

THE DISTRIBUTIONAL PATTERNS OF NEW WORLD NECTAR-FEEDING BATS¹

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ABSTRACT

Whereas in the Eastern Hemisphere, all nectar-feeding bats are members of the suborder *Megachiroptera*, in the tropical and subtropical portions of the Western Hemisphere (in the absence of megachiropterans) certain members of one family (Phyllostomidae) of the generally insectivorous suborder *Microchiroptera* have become adapted to nectar feeding. These adaptations involve such diverse areas as skulls, teeth, tongues, throat muscles, and stomach linings. Considerable diversity in these characters may be seen within the New World nectar feeders, dependent in part on whether insects or pollen are the prime protein source. The distributions of all currently recognized recent species (35 in 16 genera) are mapped. Patterns are diverse but with a majority of the genera and many species being widespread on the tropical American mainland. Origin in either South or Middle America and ecological restriction will explain the distributions of some, but for many, causes are still obscure. Of the two currently recognized subfamilies of New World nectar-feeding bats the *Brachyphyllinae* are endemic to the West Indies and have obviously been there for a long time whereas the *Glossophaginae* probably originated in South America and have reached the West Indies much more recently.

While bats were originally strictly insectivorous, many species, particularly in the tropics (where most kinds of bats live), have become adapted for obtaining a variety of food, including fish, terrestrial vertebrates, blood, fruit, and nectar. It is with the nectar-feeders that we will be especially concerned here. Because this radiation is chiefly a tropical phenomenon and since the New and Old World tropics have been separate at least since the beginning of the Miocene, it has proceeded independently in the two hemispheres. In the Eastern hemisphere, the fruit- and nectar-feeders (with the exception of one New Zealand genus) all belong to the suborder Megachiroptera, which combines primitive skull and post-cranial characters with teeth which are highly modified for handling fruit, nectar, and pollen. Some members of this suborder have tongues which are highly specialized for extraction of nectar from flowers. All the insectivorous and carnivorous species belong to another suborder, the Microchiroptera. The members of this group have a number of modifications of the skull and post-cranial skeleton related to the catching of arthropod or vertebrate prey, but their Old World representatives, in general, show little in the way of dental modification.

In the New World tropics, there are no Megachiroptera and no evidence that they ever occurred. In their absence a number of species of one of the endemic Western Hemisphere Microchiropteran families, the Phyllostomidae, have become adapted to feeding on fruit and nectar. Other members of the family feed on insects, terrestrial vertebrates, and blood. In connection with their diversity

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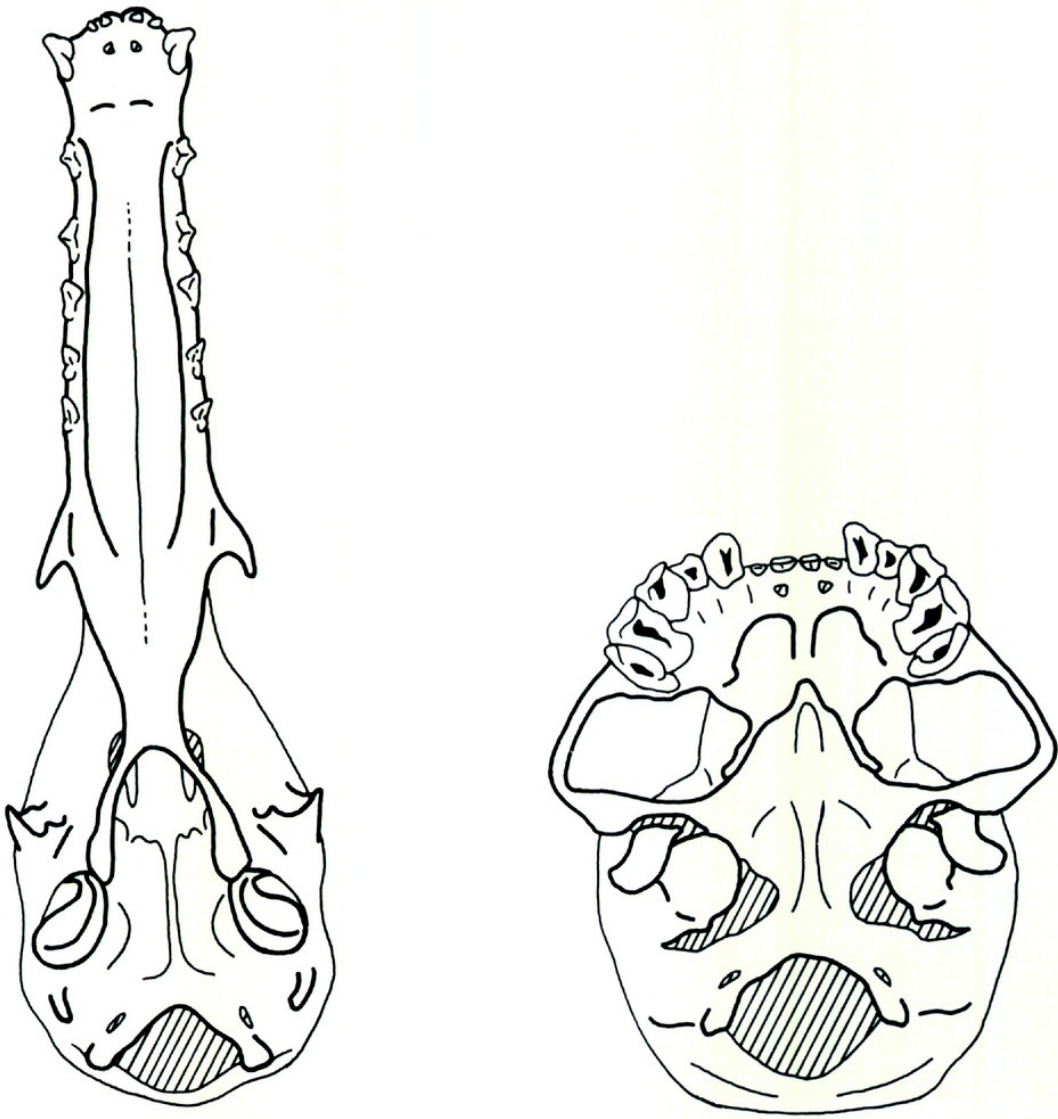
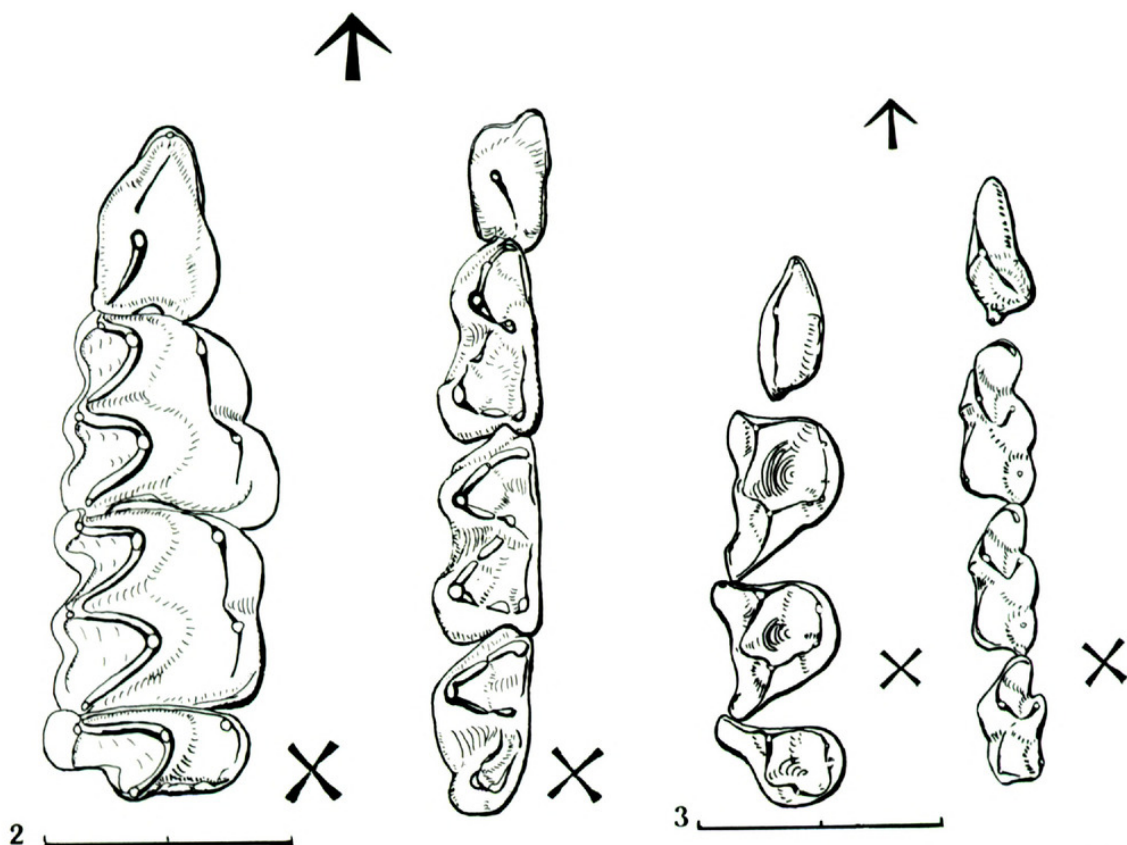


FIGURE 1. Skulls in partial view of two highly specialized phyllostomid bats; *Musonycteris harrisoni* (AMNH-235179) on the left, a nectar feeder; *Centurio senex* (AMNH-179991) on the right, a fruit eater.

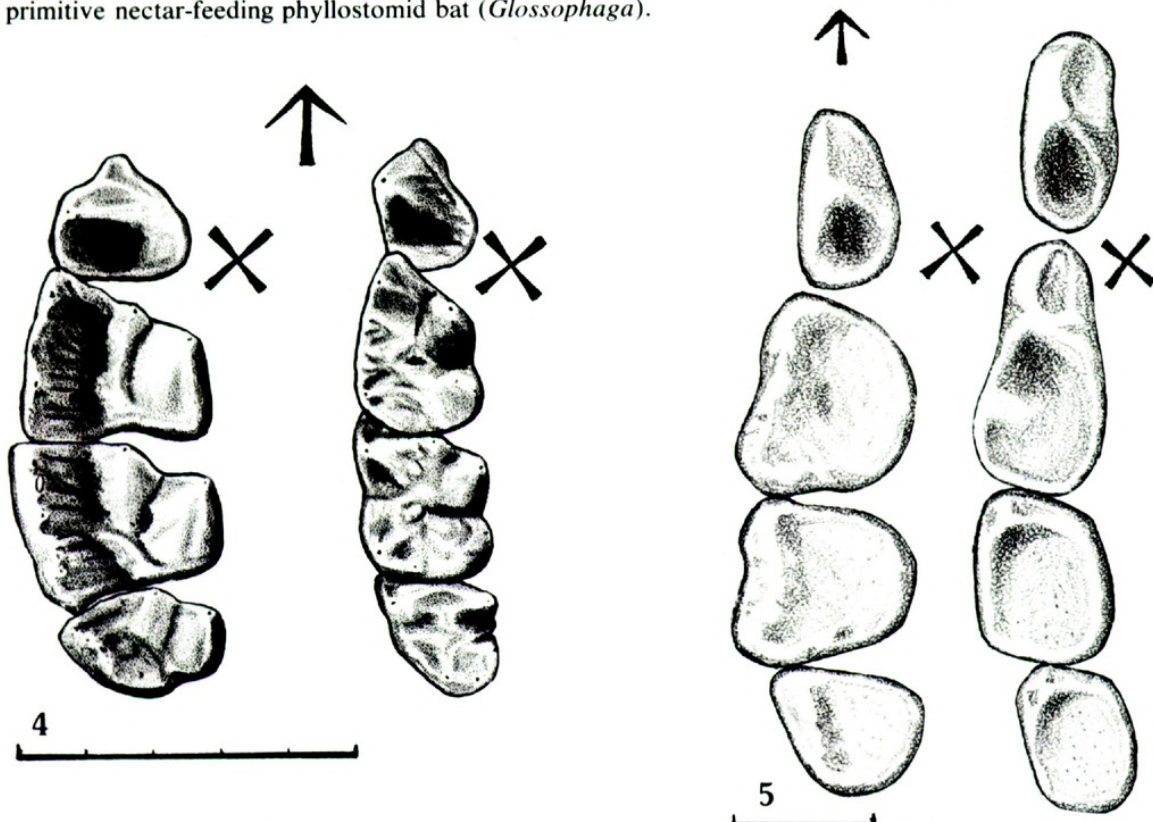
in feeding habits, the Phyllostomidae show an equal diversity in skull, tooth, and tongue morphology, some of which will be briefly discussed here.

In skull proportions, there is a tremendous spread, with a few highly specialized fruit-eaters having skulls which are almost as wide as they are long and with the rostral portion (in front of the braincase) being only about one-third of their total length. On the other hand, one of the most specialized nectar-feeders has a skull length approximately four times its breadth and with the rostral portion constituting about two-thirds of its length (Fig. 1).

Likewise the molar teeth, which in primitive members of the family are well adapted to chopping up insect exoskeletons, become highly modified in more derived species in connection with the various specialized diets, particularly fruit, nectar, and blood (Figs. 2-5). In nectar-feeders, this change involves first a weak-



FIGURES 2-3. Molars and posterior premolars of bats.—2. Upper teeth (left), lower teeth (right) of an insectivorous phyllostomid bat (*Micronycteris*).—3. Upper teeth (left), lower teeth (right) of a primitive nectar-feeding phyllostomid bat (*Glossophaga*).



FIGURES 4-5. Molars and posterior premolars of bats.—4. Upper teeth (left) and lower teeth (right) of a derived fruit and nectar-feeding phyllostomid bat (*Brachyphylla*).—5. Upper teeth (left) and lower teeth (right) of a highly derived nectar-feeding phyllostomid bat (*Phyllonycteris*).



FIGURE 6. Electron-micrograph of a portion of the tongue of *Leptonycteris*. Note the long papillae forming the nectar "mop." Taken from Howell & Hodgkin (1976).

ening (Fig. 3) and eventually a complete degeneration (Fig. 5) of the molar cuspidation. In nectar-feeders, however, the tongue does most of the work of obtaining food. As a result, it is modified in two ways. First, it is lengthened in order to reach the nectaries of flowers and this, of course, is related to the lengthening of the rostral portion of the skull. Second, the tongue papillae are greatly lengthened forming a sort of "mop" for sopping up the nectar (Fig. 6). See Griffiths (1978) for further nectar-feeding modifications of the tongue.

Nectar is a good source of carbohydrate but a poor source of protein. Primitive

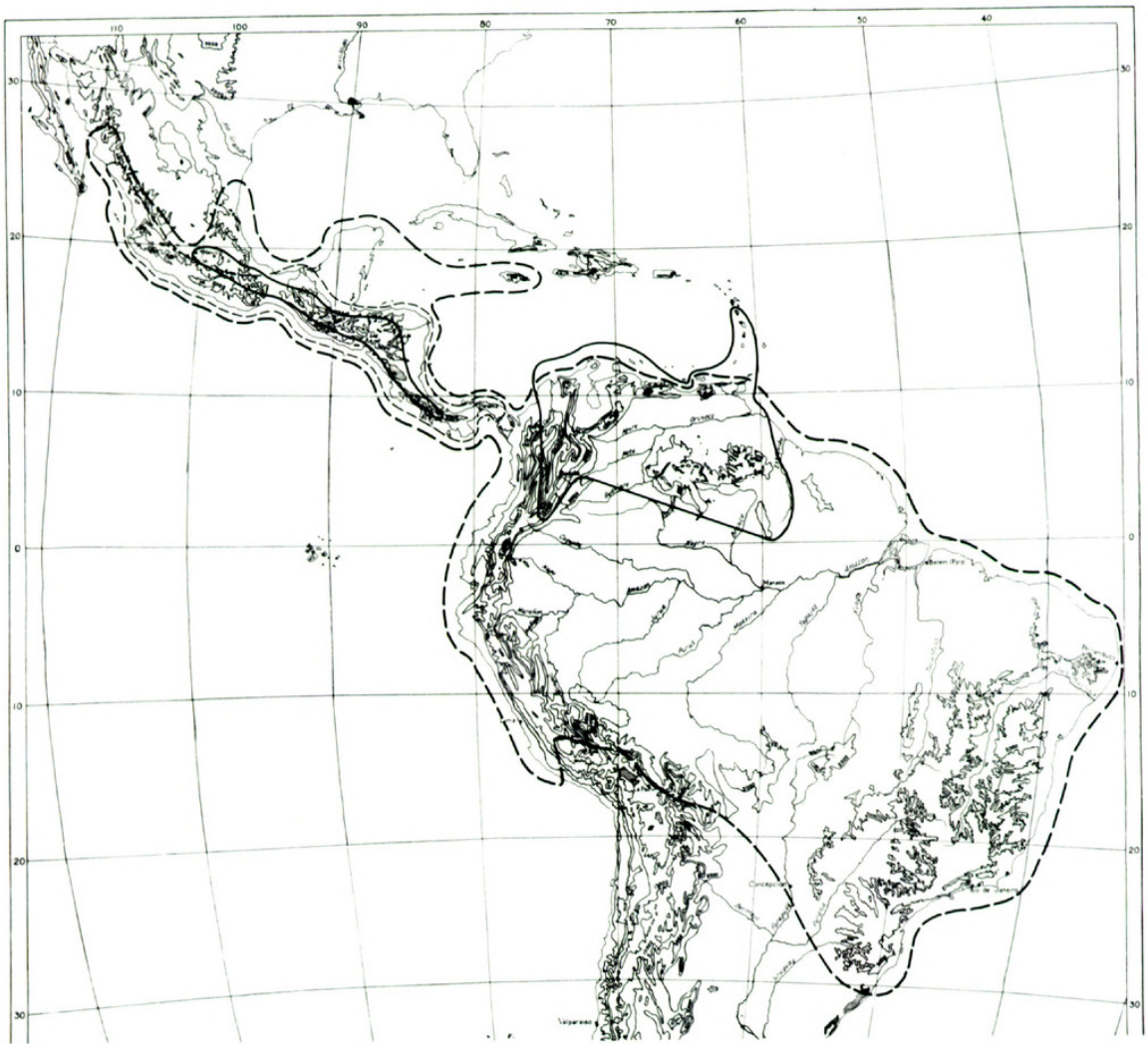


FIGURE 7. Distribution of the species of *Glossophaga*: *soricina* (bold dashed line), *commissarisi* (fine dashed line in Middle America), *alticola* (solid line in Middle America), *longirostris* (solid line in South America).

nectar feeders also eat small insects, many of which can be obtained in and around flowers. In these, there is some retention of molar cusps which are used for chewing up insects (Phillips, 1971) and of stomachs which still resemble those (Forman et al., 1979) of primitive insectivorous bats to a considerable degree. In more highly specialized nectar-feeders, pollen largely replaces insects as a significant protein source, and Howell (1974) has presented evidence that at least one such highly specialized nectar-feeder (*Leptonycteris sanborni*) obtains pollen with a richer protein content from the flowers which it pollinates than those which are normally pollinated by insects. These more highly derived nectar-feeders have teeth and stomachs which reflect the virtually total dependence of these bats on flowers for both carbohydrate and protein. The dependence is, of course, mutual since a number of flowering plants have special adaptations for pollination by bats.

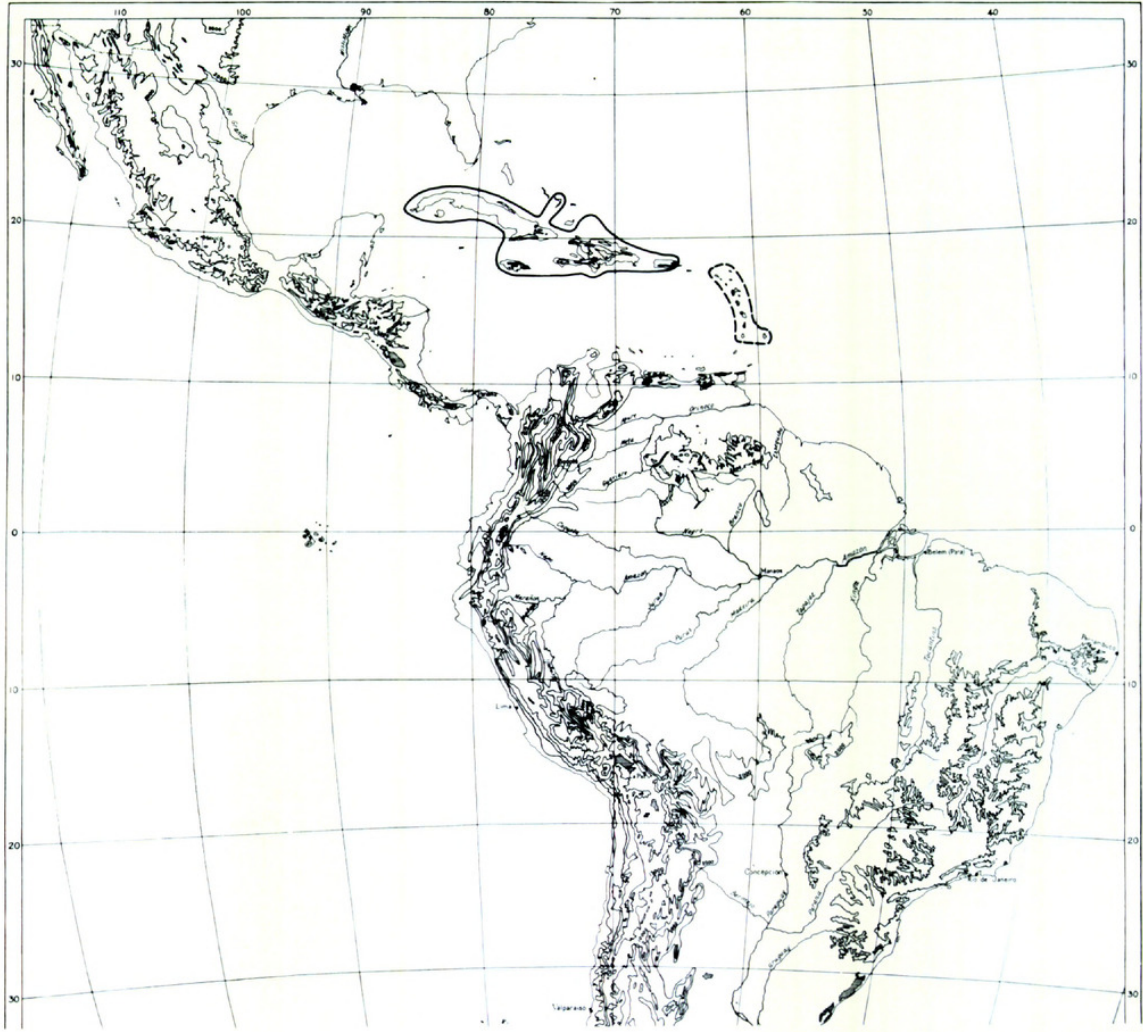


FIGURE 8. Distribution of the species of *Monophyllus*: *redmani* (solid line), *plethodon* (dashed line).

DISTRIBUTION OF NEW WORLD NECTAR-FEEDING BATS

The nectar-feeding bats of the New World are all referable to the family Phyllostomidae, which, as we have already seen, is extraordinarily diverse in both morphology and food habits. Two subfamilies are currently recognized to include the nectar-feeders. The Glossophaginae, containing 13 currently recognized genera have a wide distribution in the tropics and subtropics of North and South America as well as the West Indies. The Brachyphyllinae include three genera confined to the West Indies which possibly had a different origin within the family from that of the Glossophaginae. One of its genera (*Brachyphylla*) was until recently classified as a member of the fruit-eating subfamily Stenodermatinae since its teeth are heavier than those of other nectar-feeders (Fig. 4). While it is known to feed on nectar and pollen (Silva Taboada & Pine, 1969), it does not seem to be a specialist but is at least in part a fruit-eater. Other characters,

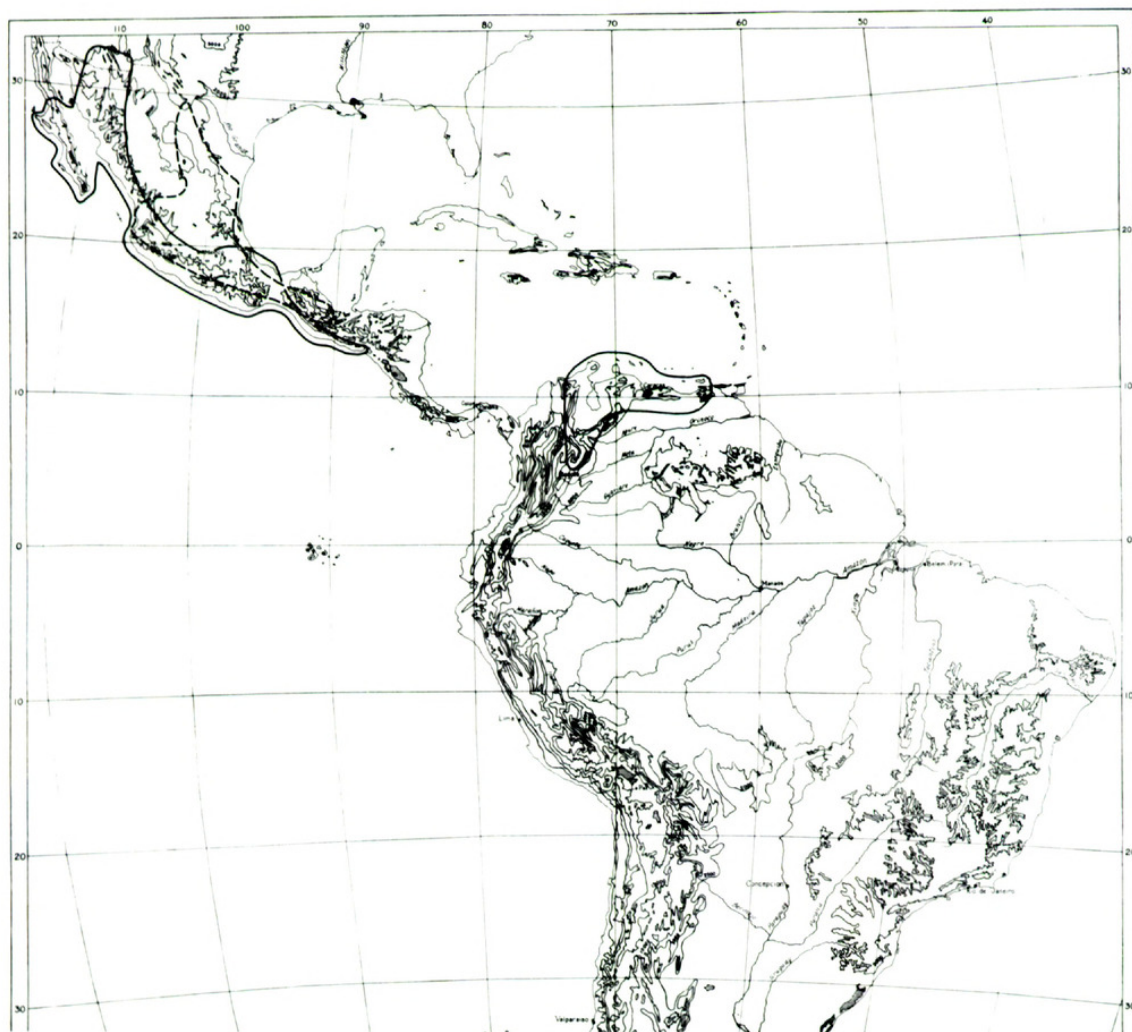


FIGURE 9. Distribution of the species of *Leptoncyteris*: *sanborni* (solid line in Middle America), *nivalis* (dashed line), *curasoae* (solid line in South America).

however, seem to ally it with the other two genera included in the subfamily Brachyphyllinae.

DISTRIBUTION OF THE GLOSSOPHAGINE

There is a great deal of disagreement concerning relationships within this subfamily, but I will use the order of genera employed by Jones & Carter (1976). It should be pointed out that several authors have regarded the glossophagines as polyphyletic. However, they disagree among themselves concerning the proper allocation of various genera to the separate clades.

Genus Glossophaga (Fig. 7).—This is a primitive genus with four currently recognized species. The commonest and most widespread, *G. soricina*, has an extensive distribution in Middle and tropical South America. It also reaches Jamaica and has been recorded from the Bahamas. Two other species, *alticola* and *commissarisi*, are known only from Middle America, though the latter is suspected to occur in northwestern South America. The fourth species, *longirostris*,

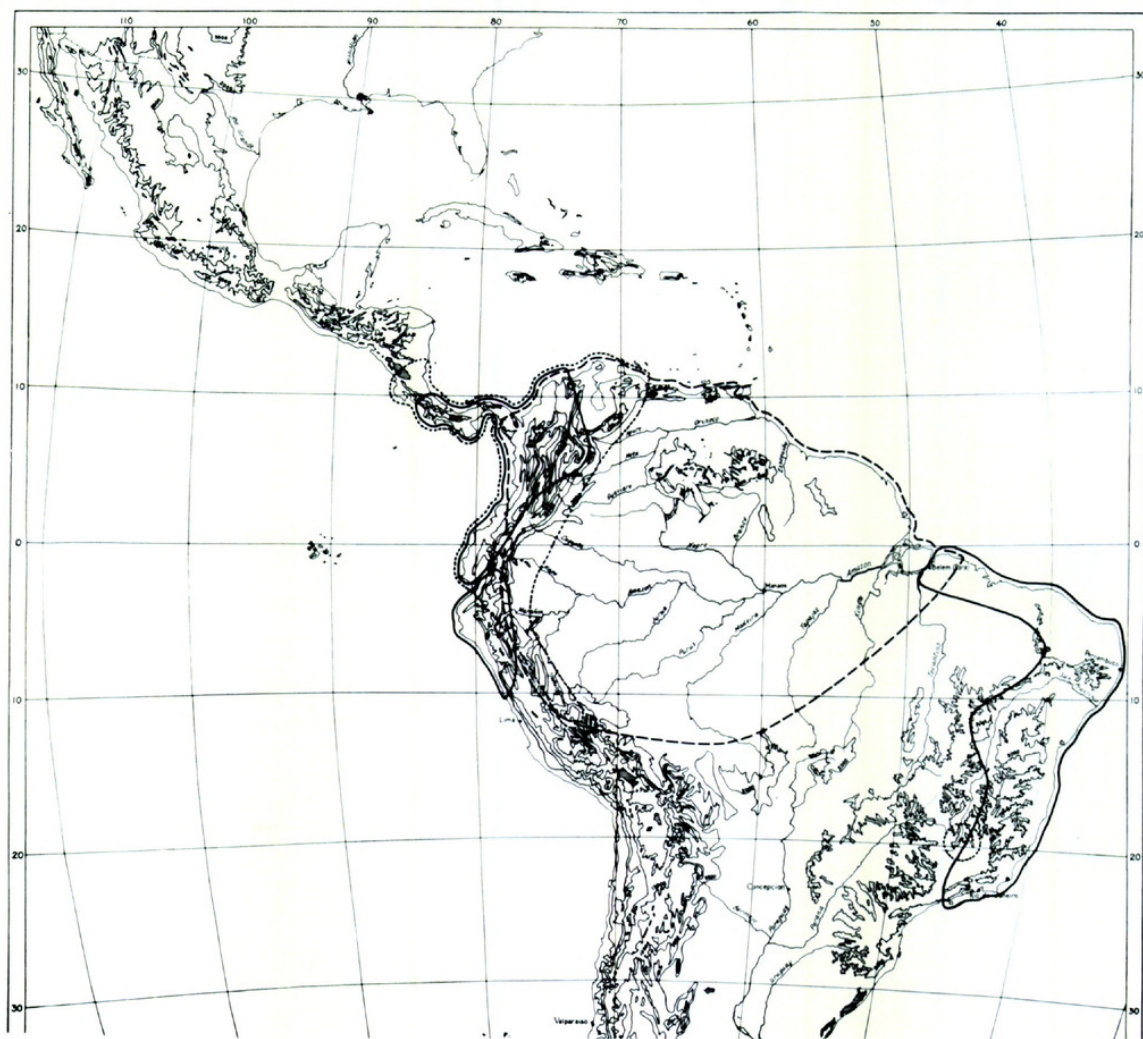


FIGURE 10. Distribution of the species of *Lonchophylla*: *thomasi* (dashed line), *mordax* (solid lines in Central and northwestern South America and in eastern Brazil), *robusta* (dotted line in Central and northwestern South America), *bokermanni* (dotted line in southeastern Brazil), *hesperia* (solid line in Peru).

occurs in northern South America but also reaches several islands off the coast including the southern Lesser Antilles.

Genus Monophyllus (Fig. 8).—This genus is closely related to *Glossophaga*, particularly to *G. longirostris*. The genus is confined to the West Indies and consists of two species. *Monophyllus redmani* is found in the Greater Antilles and southern Bahamas, whereas *M. plethodon* is at present confined to the Lesser Antilles, though it is known as a fossil from Puerto Rico (along with *M. redmani*).

Genus Leptonycteris (Fig. 9).—This is a fairly derived genus about which more is known of food habits (particularly pollen) than any other. It is probably better adapted to semiarid conditions than most other New World nectar-feeders. As a result, its distribution actually seems to avoid the wet tropics favored by most phyllostomid bats. Two of the species, *sanborni* (= *yerbabuenae*) and *nivalis*, range from the southwestern United States to northern Central America, though they are only summer residents in the northern ends of their ranges. The

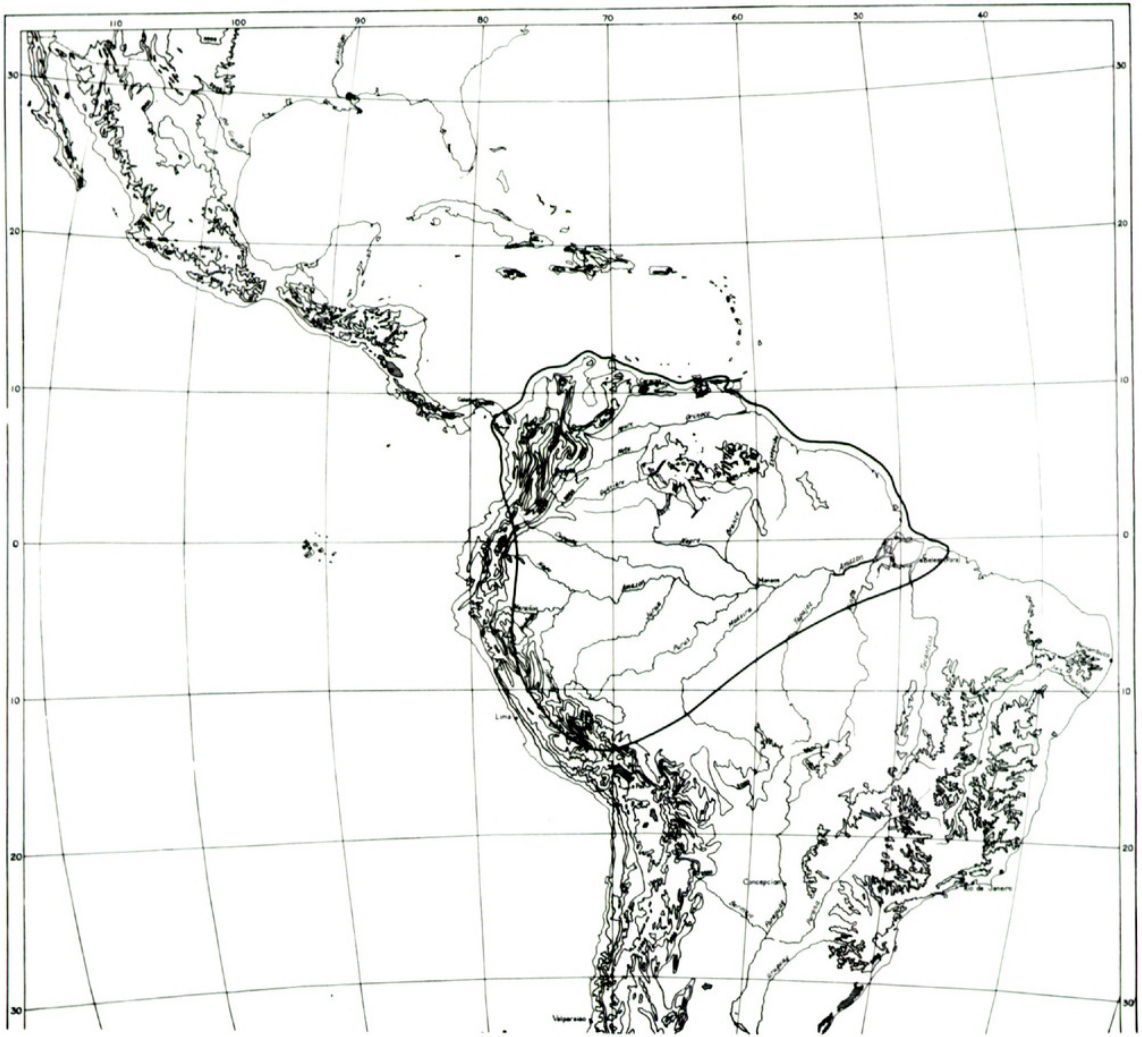


FIGURE 11. Distribution of *Lionycteris spurrelli* (solid line).

third, *curasoeae*, is confined to extreme northern South America and reaches several offshore islands.

Genus Lonchophylla (Fig. 10).—Five species may be recognized in this fairly primitive genus. *Lonchophylla thomasi* has basically an Amazonian distribution but reaches Panama. *Lonchophylla mordax* (including *concava*) ranges from Costa Rica to Ecuador and also occurs in eastern Brazil, the two discontinuous portions of the range often being considered two species. *Lonchophylla robusta* ranges from Nicaragua through lower Central America and northwestern South America to Peru. The recently described *bokermanni* (Sazima et al., 1978) is known only from a small area in southeastern Brazil. Finally, *L. hesperia* is known only from a relatively arid area in southwestern Ecuador and northwestern Peru.

Genus Lionycteris (Fig. 11).—The single species, *spurrelli*, of this primitive genus is basically Amazonian but reaches Panama.

Genus Anoura (Fig. 12).—This fairly primitive genus probably contains only three species (Nagorsen & Tamsitt, 1981). *Anoura caudifer* is confined to

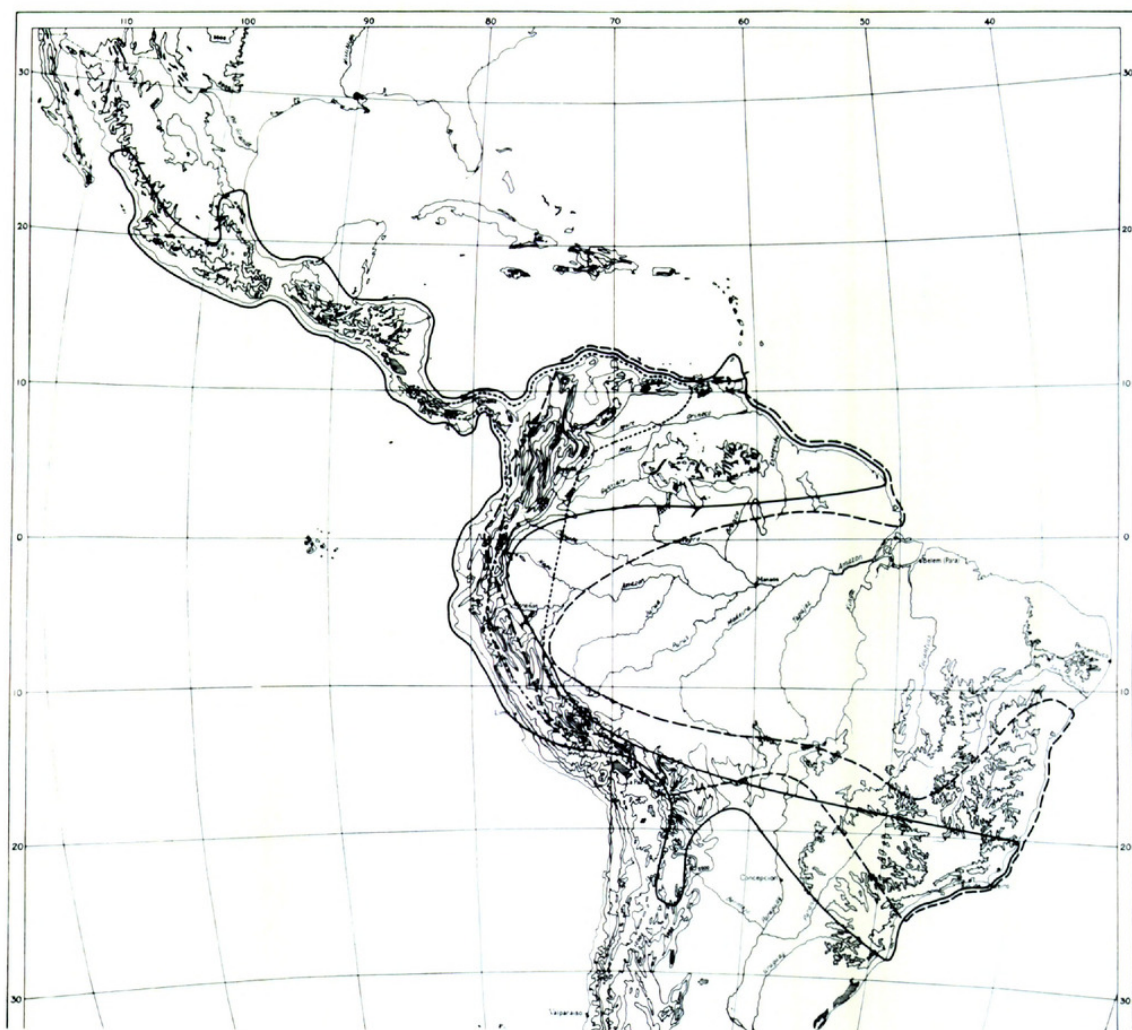


FIGURE 12. Distribution of the species of *Anoura*: *caudifer* (dashed line), *cultrata* (dotted line), *geoffroyi* (solid line).

tropical South America where it is fairly widespread but seems to avoid most of the Amazon basin. *Anoura cultrata* (including *brevirostrum* and *werckleae*, Nagorsen & Tamsitt, 1981) occurs in lower Central America and northwestern South America from Costa Rica to Peru. *Anoura geoffroyi*, like *caudifer*, is widespread in tropical South America, yet avoids most of the Amazon basin; it also extends north to tropical Mexico and onto a few off-shore islands.

Genus Scleronycteris (Fig. 13).—This highly derived genus is known by a single poorly known species, *S. ega*. The two known localities are both in the Amazon basin.

Genus Lichonycteris (Fig. 13).—This highly derived genus has two poorly defined species. *Lichonycteris obscura* ranges from Guatemala to Peru and Suriname but largely outside the Amazon basin. The few known localities for *L. degener* are all within the Amazon-Orinoco basin.

Genus Hylonycteris (Fig. 13).—This highly derived genus has a single species, *H. underwoodi*, confined to Middle America (southern Mexico to Panama).

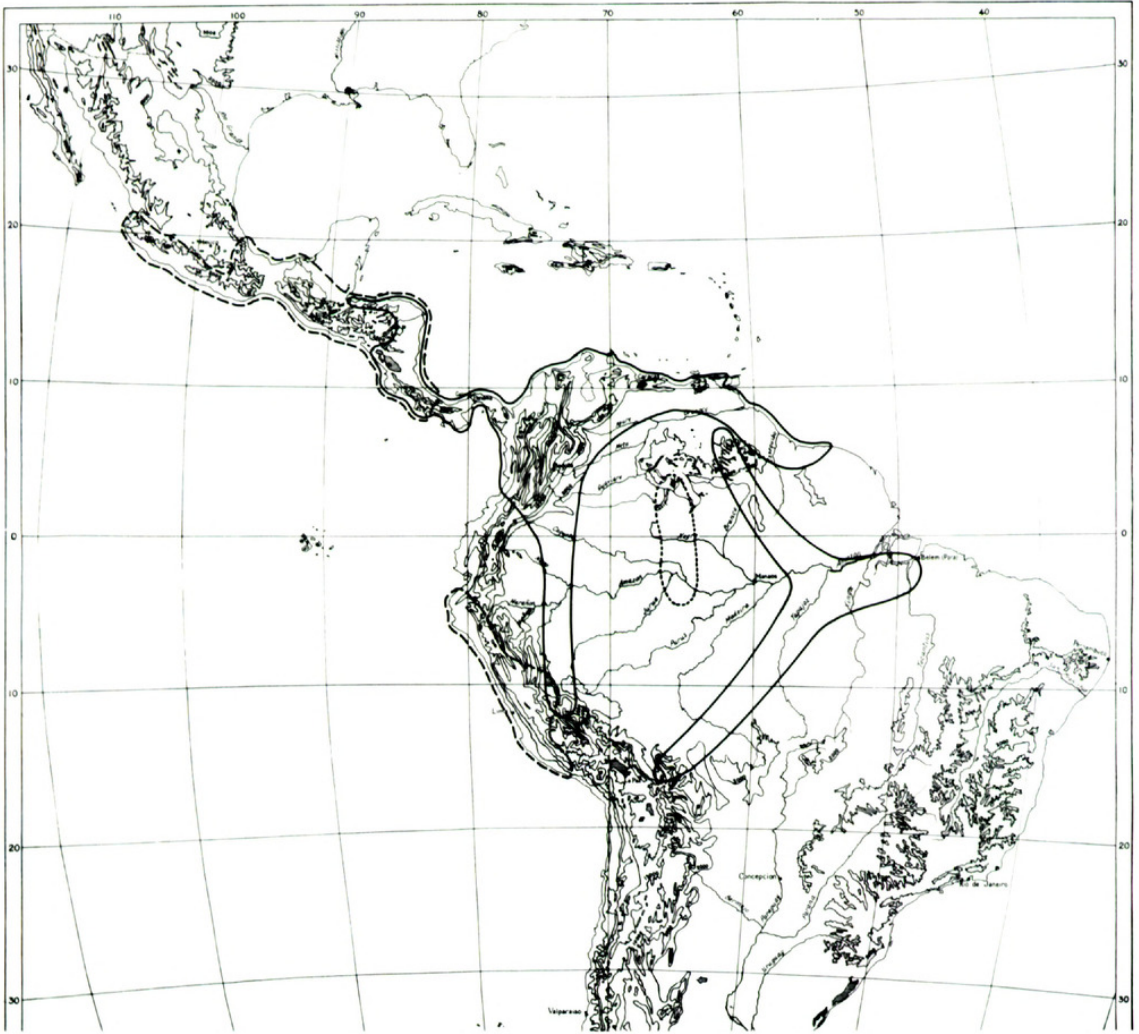


FIGURE 13. Distribution of the species of *Scleronyxteris*, *Lichonycteris*, *Hylonycteris*, and *Platalina*: *S. ega* (dotted line), *L. obscura* (solid line in Central and northwestern South America), *L. degener* (solid line in Amazon basin), *H. underwoodi* (dashed line in Middle America), *genovensium* (dashed line in Peru).

Genus Platalina (Fig. 13).—This is another highly derived genus with one species (*P. genovensium*), confined in this case to the arid coast (and some interior valleys) of Peru. It is particularly noteworthy for its very long rostrum (and presumably extra long tongue).

Genus Choeroniscus (Fig. 14).—There are four species of this highly derived genus. *Choeroniscus godmani* occurs in Middle America and northern South America (western Mexico to Guyana). *Choeroniscus minor* (including *inca*, see Koopman, 1978) is confined to northern South America and so is the closely related *C. intermedia*. *Choeroniscus periosus* is confined to a small area in the very wet forest of western Colombia.

Genus Choeronycteris (Fig. 15).—This highly derived genus has a single species, *C. mexicana*, ranging from the southwestern United States to Honduras but only as a summer resident at the northern end of its range. Though a subspecies (*ponsi*) has been described from Venezuela, it is doubtful that it belongs

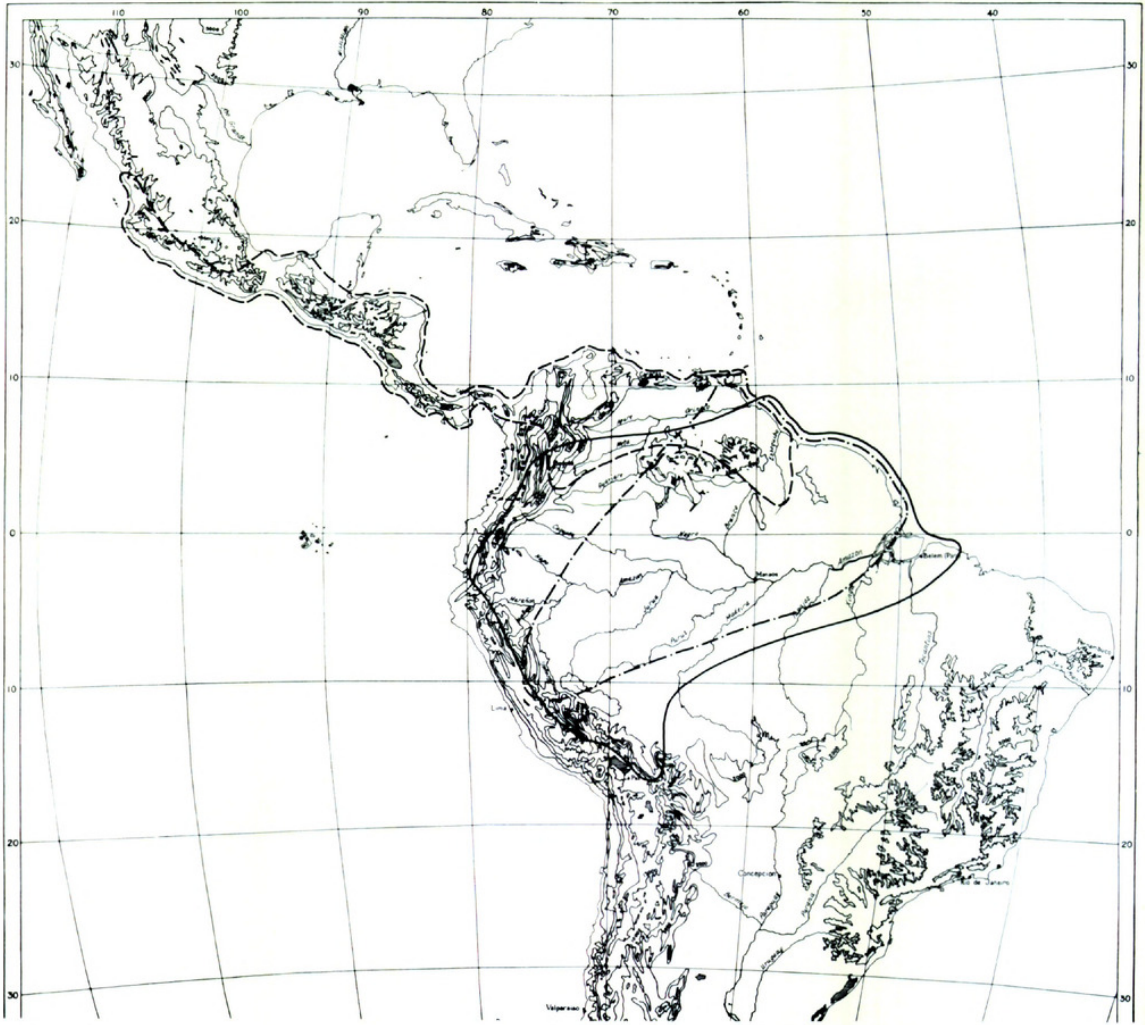


FIGURE 14. Distribution of the species of *Choeroniscus*: *godmani* (dashed line in Middle and northern South America), *intermedius* (dotted and dashed line), *minor* (solid line), *periosus* (dotted line in western Colombia).

to the Middle American species (see Jones & Carter, 1976). Like *Platalina*, *Choeronycteris* has an unusually long rostrum which almost certainly indicates a very long tongue.

Genus Musonycteris (Fig. 15).—This genus is closely related to *Choeronycteris* (with which it has been united by some) but has a still longer rostrum, in fact the longest (in relation to its width) of any bat (Fig. 1). The single species, *M. harrisoni*, is confined to southwestern Mexico.

DISTRIBUTION OF THE BRACHYPHYLLINAE

Unlike the subfamily Glossophaginae, that of the Brachyphyllinae is confined to the West Indies. Two of the three currently recognized genera (*Erophylla* and *Phyllonycteris*) have the skull and tongue proportions of typical nectar feeders, but the third, *Brachyphylla* has a head and dentition (Fig. 4) built like that of a fruit-eater. For this reason, it was for many years placed in the fruit-eating

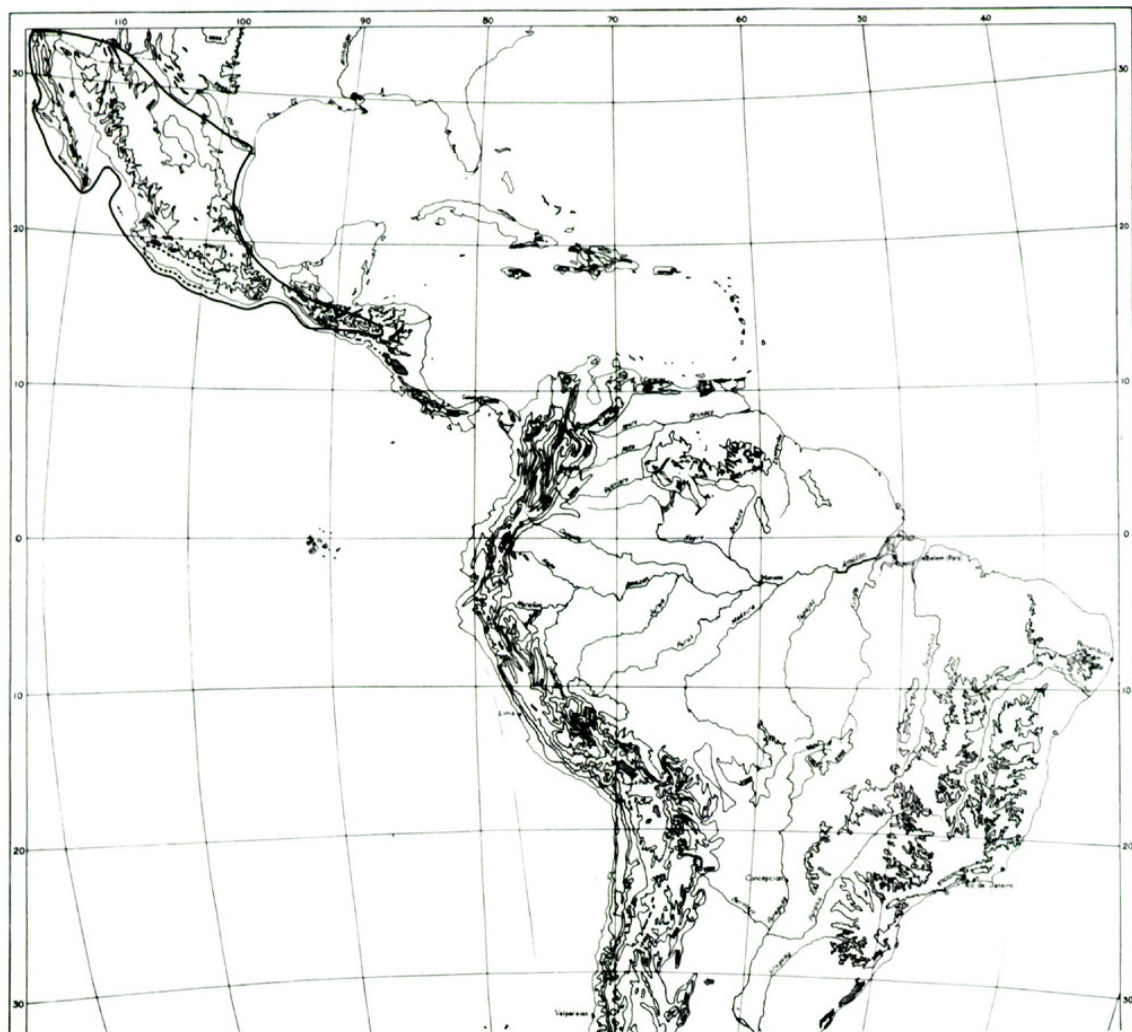


FIGURE 15. Distribution of the species of *Choeronycteris* and *Musonycteris*: *C. mexicana* (solid line), *M. harrisoni* (dotted line).

subfamily Stenodermatinae. What little is known of its food habits indicates a mixture of fruit and nectar. The other two brachyphylline genera also eat soft fruit on occasion.

Genus Brachyphylla (Fig. 16).—Two species are currently recognized, *nana* in Cuba, Hispaniola, the southern Bahamas, Cayman Islands (and known fossil from Jamaica); *cavernarum* in Puerto Rico and the Lesser Antilles.

Genus Erophylla (Fig. 16).—Again two species are recognized, *sezekorni* in Cuba, Jamaica, the Cayman Islands, and the Bahamas; *bombifrons* in Hispaniola and Puerto Rico.

Genus Phyllonycteris (Fig. 16).—This, like *Erophylla*, is a very highly specialized nectar-feeding bat. There are two living species, *poeyi* in Cuba and Hispaniola, *aphylla* in Jamaica. A third species, *major*, is known as a fossil from Puerto Rico.

ORIGIN AND DIVERSIFICATION OF NEW WORLD NECTAR-FEEDING BATS

The Phyllostomidae, the family to which all New World nectar-feeding bats belong, probably originated in tropical America since not only this family but the

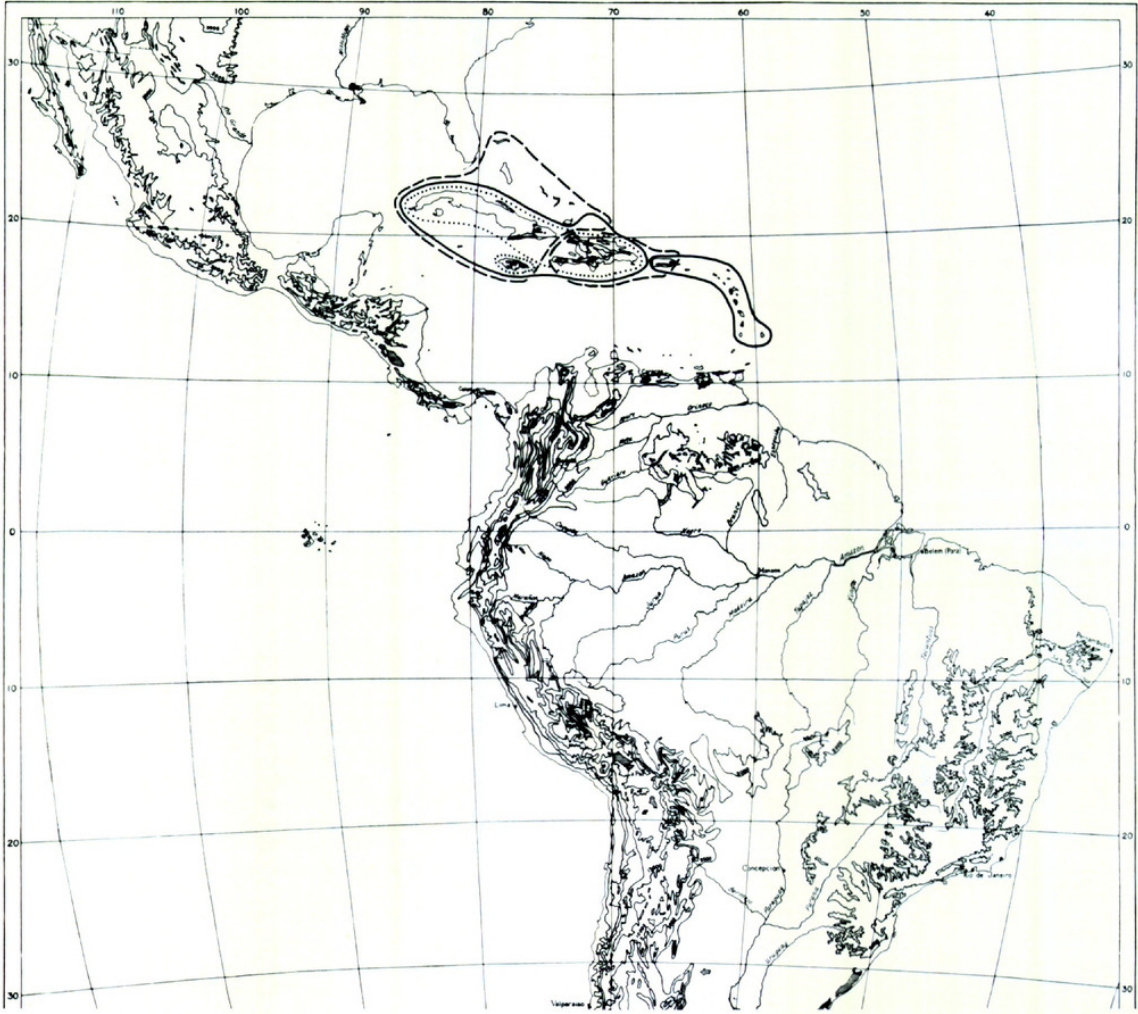


FIGURE 16. Distribution of the species of the Brachyphyllinae: *Brachyphylla nana* (solid line in the Greater Antilles), *B. cavernarum* (solid line in Puerto Rico and the Lesser Antilles), *Erophylla sezekorni* (dashed line in the Bahamas and western Greater Antilles), *E. bombifrons* (dashed line in the eastern Greater Antilles), *Phyllonycteris poeyi* (dotted line in Cuba and Hispaniola), *P. aphylla* (dotted line in Jamaica).

two most closely related families (Noctilionidae and Mormoopidae) are largely confined to this region. The earliest known fossil phyllostomid (not a glossophagine) is from the late Miocene of Colombia. At this time South America was still an island continent, separated by a marine channel from Central America, which suggests that the family originated in South America in long isolation. Unfortunately, the fossil record of bats in general and phyllostomids in particular is so poor that this can only be a suggestion. It is also highly uncertain when nectar-feeding bats evolved since none are known as fossils before the Pleistocene, but probably this occurred sometime during the middle or later Cenozoic. If both of these conclusions are valid, then the subfamily Glossophaginae probably also arose in South America, but if so there has been extensive secondary spread to Middle America. Of the 12 mainland genera here recognized, only two (*Scleronycteris* and *Platalina*) are confined to South America, whereas three (*Hylo-nycteris*, *Choeronycteris*, *Musonycteris*) are confined to Middle America (including extreme southwestern North America). Of the remaining seven genera, three

have extensive South American but restricted Middle American distributions (*Lionycteris* to Panama, *Lonchophylla* to Nicaragua, *Lichonycteris* to Guatemala). *Glossophaga*, *Anoura*, and *Choeroniscus* all have extensive distributions in both South and Middle America. *Leptonycteris* has a peculiar distribution, southwestern North America to upper Central America, also extreme northern South America, but with an apparently real hiatus in between. As suggested above, this may reflect a preference for relatively dry areas. Other glossophagine genera, however, with apparently similar ecological preferences (*Platalina*, *Choeronycteris*, *Musonycteris*) do not show the same distributional pattern.

THE COLONIZATION OF THE WEST INDIES

The West Indian nectar-feeders belong to two distinct groups. *Glossophaga* and *Monophyllus* are typical (and quite primitive) glossophagines whereas *Erophylla* and *Phyllonycteris*, together with the somewhat differently adapted *Brachyphylla*, form the highly derived endemic West Indian subfamily Brachyphyllinae. There is considerable disagreement concerning the relationships of the Brachyphyllinae. Thomas Griffiths at the University of Massachusetts is currently investigating relationships among all the New World nectar-feeding bats, and hopefully he will resolve the problem of the origin of the Brachyphyllinae. Currently, he is inclined to derive them from the base of the Glossophagine (Griffiths, oral communication). What can be said with confidence at this time is that the brachyphyllines have almost certainly been in the West Indies for a long time, probably since the Miocene, since this is the best differentiated group of endemic Antillean bats. *Monophyllus* is a much more recent invader (probably from South American *Glossophaga longirostris*), and still more recently, two different species of *Glossophaga* have colonized limited areas at the opposite ends of the West Indian chain.

ECOLOGICAL INTERACTIONS OF THE NEW WORLD NECTAR-FEEDING BATS

In view of the mutual adaptations of flower-feeding bats and the flowers with which they are associated, it would be very interesting if we could correlate their distributions and associate particular flower-feeders with the angiosperms which they pollinate. Unfortunately, not enough is known about the particular flowers visited by particular bat species to make any useful correlations. Skog (1976) has shown that head size of Greater Antillean nectar-feeding bats can be correlated with corolla size of species of *Gesneria* (which have adaptations for bat pollination) occurring on the same islands. Unfortunately, it is not known whether or not these particular species of bats do pollinate these particular species of *Gesneria*. Experience with predicting food habits on the basis of jaw and tooth characteristics in bats shows that correlations are usually far from perfect and sometimes quite poor.

Another factor that must be taken into account is that since none of the nectar-feeding bats hibernates and since all bats have surprisingly long life spans (more than 10 years), it is necessary for them to find flowers all year round. While there is apparently considerable irregular wandering (albeit undocumented) and, as we have seen, some definite migrations of north-temperate species, they still have

to find flowers blooming somewhere throughout the year. Since a given species of angiosperm is usually in flower for a limited time, a bat species dependent upon flowers must make repeated shifts. Rigid specialization for a certain type of flower is therefore unlikely, and an unusually long rostrum and tongue need not imply that only flowers with long corollas are visited. This may only mean that during one part (perhaps a very short part) of the year, this bat depends for food on nectar or pollen, which can only be reached with a very long tongue.

Nevertheless, when two or more species of nectar-feeding bats occur in the same area at the same time, one would expect some niche-partitioning of the flowers visited, assuming of course that some other necessary resource (such as roosting sites) was not in shorter supply. So far, direct evidence of this is virtually nonexistent. I have already mentioned various nectar-feeders which seem to be restricted to arid regions (*Leptonycteris*, *Lonchophylla hesperia*, *Platalina*, *Choeronycteris*, *Musonycteris*). However, most flower-feeding bats occur in the wet tropics. As indicated above, the most distinctive geographical separation is between mainland and West Indian species. There is also a weak separation on the mainland between South and Middle American species. I have checked wet tropical areas where collections have been extensive and where more than three species of nectar feeders (excluding the arid-adapted ones) are known to occur. I have come up with 10 such limited areas which merit some discussion.

Cuba. This large West Indian island has four of the species under discussion (*Monophyllus redmani*, *Brachyphylla nana*, *Erophylla sezekorni*, *Phyllonycteris poeyi*). As mentioned above, *Brachyphylla* is only partially a nectar-feeder. Judging by molar tooth patterns, *Monophyllus* has somewhat different adaptations from *Erophylla* and *Phyllonycteris*.

Hispaniola. The same species occur as in Cuba, except that *Erophylla bom-bifrons* replaces *E. sezekorni*.

Jamaica. This West Indian island also has four nectar-feeding bats (*Glossophaga soricina*, *Monophyllus redmani*, *Erophylla sezekorni*, *Phyllonycteris aphylla*.) *Glossophaga* and *Monophyllus* are at least dentally much more primitive than *Erophylla* and *Phyllonycteris*.

Sinaloa. This western Mexican state lies near the northern end of the tropics. There are four wet-tropical glossophagines (*Glossophaga soricina*, *G. commissarisi*, *Anoura geoffroyi*, *Choeroniscus godmani*). Though there is some adaptive spread among these species, it is not clear how they partition the habitats).

Oaxaca. This is another western Mexican state, but one less marginal to the tropics. There are six species of the sort under consideration (*Glossophaga soricina*, *G. commissarisi*, *G. alticola*, *Anoura geoffroyi*, *Hylonycteris underwoodi*, *Choeroniscus godmani*). Though the first three are certainly more primitive than the last three, it is not clear how this relates to niche partitioning.

Eastern Panama. This area, at the junction of South and Middle America, has seven relevant species (*Glossophaga soricina*, *G. commissarisi*, *Lonchophylla thomasi*, *T. mordax*, *T. robusta*, *Lionycteris spurrelli*, *Lichonycteris obscura*). Again, there is a fair adaptive spread, but little evidence for niche partitioning.

Mérida region. This well-collected area in western Venezuela has six species of nectar-feeders (*Glossophaga soricina*, *G. longirostris*, *Lonchophylla robusta*, *Anoura caudifer*, *A. cultrata*, *A. geoffroyi*). In view of its location near the north-

ern end of the Andes, some altitudinal stratification might be supposed. However, all six species occur in the lowlands and all but *G. longirostris* also in the highlands (above 1000 m).

Trinidad. This well-collected continental island off the northern coast of South America has four species of glossophagine bats (*Glossophaga soricina*, *G. longirostris*, *Anoura geoffroyi*, *Choeroniscus intermedius*). Though both primitive and derived species are represented, I know of no evidence of niche-partitioning on the basis of food.

Belém region. This well-collected area near the mouth of the Amazon is different from any of the others here treated in that it is completely lowland, without any mountains nearby. Six species of glossophagines occur (*Glossophaga soricina*, *Lonchophylla thomasi*, *L. mordax*, *Lionycteris spurrelli*, *Lichonycteris degener*, *Choeroniscus minor*). Again, there is considerable diversity in degrees and types of specialization, but no evidence of niche partitioning.

Amazonian slopes of central Peru. Another well-collected area in the tropical heart of South America; 10 species of glossophagines are known (*Glossophaga soricina*, *Lonchophylla thomasi*, *L. robusta*, *Lionycteris spurrelli*, *Anoura caudifer*, *A. cultrata*, *A. geoffroyi*, *Lichonycteris obscura*, *Choeroniscus minor*, *C. intermedia*). Although there is considerable evidence concerning altitudinal ranges in this area (see Koopman, 1978), this does little to explain niche partitioning among the glossophagines. All species occur in the lowlands and half of the species (those in *Glossophaga*, *Lionycteris*, and *Anoura*) reach the highlands, though the *Anoura* species reach much higher elevations than either *Glossophaga* or *Lionycteris*.

Thus, summing up this information concerning species in local areas, there is little evidence among species inhabiting the wet topics for any niche partitioning either on the basis of kinds of flowers visited or altitudes at which foraging occurs. Of course, since a bat's roosting site and its foraging range may be well separated, it is possible that there is more separation in actual places where flowers are visited than the total range would indicate. Though, on the evidence of considerable morphological diversity, I would expect some niche partitioning based on food plants, there is very little evidence of any at this time.

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Note added in proof: Since this paper was submitted, two additional species of Glossophaginae have been described. *Glossophaga mexicana* (Webster & Jones, 1980. Occ. Papers Texas Tech. Univ. 71: 1–12) is from southwestern Mexico. *Lonchophylla handleyi* (Hill, 1980. Bull. Br. Mus. Nat. Hist., Zool. 38: 233) has been split off from *L. robusta*, which does not occur south of Ecuador. *Lonchophylla handleyi* is in Ecuador and Peru.



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