Pollination by Lemurs and Marsupials: An Archaic Coevolutionary System

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Summary. Existing geographical and ecological relationships between bats, nonflying mammals, and birds that visit flowers for food suggest novel interpretations of their evolutionary history.

The earliest insect-pollinated angiosperms seem to have been visited and pollinated predominantly by insects (*1*). Angiosperms in which the flowers produce large quantities of nectar can be cross-pollinated effectively only by animal visitors with high energetic requirements (*2*). We therefore presume that angiosperm flowers with these characteristics evolved only after the appearance of small, nectar-feeding birds, bats, and nonflying mammals that fed at least seasonally on nectar and pollen. Pollination systems involving hummingbirds and hawkmoths, which are more specialized groups of flower visitors with high energetic requirements, seem to be even more recent in origin. The hypothesis that the flowers of the earliest angiosperms did not produce large quantities of nectar and were not visited by vertebrates is strengthened by the almost total absence of such pollination systems among living angiosperms that are thought to be relatively unspecialized: woody Ranales, unspecialized Hamamelidiflorae, and generalized monocotyledonous plants (*3*).

Vertebrate Pollination Systems: An Overview

Birds, bats, and nonflying mammals are the groups of vertebrates most intimately associated with the flowers of angiosperms at present. Although other kinds of vertebrates, such as lizards (*4*), also visit nectar-rich flowers on occasion, it is the three groups mentioned above that provide the great majority of flower visitors, and therefore are of the greatest historical and functional significance. Each will now be reviewed in a historical and geographical context.

Birds. The phylogenetic relationships, distribution, and history of perching birds suggest that they did not originate before the end of the Cretaceous (*5*), although some suboscine families might conceivably antedate the Paleocene. Most, if not all, modern families of perching birds are Neogene or more recent in origin. Bock's (*6*) analysis of the evolution of the Hawaiian honeycreepers (Drepanididae), which he shows could have taken place within a million years, is an important indication of the rate with which frequent or even obligate nectarivory could have originated in geological time. The history of hummingbirds is particularly enigmatic, but if they are related to swifts, they probably evolved no earlier than the Eocene (*7*). Nectarivory in birds is a trait that has originated many times independently, and there is no concrete evidence that it was widespread until the Miocene, even though some existing flower-visiting groups of birds, such as the suboscine Philepittidae of Madagascar, seem certainly to be much older.

On a geographical basis, nectarivory is, as Lein (*8*) pointed out, well represented throughout the tropics and Southern Hemisphere and virtually absent in the Palearctic region. Its presence in North America is mainly accounted for by the geologically recent invasions by the hummingbirds, doubtless of South American origin.

Bats. Although the fossil record of bats is poor (*9*), it is generally assumed that the modern attributes of bats had already been obtained by the end of the Eocene (*10*). The existence of a well-preserved Early Eocene fossil that combines to some extent the characteristics of the two living suborders of bats (*11*) is in accordance with this hypothesis. Bats, therefore, have probably contributed to the diversification of angiosperms for less than 50 million years, and presumably were absent for the first 75 million years of the evolution of the group (*12*). Megachiroptera are known to have appeared in Europe by the Oligocene (*13*, *14*). It therefore seems reasonable to assume that certain members of this suborder may have been feeding regularly both on flower parts and on fruits (*14*) and contributing to the diversification of flowering plants by the end of the Eocene.

By the close of the Eocene and the beginning of the Oligocene, many modern families of Microchiroptera appeared in the fossil record in Europe and North America (*13*). The large family Phyllostomatidae, the leaf-nosed bats, is known from the Late Miocene (*15*). This suggests that the subfamily Glossophaginae, one of the most specialized of flower-visiting bats and the most numerous, being widespread over the warmer parts of the New World, is very unlikely to be older than the Miocene (*14*). Members of another subfamily, the West Indian Phyllonycterinae, likewise feed frequently on flowers and presumably are Miocene in origin also. Most of the Phyllostomatidae, including these two specialized subfamilies, eat a varied diet including insects, fruit, and flowers (*16*). At least some glossophagine bats also obtain a portion of their nitrogen from pollen (*17*), and they certainly are not strict nectar-feeders. Individual species do not seem to be restricted to particular plants in their flower-visiting habits [for example, see (*18*)].

On a geographical basis, glossophagine bats are common and intimately associated with the flowers of plants of many families throughout the tropics of the New World (*19*). In Africa, the small, specialized pteropids that are the most reliable flower visitors are largely confined to the forested area in the west, to which the only African representative of the Macroglossinae, *Megaloglossus woermanni*, is likewise confined (*20*). In the more widespread savannah regions of Africa, fruit-eating and flower-visiting bats, including species of *Eidolon*, *Epomophorus*, and *Rousettus*, are fairly common locally and seasonally, but their role in the pollination of flowering plants is less well understood than that of bats in the New World or West Africa (*20*, *21*).

In Madagascar, there are only three

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species of fruit-eating or flower-visiting bats: *Pteropus rufus*, *Eidolon helvum*, and *Rousettus madagascariensis* (*22*). *Pteropus rufus* is found throughout the island and is mainly frugivorous; it visits flowers occasionally, but is regarded as destructive to *Ceiba* flowers in plantations in Southeast Asia (*23*). *Eidolon helvum* is found in rain forests in eastern Madagascar. Its diet and foraging behavior are similar to those of *Pteropus rufus* (*24*). *Rousettus madagascariensis*, an endemic species, is restricted to a small portion of the rain forest in the eastern parts of the island (*20, 22*).

In tropical Asia there are 11 genera of pteropid bats, two of which—*Eonycteris* and *Macroglossus*—obtain most of their food from flowers (*25*); in New Guinea there are eight genera, three of which—*Macroglossus*, *Syconycteris*, and *Melonycteris*—are flower bats (*23, 26*). In Australia, a similar, but depauperate, fauna is found in the tropical extreme north. Three species of *Pteropus* occur south to the forests of New South Wales, as does *Syconycteris australis*, another blossom-feeder (*27*). The occurrence of plant-feeding bats in Australia presumably dates from the Late Miocene or more recently (*28*). Another macroglossine genus, *Notopteris*, is endemic in western Polynesia.

Flower-visiting bats in the Old World, therefore, seem to be well represented in tropical Asia through New Guinea and western Polynesia, fairly well represented in West Africa, and less well represented in East Africa and tropical to subtropical Australia. Flower-visiting bats are also poorly represented, and by widespread genera only, in Madagascar. This pattern suggests no great antiquity in the region.

Although bat-pollination is not represented among the more archaic of the living angiosperms, it, together with bird-pollination, seems to be of early origin and establishment in Myrtaceae (especially the more advanced subfamily Myrtoideae). Increased stamen number and flower size in Myrtaceae, linked with bird-pollination by Stebbins (*29*) and Carlquist (*30*), are often regarded as primitive. It is probable that such pollination systems have existed in Myrtaceae since Paleogene time, but they were probably not characteristic of the earliest members of this family.

The small Paleotropical family Sonneratiaceae (two genera, seven species) appears to be almost exclusively bat-pollinated. Its large flowers and numerous stamens presumably evolved in relation to this system of pollination. Largely because of these features, this family is often regarded as the most primitive of the Myrtales. Such a phylogenetic position must be doubted, however, unless it can be confirmed by independent evidence. Myrtales and the family Myrtaceae itself originated before the close of the Cretaceous (*28, 31*), whereas the excellent fossil record of Sonneratiaceae extends back only to the Lower Miocene (*31, 32*), approximately the period when bats may have begun to visit flowers regularly for food in the Old World.

Nonflying mammals. A recent review (*33*) documents the extent of our knowledge of the interactions between nonflying mammals and plants. In it, Rourke and Wiens review a number of observations of such mammals as rats and squirrels visiting flowers, but also point out some relationships that appear much more significant. They argue compellingly that the inflorescences and flowers of certain members of Proteaceae and Myrtaceae in Australia are adapted to pollination by small marsupials, a suggestion first made by Porsch (*34*). They also show that rodents regularly visit and may pollinate the inflorescences of certain species of Proteaceae in South Africa and perhaps also in Australia [see also (*35*)]. In addition, as they and earlier authors pointed out, the so-called honeypossum, *Tarsipes spencerae*, seems clearly to have evolved in relation to such a source of food.

Many primates feed on flowers or parts of flowers at times, but the effect on the flowers is usually destructive [for example, see (*36*)]. *Cebus* monkeys may drink water or nectar, or both, from trees of *Ochroma pyramidale* without destroying the flowers (*37*), and might participate in their pollination. This is, however, the only well-documented case of an anthropoid which might be acting as an important pollinating agent. In Madagascar, however, the relation between lemurs and flowering plants appears to be a significant one. All of the diurnal Malagasy lemurs are mainly vegetarian and many spend a small proportion of time feeding on flowers and are destructive to them. In contrast, the following six species of nocturnal lemurs have been observed to feed regularly on flowers during at least a portion of the year, and are therefore of particular interest in terms of their possible significance in pollination systems.

1) *Lemur mongoz* [average weight, 2530 grams (*38*)]. It was reported (*39*) that 84 percent of the observed feeding of this species during the dry season was on nectar licked from the flowers of *Fernandoa madagascariensis* (*Kigelianthe*) and *Combretum phaneropetalum*, both red-flowered and normally thought to be bird-pollinated; the flowers of the introduced *Ceiba pentandra* (*40*); and the extrafloral nectaries of the native *Hura crepitans*. The animals moved rapidly from inflorescence to inflorescence and visited many trees in a single night.

2) *Lepilemur mustelinus* [weight, 600 to 900 g (*38*)]. During the driest part of the year, flowers of *Alluaudia ascendens* and *A. procera* constituted a major portion of the diet; the entire flower was eaten so the animals were evidently not effective as pollinators (*41*).

3) *Microcebus murinus* [50 to 150 g (*38*)]. Martin (*42*) reported that this small lemur ate the flowers of *Brexia madagascariensis*, *Rubus roridus*, *Uapaca* sp., and *Vaccinium emirnense* during the dry season, allowing the petals to fall to the ground. In contrast, one of us (*43*), making observations in the dry season at Ampijoroa, observed the animals licking nectar from the flowers of the introduced *Ceiba pentandra* without damaging the flowers.

4) *Microcebus coquereli* [about 400 g (*38*)]. Petter (*44*) reported this species to feed on flowers, fruits, gums, and insects.

5) *Cheirogaleus medius* [150 to 400 g (*38*)]. During the first part of the rainy season, the main part of the diet appears to be flowers, although the animals also eat insects. An important source of nectar was a native species, *Delonix floribunda* (*44, 45*).

6) *Phaner furcifer* [about 450 g (*38*)]. This species utilized both *Crateva greveana* and *Adansonia* sp. as a source of nectar at the start of the wet season, licking the flowers and moving from cluster to cluster. *Phaner furcifer* is also known to feed on gums, insects, and fruits (*46*).

Of the four remaining species of nocturnal lemurs, one—*Daubentonia madagascariensis*—has a very specialized diet, and the feeding habits of the remaining three—*Avahi laniger*, *Cheirogaleus major*, and *Allocebus trichotis*—have not been studied. In general, however, it can be asserted that nocturnal lemurs do play a significant role in the pollination of certain plant species in Madagascar.

Another group of unspecialized nocturnal primates, the bush babies of the mainland of Africa, has been reported to visit the flowers of *Adansonia* for nectar and probably other food material as well without destroying them (*47*). The species involved, *Galago crassicaudatus* [weight, 1000 to 1250 g (*38*)], has also been reported to feed on fruit, insects, and gum (*48*). A second species of *Ga-*

lago, *G. senegalensis* [weight, 225 to 300 g (*38*)], was reported by Doyle (*48*) to visit different flowering trees in succession; whether they were actually seeking insects, as he assumed, remains to be demonstrated.

In summary, certain marsupials in Australia, rodents in Australia and South Africa, lemurs in Madagascar, and galagos in continental Africa regularly visit nectar-rich flowers and lap their nectar as an important source of food, especially during the dry season. Almost all of these animals are nocturnal, and nearly all feed in part on insects, fruits, and, in some cases, gum. In general, they do not appear to compete directly with flower-visiting birds, which are exclusively diurnal, for food (*49*). The living marsupials of South America do not include forms that regularly visit flowers or eat fruits and that might conceivably be implicated in pollination systems (*50*). It would be of great interest to know more about food habits of the single nocturnal New World primate, *Aotus*, which might feed on and pollinate flowers.

Is There a Class of Flowers Adapted to Pollination by Nonflying Mammals?

This question, first raised in a comprehensive manner by Porsch (*34*), has been answered in the affirmative, with new evidence, by Rourke and Wiens [(*33*); see also (*35*)]. Whether, as Porsch supposed, certain Myrtaceae and Proteaceae of Australia fall into such a class, remains to be proved. Nevertheless, the existence of certain species with unusually large, strong flowers or inflorescences, relatively few flowers or inflorescences per plant, strong floral odors, and copious nectar, in areas where bat-pollination is absent or at best sporadic, does point in this direction.

For Madagascar, another region where plants that bear flowers with these characteristics exist, and where pollination of flowers by bats is evidently very rare, Jumelle and Perrier de la Bâthie (*51*) reported that lemurs regularly visited the nectar-rich flowers of *Symphonia nectarifera*, eating the leathery petals and drinking the nectar. Certainly lemurs may be regular visitors to the largest-flowered of the approximately 16 species of *Symphonia* found in Madagascar (*52*), and might reasonably be thought to have participated in their evolution. Porsch (*53*) considers *Symphonia* in general to be bat-pollinated, but agrees with Perrier de la Bâthie about the probability of lemur pollination in these species. He also suggests that some Bombacaceae and Lecythidaceae may be adapted for pollination by nonflying mammals.

Other Mascarene plants that have what appear to be suitable characteristics and that have been observed to be visited by lemurs eating portions of the flowers or lapping the nectar include *Adansonia*, *Brexia madagascariensis*, *Crateva greveana*, *Delonix floribunda*, *Rubus roridus*, *Uapaca* sp., and *Vaccinium emirnense*. Lemurs have also been observed to feed on nectar from the extrafloral nectaries of the pantropical *Hura crepitans* and to visit and probably efficiently pollinate the flowers of the introduced *Ceiba pentandra*. At the flowers of the normally bird-pollinated and red-flowered *Combretum phaneropetalum* and *Fernandoa madagascariensis* the visits of lemurs were undoubtedly secondary. Bats very often visit normally bird-pollinated plants, such as *Erythrina* (*54*) and *Spathodea* (*55*) for nectar. Reports of lemurs devouring the entire flower of *Alluaudia* should be confirmed, for there has been a tendency to view their activities as mainly destructive to the plants, and this has not been confirmed by many recent observations.

In any event, in Madagascar, an island where flower-visiting birds are frequent but flower-visiting bats are rare, there appears to be a strong circumstantial case for the evolution of certain plants with floral characteristics adapted to regular visitation by and consequent pollination by lemurs. Just as in temperate Australia, there is no reason to suppose that fruit-eating and flower-visiting bats were ever present in greater numbers than at present, and therefore it seems warranted to view the association between certain species of plants and lemurs as one that is archaic, rather than recently derived. Such an endemic group as Sarcolaenaceae, with some eight genera and 40 species of trees and shrubs with few, large, strong, presumably nectar-rich flowers, and large pollen shed in tetrads (*56*), might conceivably be pollinated by lemurs and might have been pollinated by them since Paleogene times.

Contemporary Relationships

Birds, bats, and nonflying mammals visit and pollinate flowers regularly at the present time. Pollination systems involving birds are well developed throughout the tropics and the temperate regions of the Southern Hemisphere; most of the flowers birds visit are brightly colored, usually red, and odorless (*57*). Systems involving bats and nonflying mammals usually include flowers that are dull-colored and odorous; they are almost invariably nocturnal, whereas systems involving birds are always diurnal, as pointed out by Fenton and Fleming (*49*). With the exception of the specialized flowers closely adapted for hummingbirds (and the analogous ones visited by hawkmoths), many of the flowers visited by birds are also visited by bats and nonflying mammals in regions where flower-visiting members of these groups are found. Aside from morphological adaptations that presumably evolved to protect the ovules of the plants concerned (*58*), the flowers of such plants are generally open, with copious nectar.

Pollination systems involving bats and those which involve nonflying mammals appear to have a reciprocal geographical distribution. Bat-pollination is common and well developed throughout tropical America, Asia, and northern Australasia, reasonably frequent in West Africa, less so in East Africa, and poorly developed on Madagascar. Flower-visiting and fruit-eating bats migrate into temperate regions seasonally, at times reaching temperate Australia and South Africa and the southern borders of the United States and of the Palearctic region. Those systems that appear to involve nonflying mammals, on the other hand, are evidently present in temperate South Africa, temperate Australia, and Madagascar—all regions where flower-visiting bats are rare, seasonal, or absent.

Evolutionary Relationships

The only extensive areas where nonflying vertebrate pollinators seem to be common are where there is a limited plant-visiting bat fauna. Can we assume therefore that competitive interactions among bats, prosimians, and phalangerid marsupials may have occurred throughout their evolutionary history? Is there any evidence that bats may have replaced arboreal tropical forest-dwelling marsupials and prosimians in certain regions during the Tertiary?

Those vertebrate taxa that are most frequent in the tropical forest canopy and most likely to be utilizing resources similar to those used by prosimians and arboreal phalangerids are bats, birds, and tree squirrels. All bats are nocturnal and most birds are diurnal. Although most mammals that dwell in tropical forests are nocturnal, anthropoid primates and tree squirrels, except flying squirrels and *Aotus*, are diurnal (*59*). Bats and birds avoid competition for many of their resources (especially insects and other prey and nectar) simply by these differences in activity pattern. It seems likely, however, that bats and nocturnal prosimians and marsupials have been major or potential competitors throughout much of Tertiary time. The success of bats in tropical Asia, Africa, and America and the relative lack of success of prosimians and arboreal marsupials in these areas may be directly related.

The great eutherian and marsupial radiations on different continents in the early Tertiary coincided with the radiation of many modern groups of angiosperms with relatively specialized flowers (*60, 61*). A major mammalian radiation, including the origin and diversification of insectivore-like primates or primate-like insectivores, the plesiadapoids (*62-66; 67*, pp. 415-433; *68, 69*), occurred in Europe and North America during the Paleocene. A similar diversification of polyprotodont marsupials occurred at the same time in South America (*61, 70*). Also in South America, some extinct groups of smaller marsupials seem to have been omnivorous (for example, Palaeothentinae, Abderitinae, Polydolopidae, and Caroloameghiniidae), and some of these groups converged markedly with living Australian phalangeroids, with some primate groups such as the fossil Carpolestidae from North America, and with living and fossil lemurs from the Old World (*50*).

Some extinct marsupials in the Cretaceous and Paleogene of South America may therefore have been flower-visitors and important in the pollination of plants at those times. None of these animals have persisted to the present. Recall that the flower-visiting bats of South America are believed to have originated by the Miocene: did they outcompete and replace earlier flower-visiting marsupials on plants that produced large flowers with copious nectar? These plants may have developed adaptations in the course of evolution that would have excluded the marsupials and favored visitation by the wider-ranging, highly specialized glossophagine bats. The bats would undoubtedly have brought about a greater degree of outcrossing in such plants (*2, 71*). A similar pattern characterizes the evolution of pollination by birds in many plant groups. At any rate, this mammalian radiation included the invasion of numerous plesiadapoids and other mammals into arboreal mixed-feeding adaptive zones (*60, 61, 65, 70, 72-74*).

A number of these early Tertiary mammals have dental morphology which suggests convergent feeding adaptations. The tiny, mouse-sized Picrodontidae were originally considered to be bats related to *Phyllonycteris* (*75*), a fruit- and nectar-feeding phyllostomatid bat, and there is still some controversy as to their relationships (*67*, pp. 415-433; *76*). Most authors suggest, however, that they are primates and merely convergent to the phyllostomatid bats (*65, 77*). Szalay (*71*, p. 16) states: "Their peculiar, phyllostomatid bat-like dental adaptation might have been the result of selection for juicy fruit or nectar feeding diet" (*78*). The carpolestids, another mouse-sized family of plesiadapoids, share dental features with certain multituberculates, with an extinct group of New World marsupials, and with some living Australian marsupials (*65; 67*, pp. 415-433; *72, 79*). The living genus of marsupial of the same size as the carpolestids, *Burramys*, feeds on seeds, fruit, insects, and nectar (*33, 80*). The dentitions of the Paleocene and Eocene genus *Phenacolemur* closely resemble those of the marsupial sugar glider *Petaurus* (*67*, pp. 415-433; *68*) that feeds on insects, insect larvae, small birds, buds, flowers, nectar, sap, and fruit juices (*24*). Kay and Cartmill (*69*), after a detailed study of the dentition of a number of Paleocene paromomyids, concluded that the genera *Palaechthon* and *Plesiolestes* were insectivorous but took a small amount of fruit, nectar, or gum; and that *Paromomys*, *Torrejonia*, and especially *Phenacolemur* fed predominantly on fruit, gum, or nectar. They also found that in the plesiadapid *Chiromyoides*, the shearing features of the molars appear somewhat reduced, suggesting a tendency toward fruit-eating. Thus, at least by the end of the Paleocene, all four families of plesiadapoids (Picrodontidae, Carpolestidae, Paromomyidae, and Plesiadapidae) contained plant-visiting genera.

Concerning these convergent adaptations, Szalay (*81*, p. 33) states:

> A previously not fully exploited primary food source of fruits and leaves, etc., became probably more and more utilized, sometime during the second half of the Cretaceous, by several groups of therians. . . . One of these groups was undoubtedly the early prosimians. In addition to the primates, mixodectids, apatemyids, condylarths, the ptilodontid multituberculates, the eutherian plagiomenids, and probably the Cretaceous marsupial *Glasbius* were also occupants of the frugivore-herbivore-omnivore adaptive zone for small mammals.

Szalay (*81*) believes that the radiation of the plesiadapoids may have led to the decline and eventual extinction of many of the more primitive Cretaceous mammals. A number of other authors have also associated early extinctions with competitive exclusion related to early eutherian radiations. However, the particular patterns of Paleocene and Eocene extinctions of some North and South American marsupials and of certain taxa of plesiadapoids and Eocene primates may be, at least to some extent, related to the rapid evolution and radiation of the bats, and their exploitation of flowers and fruits as food.

The North American marsupials declined by the end of the Oligocene and disappeared entirely by the end of the Miocene, as did the single line that reached Europe (*82*). Although most major groups of South American marsupials persisted into the Pliocene, the small, herbivorous marsupials such as the Groeberiidae, Abderitinae, and Palaeothentinae also became extinct by the middle Miocene (*61, 73*), when flower-visiting bats were becoming well established. The plesiadapoids disappeared by the Eocene, an unknown lineage giving rise to the "primates of modern aspect" (*83*) no later than the mid-Paleocene (*64*).

These Eocene prosimians ranged in size from about 60 to 1600 g (*84*), in the size range from *Microcebus* to *Lemur mongoz*. In contrast to the plesiadapoids, they showed a number of modern primate adaptations: sharp claws were replaced by flattened nails overlying friction pads; the toe and thumb were divergent and enlarged to produce effective grasping organs; and the two eyes converged toward the center of the face (*64, 85*). These adaptations (at least the first two) would have allowed the Eocene prosimians far greater access to fruits and flowers, as well as to many plant-visiting insects, making them much more efficient at locomoting and foraging in the small terminal branches of bushes and trees than were the plesiadapoids (*63, 64, 86*). Since most small nocturnal primates feed on crawling insects, many of which are captured on the ground (*42, 74*), and since most are omnivorous and include a large proportion of fruits or nectar, or both, in their diet (especially during the dry season), it is probably this improved ability to feed in terminal branches that was the most important impetus for the major adaptive shift seen in these Eocene primates. They then would become simply a more efficient version of the insectivorous-frugivorous-nectarivorous plesiadapoids.

By the Oligocene, however, these early primates of modern aspect disappear worldwide, leaving only a few, mainly specialized genera of modern forms outside of Madagascar. By the latter half of the Eocene, this group of mixed-feeding prosimians gave rise to the larger-bodied, diurnal, mainly folivorous-frugivorous anthropoids (*63; 67*, pp. 415–433). If feeding in terminal branches was a very important, new adaptive zone for a number of mammalian species during the Paleocene and Eocene, it is not unlikely that certain forms developed better adaptations to exploit this habitat throughout these time periods. It is also likely that the early prosimians of the Eocene were more efficient at exploiting terminal branches than were the plesiadapoids, and it has been suggested (*87*, pp. 1–64) that competition between Paleocene primates and primitive bats may have been one of the initial causes of bat flight. The Eocene seems to have been a period when bats and primates were refining their abilities to exploit the fruits and flowers of angiosperms, as well as the insects that also fed upon these resources. It may also have been a period of intense competitive interaction between these chiropterans and primates.

As we have mentioned, the earliest known fossil bat, *Icaronycteris index*, comes from early Eocene deposits in Wyoming (*11*). Concerning this fossil, Jepsen (*87*, p. 12) wrote:

> By the time in paleobiologic history that *I. index* was a segment in the phylogeny of chiropts the whole vast galaxy of morphic, behavioral, and ecologic characteristics that distinguish bats from non-bat predecessors had already been achieved. . . . It indicates that some bats had already evolved almost to their present grade of organization while horses were the size of modern dogs and man's ancestors were no larger than small monkeys.

By the early Eocene the evolution of primates of modern aspect was in its very early stages. The rapid development and distribution of bats in the Old and New World tropics during the Eocene corresponds with the virtual extinction of the plesiadapoids and the initial development and later disappearance of the first primates of modern aspect in Europe, North America, and presumably throughout the tropics. Jepsen (*87*, pp. 1–64) speculated that plesiadapoid and pre-bat competition led to a major adaptive shift in chiropteran evolution. Be that as it may, it does seem possible that bats may well have influenced primate evolution during the Eocene. They certainly may have been one of the major forces contributing to the extinction of many kinds of prosimians by the end of this period.

Such prosimians, and marsupials with similar habits, have survived chiefly where competition from flower-visiting and fruit-eating bats is limited or absent in Madagascar, South Africa, and temperate Australia. The reasons for the absence of such prosimians and marsupials in the temperate regions of the Northern Hemisphere remain to be explored, although these regions have certainly been an active site of evolution for many "dominant" groups of animals throughout geological history (*15, 88*). Survival for many groups of plants and animals, and we would suggest also for the unique early Tertiary coevolutionary relationships between nonflying mammals and flowering plants, seems clearly to have been facilitated in the far-flung temperate lands of the Southern Hemisphere.

Jepsen (*87*, pp. 1–64), however, warns that speculations about the causes of bat flight might be flights of fantasy, and we might add that, by making speculations about the causes of Eocene primate extinctions, we may be going out on a (terminal) limb.

Conclusion

Among the vertebrates, birds, bats, and nonflying mammals include species that regularly visit the flowers of angiosperms and have evolved in relation to these habits. Flower-visiting birds are frequent throughout the tropics and in the south temperate zone; in the north temperate region they are represented in some numbers only in North America, which the hummingbirds, a South American group of problematical origin, invaded presumably in late Tertiary time. Many unrelated groups of birds visit flowers regularly and participate in their pollination to greater or lesser degrees, but the oldest of these seem to date from the Cretaceous-Tertiary boundary, and there is no strong evidence for widespread flower-visiting among birds until the Miocene. Although they often visit the same species of plants, there appears to be little evidence for competition between birds, of which the flower visitors are all diurnal, and either bats or nonflying mammals, with which they coexist widely.

Bats seem to have originated in the Early Tertiary and may have been visiting flowers as a source of food since the Eocene. Fruit-eating and flower-visiting bats occur widely throughout the tropics. They are less well represented in Africa than in Asia or America, and rare in Madagascar and in temperate regions generally. They may, however, visit temperate regions during the course of seasonal migrations. Glossophagine and phyllonycterine bats, the two specialized groups of flower-visiting Microchiroptera, both restricted to the New World, seem to be of Miocene origin, so that the habit of eating fruits and visiting flowers for food is probably older in the Eastern Hemisphere than in the Western Hemisphere.

Among the nonflying mammals that regularly visit flowers for food, the most prominent groups are some of the phalangeroid marsupials of Australia, rodents in Australia and South Africa, lemurs in Madagascar, and bush babies in continental Africa. Where these relationships are well developed, they occur in areas in which flower-visiting bats are absent or sporadic. Almost all of these relationships involve nocturnal mammals, and there appears to have been a sort of competitive exclusion on a grand scale involving flower-visiting bats.

Although there are clearly bird-flowers and bat-flowers, whether any flowers have characteristics that evolved specifically in relation to nonflying mammals remains to be seen. The kinds of large flowers with copious nectar that are visited by vertebrates in general obviously did not occur in the course of angiosperm evolution until the end of the Cretaceous, at the earliest, and thus during the first half of their evolution different groups of flowering plants were probably visited and pollinated chiefly by beetles and by flies. Some were of course wind-pollinated. The kinds of nectar-rich flowers that evolved in certain groups of angiosperms at about the start of the Tertiary doubtless facilitated outcrossing in these plants, particularly in the kinds of widely separated populations that are characteristic of the tropics. Subsequently throughout the Tertiary more specialized forms of flowers, with flowers that structurally restrict the kinds of vertebrates that are able to obtain nectar and are thus more efficient in directing outcrossing, have evolved repeatedly. Hummingbirds, sunbirds, and plant-visiting bats have been especially important in this context; the kinds of specialized flowers they visit have evolved from antecedents of many sorts, some insect-pollinated.

On the basis of these relationships, we suggest that there have been marsupials visiting the flowers of angiosperms for food since uppermost Cretaceous times, but that this relationship, once widespread, has persisted only in temperate Australia, where placental mammals are recent arrivals. Fossil forms elsewhere that were similar to the flower-visiting arboreal phalangeroids of Australia mostly disappeared at about the end of the Paleocene in northern continents, apparently giving way to prosimian forms similar in habits to them and to the living lemurs of Madagascar. These early primates also were widespread, but apparently replaced by bats with similar habits and dentition from the Eocene onward in the Old World, with the major replacement in South America probably delayed until the presumed diversification of glossophagine bats in the Miocene. Prosimians with this mode of life have persisted only in Madagascar, where fruit-eating and flower-visiting bats are and presumably always have been rare, and to a lesser extent (*Galago*) in continental Africa. Relationships between rodents and flowers have evolved more recently in areas such as South Africa and Hawaii, where flower-visiting bats are absent. Thus the coevolutionary relationships between marsupials and certain flowering plants in Australia as well as those between lemurs and other flowering plants in Madagascar, appear to be relicts that have survived from ancient times, just as many archaic plants and animals have persisted in these isolated lands. The relationships themselves appear to be "living fossils," which have a great deal to tell us about the evolution of both the mammals, including some of our own antecedents, and of the flowering plants.

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