Zoogeography of Bats

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INTRODUCTION

The Order Chiroptera is the second largest order of mammals, with, according to my most recent revised figure, 846 species. Inasmuch as the group is world-wide, reaching many distant islands, and inasmuch as many species and higher groups are quite localized and some very distinctive, one might expect that a good deal of work on bat zoogeography would have been undertaken. However, such is not the case.

Darlington (1957, pp. 320-410) does discuss the general geographical patterns of bats, and Tate (1946) gives a useful analysis of the bats of the Malay archipelago. However, many writers on zoogeography have given them at best a very perfunctory treatment. This contrasts markedly with the attention given to bird zoogeography. From talking with various zoogeographers, I suspect the reason is that whereas birds are treated as a separate group in their own right, bats are treated as part of the Class Mammalia. Since all bats can fly, there seems to be a general assumption that they regularly cross various kinds of geographical barriers at will, with the result that they have been rather consistently downgraded with respect to flightless mammals in zoogeographical studies (see, *e.g.,* Bigalke, 1968).

Actually, except for their ability at crossing narrow water gaps without too much difficulty, bats have several advantages in zoogeographical studies over various other groups of land vertebrates. With a very few exceptions, they are not likely to fly over the open ocean as part of their normal activities. They are almost entirely free of the problems of human introduction. I know of only one case where (unintentional) human introduction has played a role, and this has not resulted in an introduced population. This was a specimen of the North American *Myotis lucifugus*, collected in Iceland, that is believed to have been inadvertently transported by ship (see Koopman & Gudmundsson, 1966). Aside from the advantages mentioned above, the large number of species, at least in the tropics, means that there are enough individual cases to enable zoogeographical patterns to be worked out.

I wish to dedicate this paper to my former major professor, Dr. Theodosius Dobzhansky, on his seventieth birthday. The insights on evolution, through population genetics and speciation, that I gained through years of association with him have stood as a cornerstone throughout my work on mammals in general and bats in particular.

General Pattern of Bat Distribution

Bats are primarily a tropical group. With the exception of one monotypic family (Mystacinidae) confined to lush pseudo-tropical New Zealand, all the families of bats occur in the tropics and many are confined or virtually confined to them. Aside from the Mystacinidae, only three families (Rhinolophidae, Vespertilionidae, Molossidae) penetrate the cool temperate zones. While a few species reach the limit of trees in both the northern and southern hemispheres (see Koopman, 1967), few species and even fewer genera are confined to atropical regions. In passing from the tropics to cool temperate regions either north or south of the equator, the number and variety of species rapidly decline. Numerous examples will be seen in the family- and region analyses. The centers of speciation and differentiation have clearly been in the tropics, and there have been no important centers outside them.

This is undoubtedly the chief reason why the primary geographical division of the Chiroptera is that between New and Old World bat faunas, corresponding to the most important separation between tropical regions. Of the 16 families recognized, only three (Emballonuridae, Vespertilionidae, Molossidae) occur in both. I think it is significant that two of these are among the few families that reach cool temperate areas. Of the families confined to the tropics, only the Emballonuridae occur in both hemispheres, and here the relationships between the two areas are far from close; all the genera are different in the two areas and are not even very closely related. It is probable that for most groups of bats, there has been no likelihood of species-exchange across the Bering Strait region since early Miocene, after which this region ceased to have a tropical (or even warm temperate) climate (see Wolfe & Leopold, 1967). Because of the wide stretches of open ocean, overwater dispersal between the tropical parts of the eastern and western hemispheres has also been difficult. While there are a few instances of apparently close special relationship between bats of Africa and South America (*Laephotis–Histiotus; Eomops–Molossops; Neoplatymops–Playtmops* and *Sauromys*), none are highly probable, and all could be explained by parallelism. Certainly there has been no exchange across the south Pacific.

This points up an important fact. In common with non-flying terrestrial mammals, broad water gaps are serious barriers to bat dispersal although a few species have managed to surmount them. On the other hand, a narrow water gap or even a series of them, as in the Malay archipelago, is not a serious impediment to a large bat fauna; although such narrow water barriers do filter out many faunal elements. As a result, while there are many species and several genera endemic to the

Australian region, there are (if New Zealand is excluded) only four endemic or nearly endemic suprageneric taxa (Dobsoniina, Nyctimenina, Notopterini, Nyctophilini)—all in my opinion of less than subfamilial rank. Six of the eight Indo-Malayan families reach Australasia. Only two families (Rhinopomatidae, Nycteridae), each with only one or two species, occur on Sumatra at the western end of the Malay archipelago, but do not reach either Australia or New Guinea. It is clear that unlike most groups of mammals, the Old World-New World division is far more fundamental than between the Australian region and the rest of the world.

Distributions of the Various Families

Before passing to an analysis of the various zoogeographical regions, I would like to summarize the geographical distribution of each of the 16 currently recognized families. Here I will try to assess the centers of origin and/or differentiation of the various families, mentioning fossil forms where these seem pertinent.

Pteropodidae:—This large and complex family (38 genera, *ca.* 150 species) includes all the fruit and nectar-feeding bats of the eastern hemisphere. The family is almost exclusively tropical (Fig. 1) but within the vast area from West Africa to Samoa, almost every island and continental area inhabited by bats has some form of pteropodid. The two subfamilies I recognize (Pteropodinae and Macroglossinae) both have a wide distribution. However, some of the tribes and subtribes are more limited: thus the Epomophorini are confined to Ethiopian Africa and adjacent small islands; the Cynopterina are virtually restricted to the Indo-Malayan region; the Harpyionycterini to the Philippines and Celebes; and, as mentioned above, the Dobsoniina, Nyctimenina, and Notopterini to the Australian region (*Dobsonia* reaches Bali). The family has obviously originated somewhere in the Old World tropics and there are several separate centers of differentiation within this area. The only place outside their present range where *Pteropodidae* are known as fossils is in the Oligocene and Miocene of southern Europe, which then presumably still had a tropical climate.

Rhinopomatidae:—This small Old World family (one genus, probably only two species) ranges from northwestern Africa to Sumatra (Fig. 2), mostly in arid regions. As a result it does not penetrate far into either the Ethiopian or Palearctic regions and its range in the Oriental region is spotty. Presumably it originated somewhere in northern Africa or southern Asia, but the number of species is too small for any definite statement to be made. There is no fossil record as far as I know.

Emballonuridae:—This family (12 genera, 44 species) occurs in both hemispheres, but is virtually confined to the tropics (Fig. 3). Of the two subfamilies, the more primitive Emballonurinae occur in both New and Old Worlds; the more specialized Diclidurinae are confined to the American tropics. In the Old World some emballonurids have been spectacular trans-oceanic colonists, having reached Samoa, Micronesia, the Mascarene islands, and Madagascar (the last from both Africa and the Malay archipelago). In the New World, however, they are virtually confined to the mainland and the adjacent continental shelf, barely reaching the West Indies on Grenada. Whether the Emballonuridae arose in the New or Old World tropics is difficult to say, there being nine genera and 18 species in the New World, three genera and 26 species in the Old World. The presence of the only known fossil genus in the Eocene or Oligocene of Europe (which at that time was probably still tropical) suggests an Old-World origin with secondary New World tropical centers for the American Emballonurinae and for the Diclidurinae.

Noctilionidae:—This small family (one genus, two species) is restricted to the Neotropical region, but is widely distributed there, being found in both South and Middle America and throughout most of the West Indies (Fig. 4). Presumably, the family originated somewhere in tropical America, but, with so few species and no significant fossil record, this is far from certain.

Nycteridae:—This small family (one genus, 13 species) is chiefly Ethiopian, including one species on Madagascar (Fig. 4). *Nycteris thebiaca*, however, though widely distributed in tropical Africa, also reaches Morocco, Egypt, and southwestern Asia. There is even a record (probably accidental) from the Greek island of Corfu. There are also two species, confined to southeastern Asia and the western end of the Malay archipelago, whose range is therefore widely separated from the rest. The most primitive species of the family (and genus) are forest forms living in Africa and southeastern Asia. Progressively more specialized species have colonized in savanna and arid regions of Africa and southwestern Asia. Africa has thus been the chief center of differentiation, but this is probably due more to ecological opportunity than to time of occupation. As nearly as I can determine, there is no fossil record.

Megadermatidae:—This small family (four genera, five species) has a discontinuous Old World tropical distribution (Fig. 5). Two genera (*Cardioderma, Lavia*) are confined to the northern part of the Ethiopian region of mainland Africa. *Megaderma* (with two species) is widely distributed in the Indo-Malayan region east to the Moluccas,

while *Macroderma* is confined to the more northern portions of Australia. Although the family Megadermatidae has a relatively good fossil record, little can be said about its area of origin except that it was probably somewhere in the Old World tropics. The relict nature of its present distribution is supported by fossil forms in areas where it does not at present occur. It is known from the Oligocene and Miocene of Europe (which was probably then still tropical) and from the Pleistocene of Palestine (Bate, 1937, pp. 157-162). Also, in the Pleistocene, *Macroderma* occurred much farther south in Australia than it does today (Cook, 1960).

Rhinolophidae:—This large widespread Old World family (11 genera, 128 species) is best divided into two subfamilies (Fig. 6), each of which was formerly considered a separate family. The Rhinolophinae are widespread in the continental portions of the Eastern Hemisphere with several species extending well into the Palearctic (England, Central Europe and Japan). They have been less successful at crossing broad water gaps, not reaching Madagascar, and not extending much beyond New Guinea and Australia in the Indo-Australasian archipelago. The Hipposiderinae are more restricted to the tropics and extend only marginally into the Palearctic. They do, however, reach Madagascar and as far as the New Hebrides in the Pacific. Of the two tribes here recognized, the Hipposiderini have the same distribution as the subfamily; but the Coelopsini are confined to the Indo-Malayan region. The family undoubtedly originated somewhere in the Old World tropics, probably either in Africa or southern Asia. The few fossil genera all occur within the present range of the family.

Chilonycteridae:—This small family (three genera, eight species) is almost restricted to the Neotropical region, barely entering the Nearctic, though it extended somewhat farther in the Pleistocene. (Its distribution includes most of the range shown on the left-hand map of Figure 7 except for the southern and eastern portions of the South American shaded area.) Until recently it was generally included in the Phyllostomatidae as a subfamily, but several lines of evidence, not all as yet published (see Machado-Allison, 1967), strongly suggest that the chilonycterines should stand as a separate family, although fairly close relationship to the Phyllostomatidae is probable. The members of this family have a somewhat spotty distribution in South America, but are widespread in Middle America and also occur throughout most of the West Indies. The Chilonycteridae undoubtedly originated somewhere in tropical America, possibly in Middle America, but the small number of recent forms and the absence of pre-Pleistocene fossils make this hypothesis tenuous.

Phyllostomatidae:—This large family (48 genera, 123 species), like the previous one, is largely confined to the Neotropical zone (Fig. 7), but does penetrate the southern edge of the Nearctic and did so somewhat more extensively in the Pleistocene. As used here, the Phyllostomatidae include the Desmodontidae, until recently regarded as a separate family. Several lines of evidence (see, *e.g.,* Machado-Allison, 1967, Forman *et al.,* 1968) suggest that the two families should be merged. Six subfamilies are probably best recognized (Phyllostomatinae, Glossophaginae, Carolliinae, Stenoderminae, Phyllonycterinae, Desmodontinae). A seventh (Sturnirinae) has generally been recognized, but again several lines of evidence suggest that it should be merged with the Stenoderminae. As is evident, the familial and subfamilial classification of the Phyllostomatoidea is at present in a state of flux, but I have tried to base my zoogeographical analysis on the systematic pattern which seems to be emerging. The first four subfamilies are widely distributed in both South and Middle America and all occur in the West Indies, though the Carolliinae do so only marginally. The Desmodontinae do not now occur in the West Indies, but did so in the Pleistocene (Koopman, 1958a). The Phyllonycterinae are confined to the West Indies, where they probably originated, and have always been confined. Of the three tribes of Stenodermininae, two (Sturnirini, Stenodermini) occur over most of the range of the family; but the Brachyphyllini (one genus) are confined to the West Indies. The family undoubtedly originated in tropical America, but a more precise area of origin is difficult to determine. South America has 36 genera and 93 species, Middle America (not counting forms which only enter Panama) 34 genera and 65 species, the West Indies (not counting species that only reach Grenada or are of only accidental or fossil occurrence) 12 genera and 25 species. Thus South America seems more probable as a center of origin than Middle America, but there remains the strong possibility that the greater number of species merely reflects the much larger area of South America. The only pre-Pleistocene fossil phyllostomatid is from the Miocene of Colombia, which is in agreement with, but hardly gives strong support for, a South American origin.

Natalidae:—This small family (one genus and probably not more than four species) is confined to tropical America (Fig. 8). It is widespread in Middle America and the West Indies, but appears to have a

FIG. 1. Distribution of Pteropodidae.

FIG. 2. Distribution of Rhinopomatidae. (Since this map was made, *Rhinopoma* has been recorded from several localities between the northern and southern portions of the range in West Africa.)

FIG. 3. Distribution of Emballonuridae.

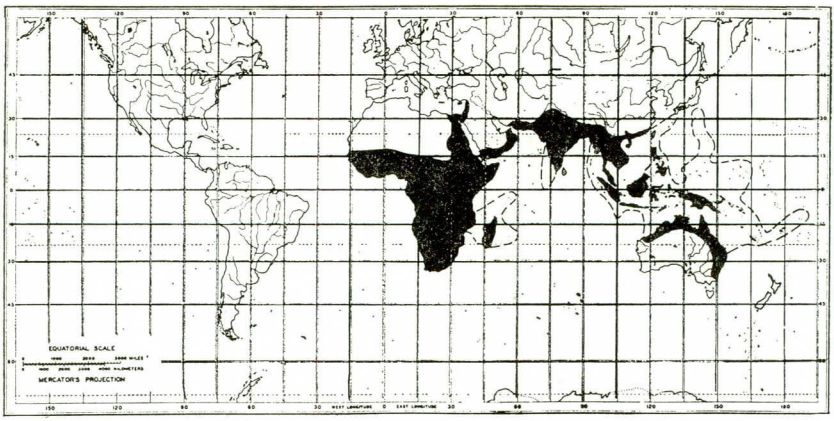

FIG. 1

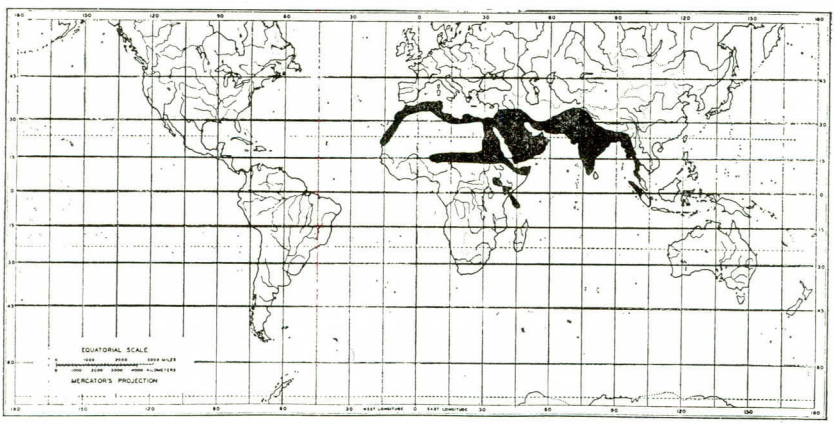

FIG. 2

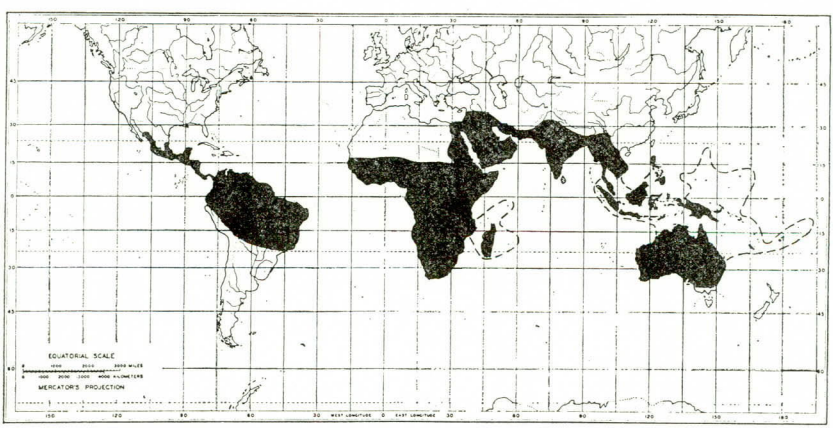

FIG. 3

rather spotty distribution in South America. Presumably the family originated somewhere in tropical America. The fact that all four species occur in, and three are confined to, the West Indies, suggests this area as the original one, but the extensive mainland distribution is not in agreement with this. There is no useful fossil record.

Furipteridae:—This small family (two genera and species) is virtually confined to tropical South America, not being known to extend beyond eastern Panama (Fig. 8). A tropical South American origin is therefore most probable, but cannot be proved. To my knowledge, no fossils are known.

Thyropteridae:—This small family (one genus, two species) is confined to the tropical American mainland, ranging from southern Mexico to southern Brazil (Fig. 9). Probably the family originated somewhere within this area. There seem to be no fossil forms.

Myzopodidae:—This monotypic family is confined to Madagascar (Fig. 9), where it probably originated. The relationships of the family are obscure. I know of no fossil record.

Vespertilionidae:—This large cosmopolitan family (34 genera, some 280 species) has the largest range of any family of bats. Not only does it occur on all continents, reaching the limits of forest in the subarctic and subantarctic, but vespertilionids have reached many oceanic islands such as Bermuda (probably only as migrants), Iceland (accidentals only), Azores, Galapagos, Hawaii, New Zealand, and possibly Samoa (doubtful record). Six subfamilies are currently recognized; but the great majority are members of the Vespertilioninae (25 genera, some 230 species), the only subfamily which occurs in all the zoogeographical regions and on most islands where the family occurs. Only one subfamily is confined to the New World, the monotypic Tomeatinae, known only from Peru. Three subfamilies (Miniopterinae, Murininae, Kerivoulinae) are confined to the Old World, but widely distributed. Of these the Miniopterinae are the most widespread, extending well into the Palearctic and reaching Madagascar and the western Pacific islands as far as the New Hebrides. The Murininae are basically eastern Asian, extending well into the eastern Palearctic but not reaching Europe or the Ethiopian region. They do, however, extend through the Malay archipelago to New Guinea. The Kerivoulinae are confined to the Old World tropics, but are otherwise widely distributed. They do not reach Madagascar, however, and do not extend eastward beyond the Bismarck archipelago.

FIG. 4. Distribution of Noctilionidae (open stipple) and Nycteridae (solid areas).

FIG. 5. Distribution of Megadermatidae.

FIG. 6. Distribution of Rhinolophidae.

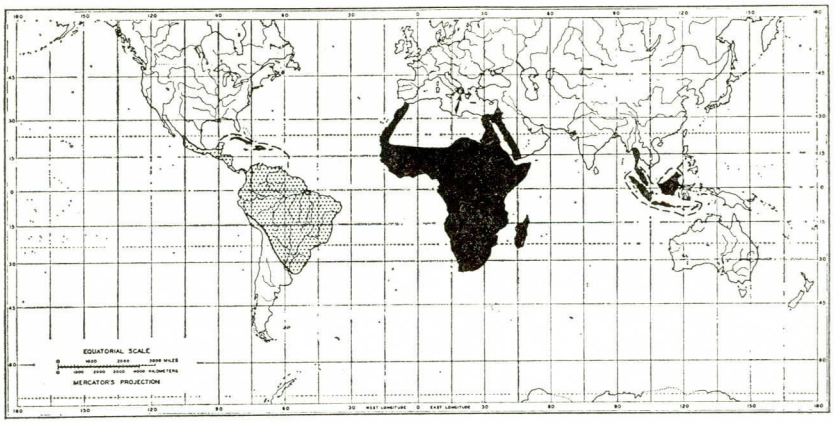

FIG. 4

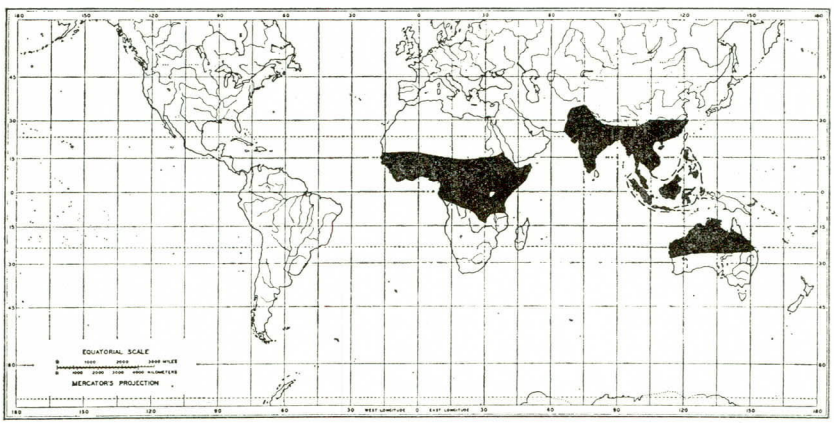

FIG. 5

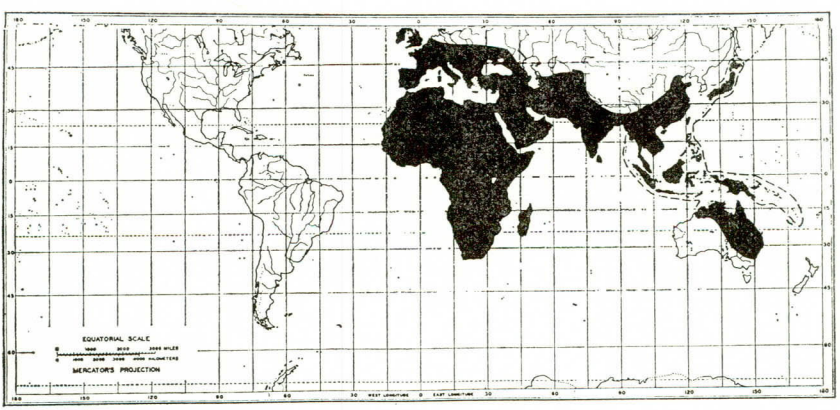

FIG. 6

As currently recognized, the Nyctophilinae have a sharply discontinuous distribution. Three genera: *Lamingtonia*, *Nyctophilus*, and *Pharotis*, are confined to the Australian region, chiefly Australia and New Guinea. They appear to form a very distinctive group of vespertilionids. With them, however, has been associated the genus *Antrozous*, which is primarily Nearctic with a marginal range in the northernmost neotropical (Mexico and Cuba). However, it is rather doubtful whether there is any special relationship between *Antrozous* and the true nyctophilines so this zoogeographical pattern may well be spurious. The subfamily Vespertilioninae is by far the most widely distributed extending to the distributional limits of the family, north and south. Several genera (*e.g.*, *Myotis*, *Pipistrellus*) have closely related species in the Palearctic and Nearctic regions, and one species (*Eptesicus serotinus*) probably occurs in both regions, even though the New World populations are currently called a separate species (*E. fuscus*). I am inclined to recognize five tribes, three of which (Myotini, Vespertilionini, Nycticeiini) occur in all the zoogeographical regions (although the Nycticeiini have a rather spotty distribution). The Lasiurini are essentially confined to the Western hemisphere where they extend from northern Canada to Tierra del Fuego. Probably because two species are migratory, they have also been unusually successful at colonizing oceanic islands. Thus they have reached the Galapagos, Hawaii, the West Indies, Bermuda, and (as accidentals) Iceland and the Orkney islands. The Plecotini are basically Holarctic (the only suprageneric group of bats of which this can be said), but do marginally penetrate the Ethiopian, Indo-Malayan, and Neotropical zones. The greater number and diversity of vespertilionids in the Old World as compared with the New, also the somewhat earlier known first fossil occurrence (early Oligocene *vs.* early Miocene), suggest an origin for the Vespertilionidae somewhere in the warmer parts of eastern hemisphere, probably tropical Asia or Africa. However, there have obviously been a number of secondary centers in various parts of the world.

Mystacinidae:—This monotypic family is confined to New Zealand (Fig. 11) where it probably originated from primitive molossid rela-

FIG. 7. Distribution of Phyllostomatidae (including Chilonycteridae) (left) and Desmodontinae (now included in Phyllostomatidae) (right). The distribution of the Chilonycteridae alone is essentially the same as that of the Phyllostomatidae, but the family is lacking in the Bahamas and from the southern and eastern parts of the shaded area in South America.

FIG. 8. Distribution of Natalidae (left) and Furipteridae (right).

FIG. 9. Distribution of Thyropteridae (America) and Myzopodidae (Madagascar).

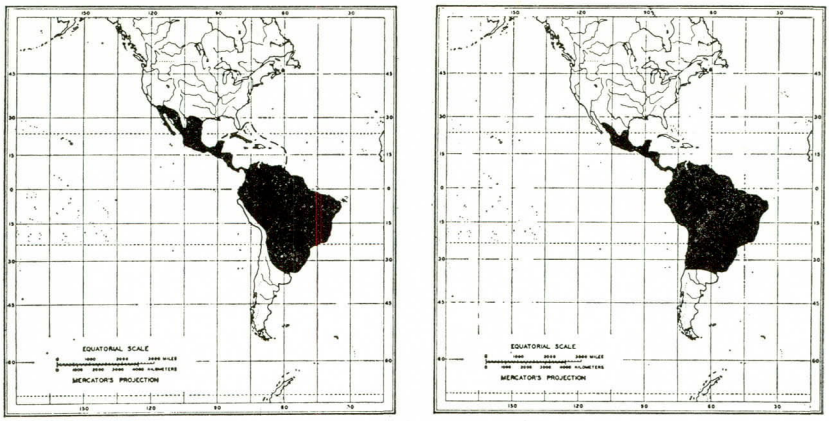

FIG. 7

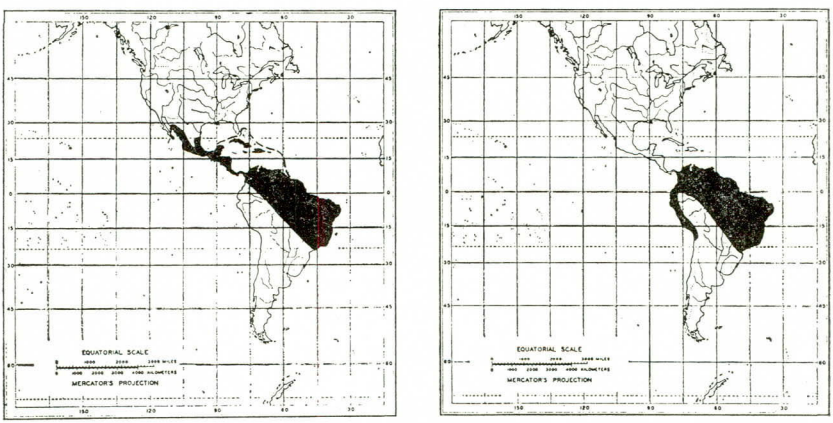

FIG. 8

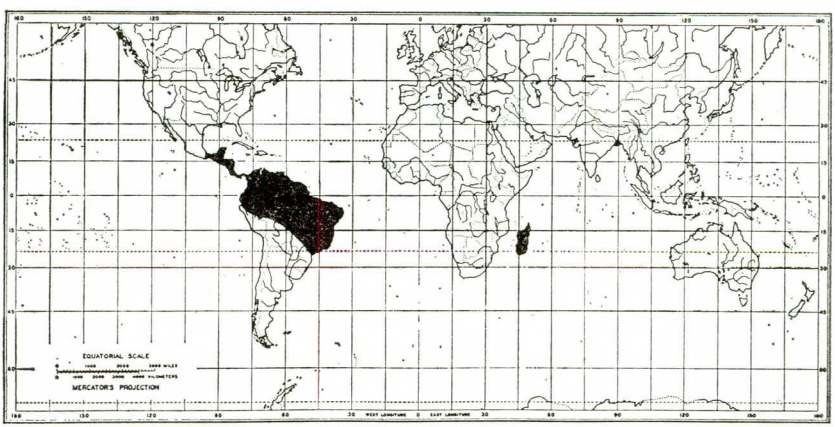

FIG. 9

tives which had come from Australia. It does not have any fossil record.

Molossidae:—This family (11 genera, 82 species) is widely distributed in the tropics and warm temperate regions of both eastern and western hemispheres (Fig. 11). Besides all the continental zoogeographical regions, these bats also have reached Madagascar several times, are widely distributed in the Indo-Pacific as far east as Fiji, and occur on practically all the West Indian islands. Curiously enough, however, most species occur in either the Ethiopian or Neotropical regions. Only 19 species do not occur in one or the other. While one genus (*Tadarida*) occurs in both hemispheres, none of the species in either of these two areas shows any very close relationships with any in the other. Hence there does not appear to be any recent exchange between the two hemispheres (such as has occurred in the Vespertilionidae). The presence of *Tadarida* (probably the most primitive genus) in the Oligocene of Europe, suggests an Old World origin for the family. On the other hand, Miller (1907) was much impressed with the molossid resemblances of the vespertilionid subfamily Tomeatinae, which is confined to Peru.

The Bat Faunas of the Various Geographical Regions
(see Tables 1 and 2)

Ethiopian region:—Nine families (Pteropodidae, Rhinopomatidae, Emballonuridae, Nycteridae, Megadermatidae, Rhinolophidae, Myzopodidae, Vespertilionidae, Molossidae) occur in this region, although the Rhinopomatidae are rather marginal and the Myzopodidae confined to Madagascar. These include 43 genera (21 endemic, 16 shared with the Palearctic, 18 with the Indo-Malayan) and 186 species. On the mainland of Ethiopian Africa occur 40 genera and 71 species. One additional species (*Nyctalus noctula*) is known by a single accidental record; another additional species (*Myonycteris brachycephala*) is known only from Sao Thomé island in the Gulf of Guinea; and two others from islands just off the east African coast (Pemba and Mafia). These two latter species belong to the genus *Pteropus* which does not occur on the mainland. The southwestern corner of Arabia has a predominantly Ethiopian bat fauna, though with Palearctic admixture. Of the 22 species, 11 are common to both regions; eight species are Ethiopian elements; and only three are Palearctic elements that do not otherwise occur in the Ethiopian region.

The most distinctive portion of the Ethiopian region consists of Madagascar and surrounding islands (including the Seychelles and Mascarenes). Of the 33 species known from these islands, 22 seem clearly of African origin (mostly still conspecific with their mainland relatives); one (*Myzopoda aurita*) belongs to an endemic monotypic

family of uncertain relationships; while nine have no close relatives on the African mainland, but are rather closely related to Indo-Malayan species. With the exception of *Emballonura atrata*, all these latter species are members of the genus *Pteropus*. It appears that the existing species of this genus on these islands (including those of Pemba and Mafia off the East African coast) were derived from four different invasions of *Pteropus* across the Indian Ocean. It should also be pointed out that of the 14 families, subfamilies, and tribes that occur on the East African coast, four (Epomophorini, Megadermatidae, Rhinolophinae, and Kerivoulinae) do not reach Madagascar or its surrounding islands.

Palearctic region:—Seven families (Pteropodidae, Rhinopomatidae, Emballonuridae, Nycteridae, Rhinolophidae, Vespertilionidae, Molossidae) occur in this region, though the first four only enter the arid southwestern portion of it. Of its 20 genera and 69 species, two genera and species (*Hipposideros caffer, Nycticeius schlieffeni*) are very marginal, entering the Palearctic only in North Africa. One species (*Rhinolophus cornutus*), which is otherwise Indo-Malayan, occurs in the Palearctic only in Japan. Several endemic species of vespertilionids have also been described from Japan. Two species (*Pipistrellus maderensis, Nyctalus verrucosus*) are endemic to Madeira and the Canaries. Several mainland species also occur on these islands, while *Plecotus auritus* and possibly *Pipistrellus savii* even reach the Cape Verdes. *Nyctalus azoreum*, of clearly Palearctic origin, is endemic to the distant Azores. One clearly American species, *Lasiurus cinereus*, is known as an accidental on the Orkney islands. The relatively small number of Palearctic species, as compared with that of either the Ethiopian or Indo-Malayan regions, reflects the usual diminution in number of bat species on leaving the tropics. Only two genera (*Vespertilio* and *Otonycteris*) are endemic to the Palearctic region, 16 are shared with the Ethiopian, 15 with the Indo-Malayan, and six with the Nearctic.

Indo-Malayan region:—Eight families (Pteropodidae, Rhinopomatidae, Emballonuridae, Nycteridae, Megadermatidae, Rhinolophidae, Vespertilionidae, and Molossidae) occur in this region. There are 43 genera and 153 species on the purely continental portion, while the total count (including the bats of the many islands which make up so much of the area) runs to 53 genera (24 endemic, 18 shared with the Ethiopian region, 15 with the Palearctic, 24 with the Australian) and 268 species. These figures for the entire Indo-Malayan region, of course, include a considerable number of Australasian species which occur on Celebes, in the Philippines, or the Lesser Sundas together with a considerable number of endemics on these islands. This insular area constitutes

"Wallacea" except that Wallacea includes the Moluccas, which have a predominantly Australasian fauna. The Indo-Malayan part of Wallacea has 32 genera and 115 species of bats. Obviously there is no clear-cut boundary between the Oriental and Australasian bat faunas.

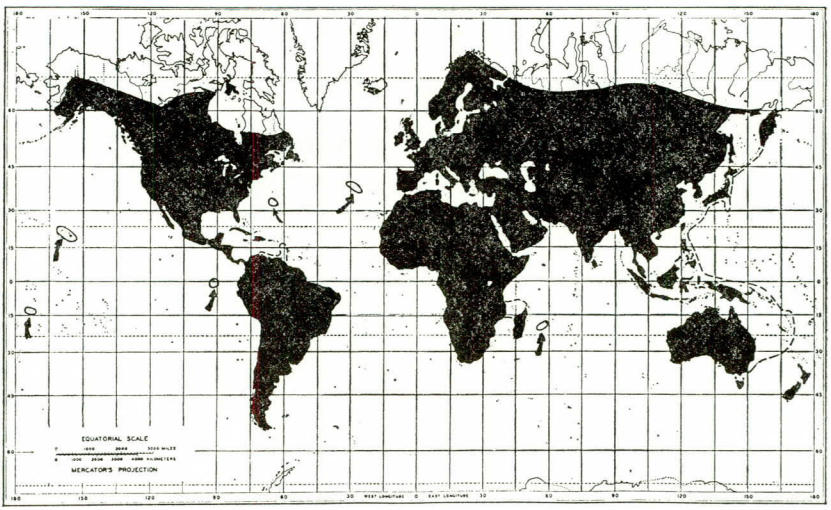

FIG. 10

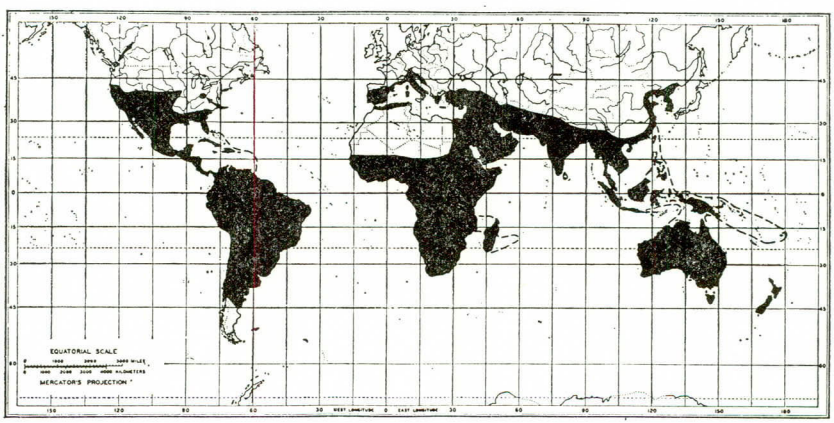

FIG. 11

FIG. 10. Distribution of Vespertilionidae.

FIG. 11. Distribution of Mystacinidae (New Zealand only) and Molossidae (solid areas). (After this map was made, the Molossidae have been recorded from a number of localities in Eurasia somewhat north of the range shown here.)

Australian region:—Seven families (Pteropodidae, Emballonuridae, Megadermatidae, Rhinolophidae, Vespertilionidae, Mystacinidae, Molossidae), with 37 genera (12 endemic, 24 shared with the Indo-Malayan region), and 134 species, occur here; one monotypic family (Mystacinidae) being confined to New Zealand. New Guinea is the richest part with 64 species, contrasting with 51 for the whole of Australia. In view of the fact that many of the latter are known only from northern Queensland, it is evident that this is another instance of decrease in number of species of bats outside the tropics. Of course, the greater relief and absence of desert in New Guinea is also an important factor. The smaller island areas of the Moluccas (45 species) and the Bismarck-Solomon group (41 species) are depauperate, relative to New Guinea. The Moluccas have some Indo-Malayan admixture, six species shared with the main portions of this region (west of Wallacea), but not otherwise occurring in the Australian region. Most depauperate of all is the bat fauna of a great expanse of islands extending from the Bonins (south of Japan) south and east to Samoa and New Zealand. Here bats are the only native land mammals, and I therefore call this expanse the "bat belt." There are only 11 genera and 29 species, but two of the genera (*Notopteris, Mystacina*) are endemic and one constitutes an endemic family. A species belonging to an additional genus (*Myotis insularum*) was described from Samoa, but it has no close relatives nearer than New Guinea and it has apparently not been collected since its original description. The status of *Myotis* in the bat belt must therefore be regarded as dubious.

Nearctic region:—Four families (Chilonycteridae, Phyllostomatidae, Vespertilionidae, Molossidae), 16 genera, and 40 species, occur here. It is thus the most depauperate of the zoogeographical regions. One species (*Lasiurus cinereus*) reaches Hawaii and also Iceland (as an accidental). This species, together with *L. borealis* and *Lasionycteris noctivagans,* is a regular migrant to Bermuda (Van Gelder & Wingate, 1961). Only two genera (*Lasionycteris* and *Euderma*), both monotypic, are endemic to the Nearctic, six are shared with the Palearctic, and 14 with the Neotropical.

Neotropical region:—Nine families (Emballonuridae, Noctilionidae, Chilonycteridae, Phyllostomatidae, Natalidae, Furipteridae, Thyropteridae, Vespertilionidae, Molossidae), occur in this region, these constituting all the New World families. The Noctilionidae, Natalidae, Furipteridae, and Thyropteridae are endemic. Some 82 genera and 221 species occur in the Neotropical region, which makes it the richest in number of genera and richer than any other except the Indo-Malayan in number of species. The number of endemic genera (68) is much

higher than for any other zoogeographical region. Only 14 are shared with the Nearctic. Within this region, South America has the richest bat fauna (172 species), Middle America next (107 species), and the West Indies least (55 species). The last, the only important island area in the Neotropical region, has seven of the nine families, though one (Emballonuridae) enters only the margin of the West Indies. Only the Furipteridae and Thyropteridae are absent. There is also considerable endemism with one subfamily (Phyllonycterinae with two genera), one monogeneric tribe (Brachyphyllini), and five additional genera (*Monophyllus, Ardops, Phyllops, Ariteus, Stenoderma*) endemic. There are also two endemic subgenera of *Natalus, Chilonatalus* and *Nyctiellus*, which until recently were regarded as separate genera. The only other really oceanic islands in the Neotropical region, with bats, are the Galapagos. Two species of *Lasiurus* have been recorded from there, both of which are, however, probably conspecific with mainland species.

Conclusions

Bats comprise a large, widespread, successful order (Chiroptera) which is, however, primarily tropical with a relatively poor representation in temperate, particularly cool-temperate regions. All bats can fly and as a result tend to cross *narrow* water barriers more easily than do other non-aquatic mammals or most flightless terrestrial vertebrates. However, in common with other non-marine mammals, *wide* stretches of ocean do pose serious barriers to bat dispersal. These attributes of bats had probably already been attained by the end of the Eocene and were certainly already well developed by the beginning of the Miocene, when the separation of New and Old World tropical zones were completed. Since then the bat faunas of the eastern and western hemispheres have evolved largely independently.

Later changes have been of secondary importance. The land connection established between North and South America in the Pliocene doubtless facilitated exchange of species between the two continents, though almost certainly there had been some exchange before this. Perhaps the previous relationships were more like that between the mainland and the West Indies today. It may be that exchange of species between the Indo-Malayan and Australian region was facilitated by new island-building in the intervening area, although it is uncertain how much of this there was. On the other hand, the increasing aridity of much of northern Africa and southwestern Asia has certainly had the effect of inhibiting exchange between the Ethiopian region and the Palearctic and Indo-Malayan regions.

Research on bat zoogeography is affected by various aspects of bat biology chiefly indirectly through their contribution to chiropteran

systematics. The relationship of systematics to bat zoogeography is discussed below. The principal contribution that zoogeography can make to other aspects of bat biology is to emphasize the fact that bats are essentially a tropical group. It is therefore evident that physiological adaptations of North American and European bats to cool-temperate conditions must be secondary, and probably have been evolved independently by various groups which have invaded these ecologically peripheral areas from the tropical centers. It is rather unfortunate that most of our knowledge of such aspects of bat biology as reproduction, thermoregulation, and physiological ecology is based on such ecologically peripheral species. Obviously the greatest opportunities for a better understanding of the overall biology of bats lie with the tropical Chiroptera.

To anyone with first hand experience in bat zoogeography, it is evident that this field is a constantly changing one. It is virtually impossible to study any really extensive bat collection, particularly from anywhere in the tropics without turning up range extensions. Some of these are likely to be spectacular. While most new records do not affect the overall world pattern, many details will be altered, particularly as regards boundaries of zoogeographical regions. New species and other taxonomic changes are also likely to emerge from study of unworked collections from the tropics. Island faunas which tend to be less adequately studied than those from continental areas, often show spectacular increases in numbers of species with more collections, and even more careful study of existing collections.

There is a strong trend in vertebrate paleontology today toward collection and study of small animals, and as a result fossil Chiroptera should become better known. Investigation of Pleistocene and late Tertiary bats should correct many errors based on recent extinctions. (This approach has been particularly fruitful in the West Indies.) Study of the early Tertiary record should help to elucidate many doubtful points concerning the place of origin of families and higher groups. In this it is important to make intercontinental comparisons, since, as indicated above, the Eocene, Oligocene, and early Miocene were almost certainly the periods when the major patterns of bat distribution developed.

Probably the most important advances in bat zoogeography, however, will come about as a result of improved systematics. A number of large genera of bats, particularly in the Indo-Malayan region, have either never been revised or have not been revised in the last 50 years. In the Malay archipelago and Philippines the situation is particularly chaotic in genera such as *Pteropus, Rhinolophus, Myotis*, and *Pipi-*

strellus. Much of the zoogeographical fuzziness in this area should disappear if and when these difficult genera are competently revised.

ACKNOWLEDGMENTS

I have profited greatly from discussions, both formal and informal, with participants and others at this symposium. Dr. Richard G. Van Gelder, Mr. Hobart Van Deusen, and Dr. Guy G. Musser have all read the manuscript and made valuable suggestions. The maps are taken from *Recent Mammals of the World,* edited by Sydney Anderson and J. Knox Jones, Jr. and are reproduced with the permission of the publisher, Ronald Press, New York (copyright © 1967).

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TABLE 1

Numbers of Species for Each Genus of Bats in Each Zoogeographical Region

	Ethiopian	*Palearctic*	*Indo-Malayan*	*Australian*	*Nearctic*	*Neotropical*
Eidolon-1	1	----	----	----	----	----
Rousettus-6	3	1	3	1	----	----
Myonycteris-2	2	----	----	----	----	----
Boneia-1	----	----	1	----	----	----
Pteropus-65	9	----	24	39	----	----
Acerodon-5	----	----	5	----	----	----
Neopteryx-1	----	----	1	----	----	----
Pteralopex-1	----	----	----	1	----	----
Styloctenium-1	----	----	1	----	----	----
Dobsonia-7	----	----	3	5	----	----
Harpyionycteris-1	----	----	1	----	----	----
Plerotes-1	1	----	----	----	----	----
Hypsignathus-1	1	----	----	----	----	----
Epomops-3	3	----	----	----	----	----
Epomophorus-8	8	----	----	----	----	----
Micropteropus-3	3	----	----	----	----	----
Nanonycteris-1	1	----	----	----	----	----
Scotonycteris-2	2	----	----	----	----	----
Casinycteris-1	1	----	----	----	----	----
Cynopterus-4	----	----	4	----	----	----
Megaerops-2	----	----	2	----	----	----
Ptenochirus-1	----	----	1	----	----	----
Dyacopterus-1	----	----	1	----	----	----
Chironax-1	----	----	1	----	----	----
Thoopterus-1	----	----	1	1	----	----
Sphaerias-1	----	----	1	----	----	----
Balionycteris-1	----	----	1	----	----	----
Aethalops-1	----	----	1	----	----	----
Penthetor-1	----	----	1	----	----	----
Haplonycteris-1	----	----	1	----	----	----
Nyctimene-9	----	----	2	9	----	----
Paranyctimene-1	----	----	----	1	----	----
Eonycteris-3	----	----	3	----	----	----

TABLE I (cont.)

	Ethiopian	*Palearctic*	*Indo-Malayan*	*Australian*	*Nearctic*	*Neotropical*
Megaloglossus-1	1	----	----	----	----	----
Macroglossus-2	----	----	2	1	----	----
Syconycteris-3	----	----	----	3	----	----
Melonycteris-3	----	----	----	3	----	----
Notopteris-1	----	----	----	1	----	----
Rhinopoma-2	2	2	2	----	----	----
Emballonura-10	1	----	4	7	----	----
Coleura-2	2	----	----	----	----	----
Rhynchonycteris-1	----	----	----	----	----	1
Saccopteryx-4	----	----	----	----	----	4
Centronycteris-1	----	----	----	----	----	1
Peropteryx-3	----	----	----	----	----	3
Cormura-1	----	----	----	----	----	1
Balantiopteryx-3	----	----	----	----	----	3
Taphozous-14	6	2	6	4	----	----
Cyttarops-1	----	----	----	----	----	1
Depanycteris-1	----	----	----	----	----	1
Diclidurus-3	----	----	----	----	----	3
Noctilio-2	----	----	----	----	----	2
Nycteris-13	11	1	2	----	----	----
Megaderma-2	----	----	2	1	----	----
Macroderma-1	----	----	----	1	----	----
Cardioderma-1	1	----	----	----	----	----
Lavia-1	1	----	----	----	----	----
Rhinolophus-68	18	7	45	5	----	----
Rhinomegalophus-1	----	----	1	----	----	----
Hipposideros-44	11	1	26	11	----	----
Anthops-1	----	----	----	1	----	----
Asellia-2	2	1	----	----	----	----
Aselliscus-2	----	----	1	1	----	----
Cloeotis-1	1	----	----	----	----	----
Rhinonicteris-1	----	----	----	1	----	----
Triaenops-4	4	1	----	----	----	----
Coelops-3	----	----	3	----	----	----
Paracoelops-1	----	----	1	----	----	----
Chilonycteris-4	----	----	----	----	----	4
Pteronotus-2	----	----	----	----	----	2
Mormoops-2	----	----	----	----	1	2
Micronycteris-10	----	----	----	----	----	10
Macrotus-1	----	----	----	----	1	1
Lonchorhina-1	----	----	----	----	----	1
Macrophyllum-1	----	----	----	----	----	1
Tonatia-5	----	----	----	----	----	5
Mimon-2	----	----	----	----	----	2
Phyllostomus-4	----	----	----	----	----	4
Phylloderma-1	----	----	----	----	----	1
Trachops-1	----	----	----	----	----	1
Chrotopterus-1	----	----	----	----	----	1
Vampyrum-1	----	----	----	----	----	1
Glossophaga-3	----	----	----	----	----	3
Lionycteris-1	----	----	----	----	----	1
Lonchophylla-4	----	----	----	----	----	4

TABLE I (cont.)

	Ethiopian	*Palearctic*	*Indo-Malayan*	*Australian*	*Nearctic*	*Neotropical*
Platalina-1	----	----	----	----	----	1
Monophyllus-2	----	----	----	----	----	2
Anoura-5	----	----	----	----	----	5
Scleronycteris-1	----	----	----	----	----	1
Hylonycteris-1	----	----	----	----	----	1
Choeroniscus-5	----	----	----	----	----	5
Choeronycteris-2	----	----	----	----	1	2
Leptonycteris-1	----	----	----	----	1	1
Lichonycteris-2	----	----	----	----	----	2
Carollia-4	----	----	----	----	----	4
Rhinophylla-3	----	----	----	----	----	3
Sturnira-10	----	----	----	----	----	10
Brachyphylla-2	----	----	----	----	----	2
Uroderma-2	----	----	----	----	----	2
Vampyrops-5	----	----	----	----	----	5
Vampyrodes-1	----	----	----	----	----	1
Vampyressa-5	----	----	----	----	----	5
Chiroderma-4	----	----	----	----	----	4
Ectophylla-2	----	----	----	----	----	2
Enchisthenes-1	----	----	----	----	----	1
Artibeus-8	----	----	----	----	----	8
Ardops-1	----	----	----	----	----	1
Phyllops-2	----	----	----	----	----	2
Ariteus-1	----	----	----	----	----	1
Stenoderma-1	----	----	----	----	----	1
Pygoderma-1	----	----	----	----	----	1
Ametrida-1	----	----	----	----	----	1
Sphaeronycteris-1	----	----	----	----	----	1
Centurio-1	----	----	----	----	----	1
Erophylla-2	----	----	----	----	----	2
Phyllonycteris-3	----	----	----	----	----	3
Diphylla-1	----	----	----	----	1	1
Diaemus-1	----	----	----	----	----	1
Desmodus-1	----	----	----	----	----	1
Natalus-4	----	----	----	----	----	4
Furipterus-1	----	----	----	----	----	1
Amorphochilus-1	----	----	----	----	----	1
Thyroptera-2	----	----	----	----	----	2
Myzopoda-1	1	----	----	----	----	----
Myotis-68	6	18	22	4	15	11
Lasionycteris-1	----	----	----	----	1	----
Eudiscopus-1	----	----	1	----	----	----
Pipistrellus-53	13	10	28	4	2	1
Nyctalus-9	----	5	5	----	----	----
Glischropus-2	----	----	2	1	----	----
Eptesicus-26	12	6	3	1	1	4
Vespertilio-3	----	3	----	----	----	----
Laephotis-1	1	----	----	----	----	----
Histiotus-3	----	----	----	----	----	3
Philetor-1	----	----	1	1	----	----
Tylonycteris-2	----	----	2	----	----	----

TABLE I (cont.)

	Ethiopian	*Palearctic*	*Indo-Malayan*	*Australian*	*Nearctic*	*Neotropical*
Mimetillus-1	1	----	----	----	----	----
Hesperoptenus-4	----	----	4	----	----	----
Chalinolobus-13	7	----	----	6	----	----
Nycticeius-12	3	1	2	6	1	1
Rhogeesa-2	----	----	----	----	----	2
Baeodon-1	----	----	----	----	----	1
Scotomanes-1	----	----	1	----	----	----
Scotophilus-7	3	----	4	----	----	----
Otonycteris-1	----	1	----	----	----	----
Lasiurus-6	----	----	----	----	4	6
Barbastella-2	1	2	1	----	----	----
Plecotus-5	1	1	----	----	4	1
Euderma-1	----	----	----	----	1	----
Miniopterus-6	3	1	3	4	----	----
Murina-11	----	2	10	1	----	----
Harpiocephalus-1	----	----	1	1	----	----
Kerivoula-22	9	----	8	5	----	----
Antrozous-3	----	----	----	----	1	2
Lamingtonia-1	----	----	----	1	----	----
Nyctophilus-7	----	----	----	7	----	----
Pharotis-1	----	----	----	1	----	----
Tomopeas-1	----	----	----	----	----	1
Mystacina-1	----	----	----	1	----	----
Tadarida-45	25	2	7	5	3	7
Otomops-5	1	----	2	2	----	----
Neoplatymops-1	----	----	----	----	----	1
Sauromys-1	1	----	----	----	----	----
Platymops-1	1	----	----	----	----	----
Myopterus-3	3	----	----	----	----	----
Molossops-6	----	----	----	----	----	6
Eumops-10	----	----	----	----	3	10
Promops-3	----	----	----	----	----	3
Molossus-5	----	----	----	----	----	5
Cheiromeles-2	----	----	2	----	----	----

TABLE 2

Numbers of Genera and Species in the Various Zoogeographical Regions and Major Portions Thereof

	Genera	*Species*
Ethiopian region	43	186
Continental	40	170
Madagascar and surrounding islands	15	33
Palearctic region	20	69
North African portion	17	37
Eurasian portion	18	64
Indo-Malayan region	53	268
Continental	43	157
Sunda shelf islands	35	117
Western Wallacea	32	115
Australian region	37	134
Australia	19	51
New Guinea	25	64
Moluccas and nearby islands	20	45
Bismarck and Solomon archipelagos	19	41
"bat belt"	11	29
Nearctic region	16	40
Neotropical region	81	221
South America	66	172
Middle America	61	107
West Indies	28	55