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# Two cases of bat pollination in Central America

by

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Pollination of the flowers of trees and vines by bats (Chiroptera) is characteristically a tropical phenomenon. Adaptations to nectar-lapping and pollen-feeding are to be seen in the bats while the plants show all or most of a syndrome of characters. The latter include nocturnal anthesis, whitish or drab colors, large and strong flowers or inflorescences, large quantities of nectar (particularly available at night), a sour smell, large quantities of pollen, and positioning of the flowers in such a manner that they can be reached by the bats without impedance by the foliage (VAN DER PIJL, 23; FAEGRI and VAN DER PIJL, 13). The flowers may have a broad tubular form (into which the bat inserts its head and the upper part of its body) or, at the opposite extreme, resemble a "shaving brush" with stamens and styles bristling out from the flower so that they are pressed against the body of a bat which clasps it. In the latter case an inflorescence of many flowers may function as a unit in producing the "shaving brush" (BAKER, 4).

In the Old World, all of the flower - visiting bats belong to the suborder Megachiroptera and they show their adaptation to their vegetarian diet by modifications in dentition, by the possession of long, narrow tongues and a stomach structure appropriate for the digestion of largely liquid food (ALLEN, 2).

It appears that the order Chiroptera had its origin in the Old World and that migration of bats to the New World took place through boreal regions at about the beginning of the Tertiary Period. Apparently the migrants were insectivorous members of the Microchiroptera. However, when their range expansion brought them to the American tropics they encountered plants with appropriate flowers and a radiation into the flower-visiting niche (comparable with that occupied by the Megachiroptera in the Old World) ensued. The flower-visiting

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Microchiroptera in the American tropics belong to the family Phyllostomatidae, the leaf-nosed bats.

In recent years, a moderate amount of attention has been given to the pollinatory activities of bats in the Old World tropics (see reviews by JAEGER, 16; VAN DER PIJL, 21; HARRIS and BAKER, 15). By contrast, relatively few observations have been made in the New World. Exceptional are the accounts of bat pollination published by VOGEL (24, 25), CARVALHO (10, 11) and, outside of the tropics, by several biologists in Arizona (1, 18).

Because the activity of most flower-visiting bats takes place at dusk or after dark, accurate observations are not easily made, a fact which must be partially responsible for the neglect of the subject. With the advent of the stroboscopic flash-gun for high-speed nighttime photography, however, the situation is changed. Now, photographs of visits by bats to flowers may be taken in the field and analyzed subsequently in the laboratory.

During a botany course conducted by the Organization for Tropical Studies in July, 1968, two opportunities for photographic work of this sort were available. One was at the botanical garden in Lancetilla, Honduras, and the other was at Santa Ana, near San José, Costa Rica. In the former case, a tree of *Durio zibethinus* Murr. (Bombacaceae) was the focus of attention; in the latter case it was a vine of *Mucuna andreana* Micheli (Leguminosae). The photographic apparatus used included an Exakta camera (35 mm film) with 50 mm, 135 mm and 200 mm focal length lenses, a Meteor Ultrablitz flash-gun (flash duration 1/1400 second), and Kodak Tri-X film (ASA rating 400). The film developer was made with sodium sulfite instead of water to cut down on graininess.

## *Durio zibethinus* (Bombacaceae).

The durian tree is native to south-eastern Asia. There, its flowers are known to be visited by bats of the suborder Megachiroptera (VAN DER PIJL, 23). The point of interest was whether these flowers would be equally attractive to bats of the other suborder which had evolved the flower-visiting habit quite independently in the New World. *Durio zibethinus* belongs to a family in which bat-pollination is well known in the Old World (e.g. *Adansonia*, 15, 17; *Ceiba pentandra* [L.] Gaertn., 4. 5, 9); in the New World it occurs in *Ceiba acuminata* Rose (7) and *Ochroma* (6).

*Durio zibethinus* exhibits a number of characters which fit in the bat-pollination syndrome. Thus, its flowers are borne in clusters on the larger branches, are creamy-white in color, open in the evening (with their corollas and stamens being shed as a unit the next morning), produce a copious supply of nectar and have a smell which has been aptly described by BACKER (3) as resembling sour milk. The stamens, although only five in number, each have the filaments divided near their bases into 4 to 18 branches, each of which bears an anther. As a consequence, a "shaving brush" arrangement of anthers is produced with an ample pollen supply.

The stout style in each flower stands among the stamens. At anthesis the capitate stigma is on a level with the anthers but the style continues to elongate during the night (and even after the corolla and androecium are shed next morning). As a consequence, the stigma becomes more and more likely to receive pollen from another flower as the night wears on.

A single tree of this species, planted in the botanical garden of the Tela Railroad Company at Lancetilla, Honduras, was watched for four hours after dusk on July 15, 1968. Photographs were taken of visitors to the flowers as they could be perceived dimly silhouetted against the sky. There was no evidence that the flash was disturbing to the visitors which never spent more than two or three seconds at the flowers. Figs. 1-5 show that the visitors were one species of bat and one species of hawkmoth, respectively. This is not the first time that these two kinds of animals have been seen to be attracted to (and photographed on) the same flowers (cf. *Kigelia africana* Benth., Bignoniaceae, in Ghana, HARRIS and BAKER, 15), but it is of interest in once again challenging the popular belief that it is only *sweet* smells which are attractive to moths.

It is clear that the microchiropteran pictured in Figs. 1-4 is capable of carrying pollen from one flower to another for its head is liberally dusted with the abundant *Durio* pollen. It would seem that cross-pollination with another tree is necessary for fruit-setting, however, because the isolated tree at Lancetilla has not been known to set fruit.

The hawkmoth also appears capable of cross-pollination, for small masses of pollen may be seen (Fig. 5) adhering to the extended proboscis of the moth as it approaches a fresh group of flowers.

Visits by the bats were less frequent than might have been expected if the flowers provided their whole food supply for the night. Thus, intervals of as much as 20 minutes occurred during which no bat activity could be detected in the vicinity of the tree. It is probable that in this case, as in others studied by me elsewhere in tropical America, these microchiropterous bats were engaged in hawking for insects between their very brief visits to the flowers to lap nectar. Before it is concluded that this reduces their efficiency as cross-pollinators, however, it should be considered that this behavior may lead to a higher *proportion* of pollen transfers from one tree to another than the more concentrated attack upon one tree at a time which megachiropterans may make in the Old World.

## *Mucuna andreana* (Leguminosae-Lotoideae)

In 1941, VAN DER PIJL (22) pointed out that flagelliflory (the production of clusters of flowers at the end of long, dangling peduncles) is an extremely appropriate adaptation to the visitation of the flowers by larger flying animals because it allows them free flying room unimpeded by branches and foliage. Such flagelliflory may be developed from cauliflory (if the dangling peduncles are developed from buds on the trunk or major branches of the plant) and, in these circumstances, the peduncle may be as much as a centimetre in

diameter and capable of carrying the weight of the visitor as well as the flowers and their products.

Flagelliflory is nowhere better developed than in the vine genus *Mucuna* where some Central American species (such as *M. rostrata* Benth.) have orange or red flowers and are known to be visited by nectar-seeking birds. Even the purple-flowered *Mucuna urens* (which is frequent in the warmer parts of the area) is reported by DUCKE (12) to be visited exclusively by hummingbirds (and ignored by bees) in Brazil.

Several species of *Mucuna,* however, have white or greenish-white flowers. Thus, in Java, *M. reticulata* Burck and *M. junghuhniana* Back. have "dirty-white" petals and are believed by VAN DER PIJL (22) to be pollinated by bats. Although Van der Pijl made no direct observations of bat visits to the flowers of these species, they were adjudged to have received them because of the claw marks which appeared on their corollas as early as one hour after nightfall.

*Mucuna andreana* Micheli is a New World species which shows both cauliflory and flagelliflory (in the sense that the inflorescences arise from buds on the rather stout ascending stems on the vine but hang down on peduncles which may be two metres in length. Fig. 6). *M. andreana* is common in the forests and thickets of the tierra templada in Costa Rica (PITTIER, 20). In the type description of the species (MICHELI, 19) the flowers of the Colombian type material are said to be sordid-white but, for Costa Rica, waxy greenish-white would seem to be more appropriate. In any case, chiropterophily seemed likely in this species, and the occurrence of vines in the orchard of the Finca Lornessa, Santa Ana, San José Province, Costa Rica, provided the opportunity for its confirmation. I am greatly indebted to Mr. and Mrs. L. Ross for permission to make the study on their property and for their generous hospitality.

The detailed morphology of the flowers of the vines at Santa Ana includes some discrepancies from that of the Colombian type material as described by MICHELI (19) beyond the slight difference in petal color. Most significantly for bat-visitation these concern the disposition of the flowers and the sizes of the flower-parts. Thus, as Fig. 6 shows, despite the fact that the inflorescence is dangling, with its apex *toward* the ground, the flowers themselves are held in what is the usual "upright" position for a papilionaceous blossom. This implies a twist of 180° in the pedicels on which they are borne. VAN DER PIJL's (22) photographs of Javan species show similarly positioned flowers. However, the illustration of the type specimen which accompanies MICHELI's (19) account of it shows the flower "upside down". I believe that this may be simply the result of a mounter of the herbarium specimen arranging the flower in what seemed to him (or her) a natural position in keeping with the direction in which the inflorescence is pointing. Micheli's illustration also gives the impression of somewhat smaller flowers than those of the Costa Rican material. Whether or not the Costa Rican material should be described as belonging to another species closely related to *M. andreana,* it appears to be at least as well adapted to bat-pollination as the Asiatic species which it resembles.

The flowers of *Mucuna* have an explosion mechanism of pollen-delivery

to the animals which visit them — a feature which they share with the flowers of many other genera in the Leguminosae. Pressure must be applied to the wings and keel of "unexploded" flowers to force them apart. After this, continued pressure causes the two petals which make up the keel to split apart from the base upwards. As the bat leaves the flower, the staminal tube is allowed to spring out from its place in the keel through the newly formed gap. It does so, projecting its pollen onto the underside of the animal visitor. Nectar has accumulated between the base of the staminal tube and the wings of the corolla and is now available to subsequent visitors. Flowers are ready to be "exploded" in the evening and they are visited by bats from about 7:30 PM (19:30 hours) onwards. At Santa Ana the majority of the bat visits are made in the first half-hour but they continue at intervals throughout the night.

The attractiveness of the flowers presumably depends upon their scent which is more apparent at this time, although never very strong; it resembles the odor of fresh *Phaseolus* beans.

An analysis of the photographs (all taken from a distance of about 2 metres with a 50 mm lens) shows that bat visitors are members of the Phyllostomatidae. The nose leaf is particularly obvious in the bat in Fig. 7. When taking nectar the bats may either cling quite tightly to the inflorescence (which would certainly "explode" unopened but mature flowers) (Fig. 8) or else support themselves by flapping motions of their wings (Fig. 9) (in which case the snout of the bat will perhaps be weighty enough to "explode" the flowers). In either case, the bat stays only for a very few seconds and receives pollen on its chest or the underside of its jaw. The utility of the explosive dusting of the pollen becomes obvious in view of the short time of contact between bat and flower. Contact with the capitate stigma of an "exploded" flower is possible because the style stands among or slightly above the stamens (Fig. 7).

When the bat's visit is completed, it appears to throw itself off backwards and to fall clear of the inflorescence (Fig. 10) before flying away (Fig. 11). This behavior has also been recorded for megachiropterans visiting the globular inflorescences of *Parkia clappertoniana* Keay (Leguminosae-Mimosoideae) in Africa (8) and, judging from the photographs published by VOGEL (25), it is also shown by *Phyllostomus discolor* (Microchiroptera) after visiting the flowers of *Couepia longipendula* Pilger (Chrysobalanaceae). It is almost necessitated because these bats, unlike hummingbirds, cannot fly backwards.

*Mucuna andreana* sets fruit in Costa Rica. Although it was too early in the flowering season for this to be observed at Santa Ana, Mr. Robin Foster (personal communication) was able to make observations on the numbers of fruits and seeds produced by inflorescences on a number of vines growing in the vicinity of Las Cruces field station, near San Vito, Puntarenas Province, Costa Rica.

Mr. Foster found that although the inflorescences contain an average of 46 flowers, the mean number of fruits which mature in any inflorescence is only 1.8. The ovaries in *M. andreana* regularly contain four ovules; however, the number of seeds produced by a fruit may fall as low as two, partly because of

insect attack, giving a mean of 2.9 seeds per fruit. Each one of the flowers that he examined showed claw marks on the petals on a number of separate plants that were available, so we may assume that pollination was not inadequate. Voluntary shedding of fruits that it is beyond the capacity of the plant to support is not infrequent among woody tropical plants (e.g. *Parkia,* BAKER and HARRIS, 8; *Ceiba,* BAKER, 5).

## GENERAL OBSERVATIONS

It is apparent that bats of the suborder Microchiroptera are more difficult subjects for the study of flower-visiting habits than their Old World cousins of the suborder Megachiroptera. Nevertheless, with patience their activities can be observed and photographed. There can be no doubt that they are effective pollinators of many New World tropical and subtropical woody plants and that the syndrome of characters involved in the plants to which they are attracted is much the same as attracts Megachiroptera in the Old World. In the great majority of cases this must be presumed to be independent, parallel evolution, probably most often from bird-pollination or moth-pollination ancestry.

## ACKNOWLEDGEMENTS

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At Lancetilla, Honduras, the course was accomodated at the Botanical Garden through the kind cooperation of the Tela Railroad Company. At Santa Ana, Costa Rica, we received enormous hospitality and cooperation from Mr. and Mrs. Ross. Finally, my wife helped in the field and then was responsible for all of the processing of the photographs; to her technical skill I am greatly indebted.

## SUMMARY

Visits by bats of the family Phyllostomatidae (in the suborder Microchiroptera) to the flowers of *Durio zibethinus* growing in Honduras and *Mucuna andreana* growing in Costa Rica are described and illustrated photographically. In *Durio* we have a case of flower-type which evolved in relation to visits from Megachiroptera in the Old World proving attractive to Microchiroptera which developed the flower-visiting habit in the New World. Hawkmoths also visit these flowers. Both kinds of visitor are capable of causing cross-pollination (which is necessary for fruit production by this species because it appears to be self-incompatible). In *Mucuna andreana,* a native American vine demonstrates a close adaptation to pollination by native bats; again a parallel to similar evolutionary development in the Old World.

## RESUMEN

Se registra y se documenta con fotografías las visitas de murciélagos de la familia Phyllostomatidae (suborden Microchiroptera) a las flores de *Durio zibethinus* cultivado en Honduras y a *Mucuna andreana* en Costa Rica. En *Durio* vemos un tipo de flor que evolucionó en adaptación a visitas de Megachiroptera en el Viejo Mundo, y que resultó atractivo a microquirópteros que desarrollaron el hábito de visitar flores en el Nuevo Mundo.

Mariposas esfíngidas también visitan estas flores. Ambos grupos de visitantes son capaces de realizar polinización cruzada, necesaria para la fructificación pues esta especie parece no ser auto-compatible.

*Mucuna andreana,* oriunda de América, muestra una adaptación íntima a la polinización por murciélagos nativos, otro paralelo al desarrollo evolutivo en el Viejo Mundo.

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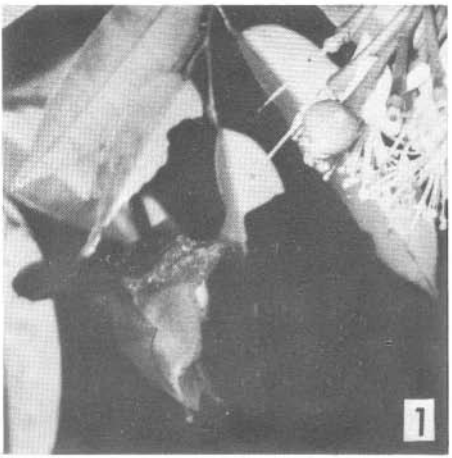
Figs. 1-4. Bats visiting flowers of *Durio zibethinus*. Lancetilla, Honduras, July 1968.

Fig. 5. Hawkmoth visiting flowers of *Durio zibethinus* during bat visitation. Lancetilla, Honduras, July 1968.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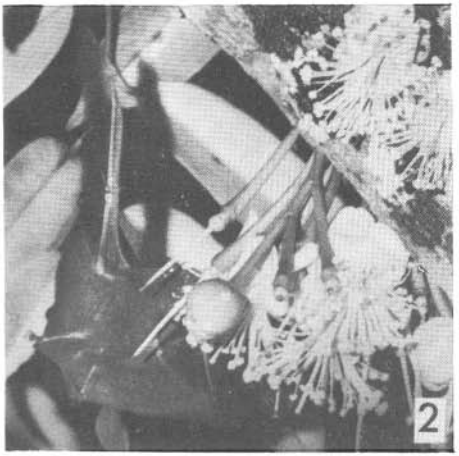
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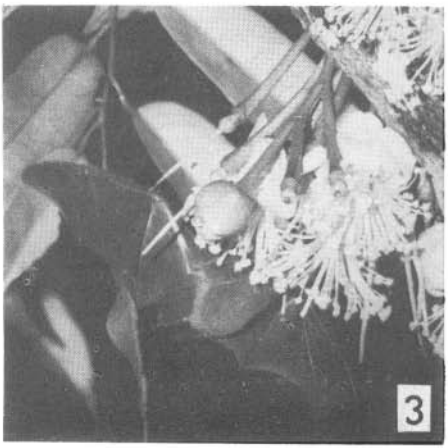
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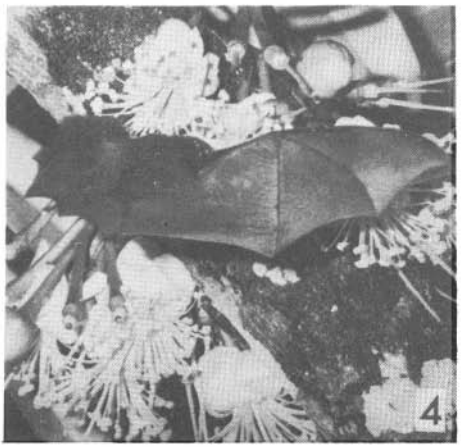
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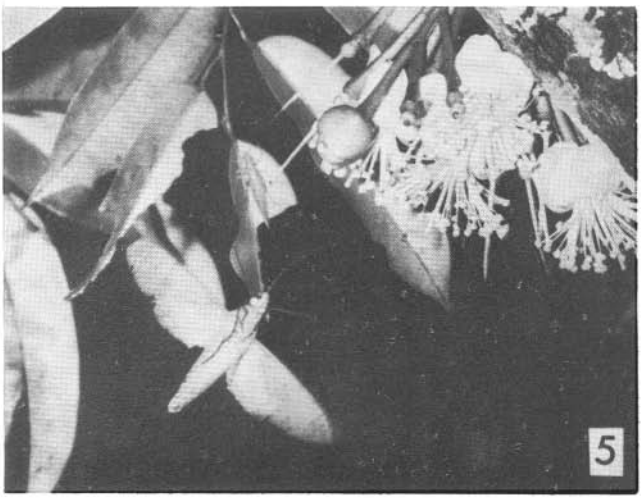
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Fig. 6. Flagelliflory in *Mucuna andreana,* Santa Ana, Costa Rica, July 1968.

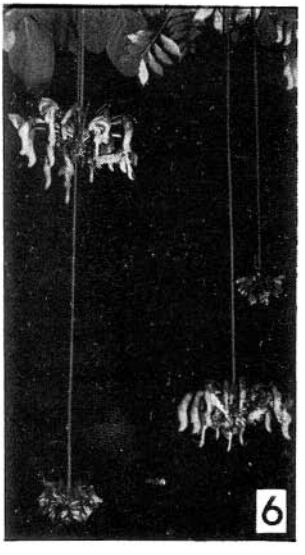
Fig. 7. Approach by bat of the family Phyllostomatidae to flowers of *Mucuna andreana.*

Fig. 8. Bat clinging to "exploding" flower of *M. andreana,* taking nectar from base of staminal column.

Fig. 9. Bat taking nectar from flower while flapping wings. Snout inserted into flowers.

Fig. 10. Bat leaving inflorescence, having thrown itself off backwards.

Fig. 11. Bat flying from inflorescence.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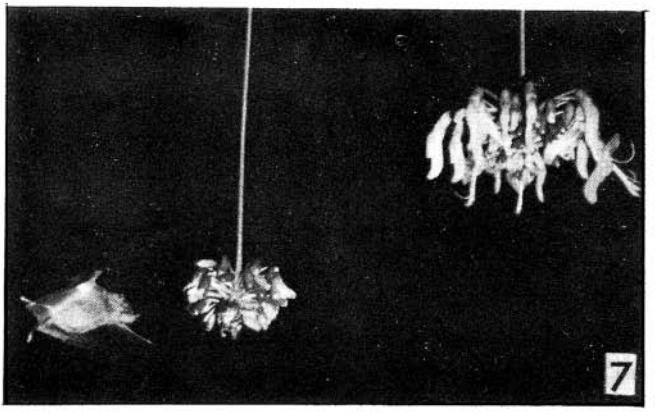
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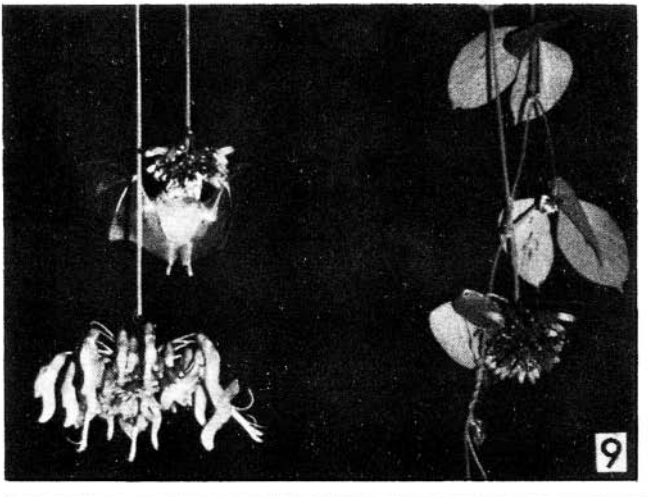
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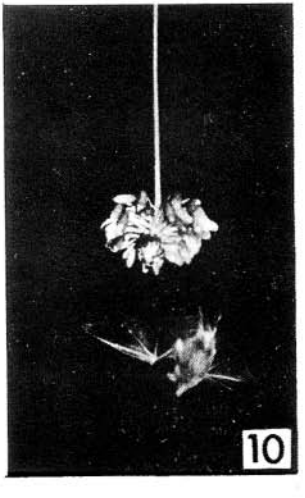
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