POLLINATION OF SOME TRINIDAD PLANTS BY GLOSSOPHAGINE BATS
(ANOURA AND GLOSSOPHAGA)

By O. Marcus Buchanan

Introduction :

Interest in the flower-attending behaviour in bats was stimulated over a century ago with the description by Gould (1863) of the feeding by the Megachiropteran, **Pteropus alecto,** on the blossoms of a Eucalyptus (Myrtaceae : **Eucalyptus** ssp.) in Australia. Since Gould's time, numerous naturalists have described flower-feeding or nectar-drinking at approximately 30 different species of tropical and sub-tropical plants. Many of these are of economic or aesthetic importance in the tropics. Allen (1940) summarized the earlier literature, and the more recent detailed studies of Baker (1960), Baker and Harris (1957, 1959), Harris and Baker (n.d., 1958), and Vogel (1958) have added much to our knowledge of the significance of the nectar-drinking aspect of this behaviour in the evolution of some night-blooming plants.

With the exception of the observations of Vogel **(op. cit.)** on a number of bat and plant species in Colombia, and the early notes of Hart (1897) on **Bauhinia megalandra** in the Royal Botanic Gardens, Port-of-Spain, and of Porsch (1931) on **Crescentia cujete** and **Parmentiera alata** in Costa Rica, little has been recorded on the role of bats in pollinating plant species in the New World tropics. It is of some interest, therefore, to add the following observations made on Trinidad between 1967 and 1970.

Methods :

All observations reported herein were made during the course of a study of the life-history of the "Tailless, Long-tongued Bat", **Anoura geoffroyi** Gray, 1838, and while collecting comparative data on the other common Trinidad glossophagine, **Glossophaga soricina** (Pallas), 1766. Most of the field observations were made in and around the William Beebe Tropical Research Station of the New York Zoological Society at Simla in the Arima Valley.

Field observations at night-blooming species were greatly facilitated with the aid of two powerful 12-volt, swivel-mounted, "night-cultivating" farm tractor lights operated from an independent battery source and placed on a roof-rack on the author's car. Glossophagine bats are not disturbed by such lights, and the entire crown of a large tree could be abundantly illuminated by juxtaposing the wide, intense beams of these lights one above the other. Bat species documentation was made by the use of Japanese mist nets where possible; in the case of very tall trees, specimens were collected with a .22 smooth-bore or a .410 shotgun hand-loaded with light "dust" shot.

Presence or absence of pollen was determined by gross visual observation of the fur in the facial region, and by examination of stomach contents with a compound microscope.

Plant Species Accounts.

Ipomaea bona-nox. Moon Flower.

This species, with large (15 cm diam.) white night-blooming flowers, is found growing in two distinct situations on Trinidad, and these situations apparently influence the nature of the pollinating species. As an ornamental, **I. bona-nox** is frequently encountered as a verandah-screen, or it is allowed to grow more or less freely among border shrubs such as **Ixora** or **Hibiscus.** It also grows as a wild plant, "parasitizing" tall forest trees. In the study area, it was frequently encountered on Nutmeg (**Myristica fragrans**) and Cocoa **(Theobroma cacao),** as well as taller species such as the Balata **(Manilkara bidentata),** Crappo **(Carapa guianesis),** and Mountain Immortelle (**Erythrina micropteryx**). Under the latter circumstances, **I. bona-nox** flowers are frequently to be seen at heights of 12 - 30, or more, meters above the ground, and it is under these conditions that bat-visitation has been observed. As a garden-plant, we have observed visitation only by a very large species of Sphingid moth.

During September and October, 1968, **Ipomaea bona-nox** were flowering profusely in several habitats between 600 and 800 - ft. elevation in the Arima Valley. In addition to the Sphingidae, which were persistently evident, glossophagine bats were observed visiting flowers on the crowns and crown-periferies every night between 29 September and 6 October. Bat-visitation was observed as early as 1923 hrs., and extended at least to 2245 hrs. at intervals, and possibly later. At that season, blossoms of **I. bona-nox** began opening in deep shade parts of the Valley as early as 1729 hrs., and the bulk were open by 1805 hrs. Thus, the earliest visitation by bats observed occurred ca. 1½ hrs. after the opening of the blossoms.

Although **I. bona-nox** blossomed freely on lower under-story trees and some shrubby roadside vegetation in the vicinity, no bats were observed to visit these lower flowers. Rough triangulation measurements showed the lowest flowers visited by bats to be between 12 and 15 meters above the ground.

On 2 October, two specimens of **Glossophaga soricina** were collected at one flowering **I. bona-nox** vine at ca. 1945 hrs., and on 5 October three specimens of **Anoura geoffroyi** were collected at the same vine. All five of these specimens had the fur of the nasal and face regions covered with pollen; four had the stomachs filled with a thick, viscous mixture of pollen and nectar, the stomach of one individual (an **Anoura geoffroyi**) being empty.

Jacaranda caerulea. Fern Tree.

A strikingly ornamental member of the Bignoniaceae, this species is occasionally met as a garden-tree on Trinidad. Its bluish-violet, tubular flowers appear in pendant clusters, usually profusely throughout the long dry-season (January-May), and are diurnal. Many of the flowers, however, remain at least partially open during the night hours. The flowers of **J. caerulea** are visited during daylight hours by large numbers of both avian and insect species, and it is likely that these play the predominate role in the pollination of this species.

A large, old example of **Jacaranda caerulea,** located in the garden at Verdant Vale, Simla, has been under almost daily observation since March, 1967. In April, 1967, bats were observed attending some of the flowers remaining partially open after dark. On three successive nights, 9–11 April, a 12 meter mist net set touching a long, drooping flowering limb of this tree yielded 6 **Glossophaga soricina** and 1 **Anoura geoffroyi.** The **A. geoffroyi** and 2 of the **G. soricina** had their faces dusted with pollen and their stomachs contained fairly dry pollen with little or no nectar.

Glossophagine bats do not visit the Verdant Vale tree on a nightly basis : Several weeks may pass, during the flowering season, before they are seen in attendance. However, we have one or more sight records of bat-attendance at this tree for every month of the flowering season between 1967 and 1970. Visitation of **Jacaranda caerulea** flowers by bats has been observed as early as 1940 hours., and as late as 2315 hours. Apparently all blossoms are sufficiently closed during early morning darkness to make tongue-entry by a hovering bat difficult, if not impossible.

Hylocereus lemairei. Night-blooming Cereus.

A night-blooming, epiphytic Cactaceae, **Hylocereus lemairei** is frequently encountered in forested regions throughout Trinidad. Large examples, with their characteristic triangular and thorny stems, are often found growing on Samaan **(Pithecellobium saman),** Crappo **(Carapa guianensis),** and other large, durable species of trees in the Arima Valley and other parts of the Northern Range. Its large (15-22 cm diam.) greenish-yellow and white flowers, are unusually striking.

An unusually large specimen of **Hylocereus lemairei,** growing on an old **Pitchecellobium saman** near the Arima River at Simla, flowered in July, 1967. Although observations were made on several nights, bats were observed in attendance on only one occasion, at ca. 2030 hours on 13 July. One speçimen was caught in a hand-net, and proved to be **Glossophaga soricina.** Its face was covered with pollen, and its stomach contained both pollen and nectar.

Reports are occasionally received at Simla of bats visiting flowers of the related species, **Epiphyllum hookeri,** but we have no personal observations. Certainly the floristic characteristics and mode of growth make this latter species also a potential bat-attended form.

Tecoma serratifolia. Yellow Poui.

One of the most beautiful as well as characteristic trees of the secondary montane rain forest of the Northern Range, **Tecoma serratifolia** produces masses of yellow, trumpet-shaped flowers when the tree is devoid of foliage during the long dry-season, January-May. Like **Jacaranda caerulea,** the flowers are diurnal, but with many remaining at least partially open during the night. Similarly, the flowers of **T. serratifolia** are also visited during the daytime by many birds and insects, and these unquestionably account for most of the pollination in this species.

A large **Tecoma serratifolia** stands on a very steep hillside just below the terrace at Simla, thus bringing the crown of the tree only 3-5 meters above eye-level to an observer on the terrace. Glossophagine bats were first observed frequenting the flowers of this tree in late March, 1967, and subsequently have been observed at flowering intervals during every dry-season to date (June, 1970). On February 17, 1968, a group of approximately 12-15 bats were observed at the flowers of this tree at ca. 1950 hours. They disappeared after about 5 minutes of feeding, and were not noted again until 2145 hours, when a single specimen of **Glossophaga soricina** was collected from the group. Its facial fur was covered with pollen, and the upper alimentary tract contained semi-dry pollen.

Ceiba pentandra. Silk-cotton Tree.

Baker's (**op. cit.**) studies on the bat-pollination of this tree in West Africa, by nectar-feeding Megachiropterans, are classical. On Trinidad **Ceiba pentandra** is a common and widely distributed species, occurring from near sea-level (i.e., Caroni sugar estates; Cedros) to the heights of the Northern Range. This Bombicacid is a night-bloomer, flowering during the long dry-season when the tree is out of leaf. Unlike the other night-blooming species treated here, the flowers are comparatively small : ca. 5 cm diam. and 1.3-1.5 cm. deep.

The only tree of this species from which persistent data has been obtained is an old, tall representative near the 4-mile marker on the Blanchisseuse Road. This tree variously flowered in either February, March, April, or early May during the years 1967 through 1970. Because of extrinsic factors, bats could not be collected while attending flowers on this tree. However, glossophagines were observed in attendance on 21 April and 7 May 1967, 26 February 1968, and 11 March 1970. All observations were between 1900 and 2200 hrs. Although species-documentation could not be made, two distinct flight characteristics were believed to be represented on 11 March 1970, and therefore at least two species of glossophagines are suspected of attending **Ceiba pentandra** blossoms at this locality.

Crescentia cujete. Calabash.

The second species of New World plant to be recognized as bat-pollinated (Porsch, **op. cit.**), **Crescentia cujete** is widely distributed in Trinidad. The solitary flowers are night-blooming and are borne directly on the main branches. Flowering usually occurs about one month after the short fall dry-season (i.e., in November and early December).

Crescentia cujete is locally extremely abundant in the vicinity of Simla. One such group of 5 trees was located within 10 metres of a permanent station where systematic mist-netting for bats of all species was

carried out on a weekly basis from November, 1967 until May, 1968. The net paralleled the long axis of the plantation of **C. cujete,** and between 1 November and 10 December 1967 yielded a total of 42 captures of **Glossophaga soricina** and 15 of **Anoura geoffroyi.** This is the highest percentage of captures of glossophagine bats taken in any of the random or systematic netting-programmes conducted at Simla over a three-year period. This unusually high capture of **Glossophaga** and **Anoura** coincided with the flowering-season of these **Crescentia;** it is probably highly significant that no further glossophagines were taken in this net between 11 December 1967 and 18 May 1968, when the netting programme was terminated.

All individuals taken had pollen grains adhering to the facial fur, and the 5 **Glossophaga soricina** and 5 **Anoura geoffroyi** had a pollen-and-nectar mass in the stomachs. Both **Glossophaga** and **Anoura** were taken at this site at all hours between 1900 hrs. and daylight.

Other Bat-Flowers and potential Bat-Flowers on Trinidad.

In addition to the observations reported here, bat-attendance has been previously reported in two other species of plants on Trinidad. Hart **(op. cit)** reported bat-pollination in Napoleon's Hat, **Bauhinia megalandra;** and, in 1908 Knuth cited Hart on the pollination of the Wallaba, **Eperua falcata,** by **Anoura geoffroyi.** Both of these observations were made in the Royal Botanic Gardens in Port-of-Spain.

The potential number of bat-attended plant species on Trinidad is considerable. These represent plant species in which bat-attendance has been reported in other areas of either the Old or New World Tropics, but not on Trinidad. Table 1 summarizes those observations. It will be noted that this list includes only plant species also found on Trinidad, or else with very closely related species on Trinidad, and includes both native and introduced plant species.

Discussion.

Bat-attendance at flowering plants may be divided into three rough categories : 1) Flower-eating; 2) Nectar-drinking; and 3) Pollen-eating. This categorization does not imply that any one of these behaviour patterns is exclusive to any given bat or plant species, and field observations and stomach contents analysis indicate considerable over-lap in the last two named categories in the New World Glossophagine bats.

Flower-eating is apparently a frequent pattern in some Old World Megachiropterans (Rosevear, 1965). I have not observed this pattern in any New World species with the exception of the Short-tailed Fruit Bat, **Carollia perspicillata.** Possibly other predominately fruit-eating Phyllostomid bats engage in this behaviour. The dentition of the nectar-feeding Glossophagines, however, is ill-adapted for such feeding and this behaviour is not to be expected in this Phyllostomid sub-family.

Table 1.. Potential Bat-attended or Pollinated Flowers on Trinidad.

Plant Species	Locality Observed	Source
Erythrina ssp.	Tonga	Moseley, 1879
Eucalyptus ssp.	Australia	Gould, 1863
Kigelia aethiopica	Dutch West Indies	Heide, 1927
K. pinnata ınata	India	McCann, 1931
K. africana ricana	Ghana	Harris & Baker, 1958
Oroxlyon indicum	India	McCann, 1931
Parmentiera alata	Costa Rica	Porsch, 1931
Adansonia digitata	Java	Altmann, cited in van der Pijl, 1936
A. digitata	French West Africa	Jaeger, 1945
Musa paradisiaca	Java	van der Pijl, 1956
Parkia roxburghii & other ssp.	Java	Danser, 1929; van Heurn, 1929; Docters van Leewen, 1933
P. clappertoniana	Ghana	Baker & Harris, 1957
Trianaea, Campanea, Symbolanthus, Cobaea, Purpurella, Mucuna, Ochroma, Cayaponia, Marcgravia, Lafoensia, and **Cleome** ssp.	Colombia	Vogel, 1958

The mutual benefits accrued to both the feeding bat and the plant species being fed upon in the case of nectar-and/or-pollen feeding appear clear. Unlike flower-eating, the reproductive parts of the plant are not destroyed, and an efficient pollination mechanism is established, particularly in respect to strictly night-blooming species. Damage to the flowering parts is usually limited to some shredding of the outer petal areas by the thumbs of the hovering bat, and is inconsequential in terms of the reproduction of the plant.

Less well-known are the benefits to the feeding bat. Traditionally, nectar-feeding bats have been compared with their avian "counterparts", the hummingbirds. Like hummingbirds, nectar-feeding bats have an unusually high protein requirement, and like hummingbirds, it has been assumed that this requirement has been fulfilled primarily by ingesting small Diptera found in the carolla of the flowers upon which they feed. That this is not the case in **Anoura geoffroyi** and **Glossophaga soricina**, at least, has been abundantly demonstrated by detailed stomach contents analysis made during the past three years at Simla. Of randomly-netted individuals, only 7% (6 out of 83) **Anoura geoffroyi** and 9% (4 out of 47) **Glossophaga soricina** stomachs contained any remains that could be identified as insect in origin. At the same time, all stomachs of individuals that had recently fed contained pollen, and this usually in very large amounts. It is suggested, therefore, that pollen and not insects form the basic protein source in these two Glossophagines. The relatively dry pollen content of some stomachs reported upon above further suggests that some flowers (e.g., the basically diurnal **Tecoma serratifolia** and **Jacaranda caerulea**) may be visited primarily, if not exclusively, for pollen-eating (Buchanan, **unpubl. mss.**).

The potential role of nectar-and-pollen feeding bats in the reproduction, ecology, and economics of certain tropical plants is clearly evident. Equally clear is the fact that if such species continue to be classified as pests, and destroyed whenever opportunity affords, there may ultimately be a negative effect upon the local ecosystem.

Summary.

Nectar and/or pollen feeding is described at six species of Trinidad plants (**Ipomaea bona-nox, Jacaranda caerulea, Tecoma serratifolia, Crescentia cujete, Ceiba pentandra,** and **Hylocereus lemairei**) variously by two species of Glossophagine bats (**Anoura geoffroyi** and **Glossophaga soricina**). Time of feeding, presence of pollen on the facial fur, and stomach contents are noted. The evidence suggests that some species may be visited solely for pollen-feeding, and the stomach analysis indicate that pollen and not insects form the major protein sources in **Anoura geoffroyi** and **Glossophaga soricina.** The significance of this data is discussed, and a list of potential bat-flowers on Trinidad is abstracted from the literature.

New York Zoological Society, William Beebe Tropical Research Station, Simla, Arima Valley.

Literature Cited

Allen, G.M.

Bats. Cambridge, Mass. 1940.

Barker, H.G.

Apomixis and polyembryony in **Pachira oleaginea** (Bombacaceae). Amer. Journ. Botany, 47(4):296-302. 1960.

————————, and B.J. Harris.

Pollination of **Parkia** by bats and its attendant evolutionary problems.
Evolution, XI(4): 449-460. 1957

————————————— .

Bat-pollination of the Silk-Cotton Tree, **Ceiba pentandra** (L.) Gaertn. **(Sensu Lato)**, in Ghana.
Journ. West African Science Assoc., 5(1):1-9. 1959.

Gould, J

The Mammals of Australia, Vol. 3. London, 1863.

Harris, B.J., and H.G. Baker.

Pollination of flowers by bats in Ghana.
The Nigerian Field, XXIV (4) : 151-159. n.d.

————————————— .

Pollination in **Kigelia africana** Benth.
Journ. West African Sci. Assoc., 4(1):25-30. 1958.

Hart, J.H.

Bats fertilising the flowers of **Bauhinia megalandra** Griseb.
Bull. Misc. Inform. Trinidad, 2(3): 30-31, 1897.

Heide, F.

Observations on the pollination of some flowers in the Dutch East Indies.

Dansk Botanisk Arkiv. 5(3):1-42. 1927.

Jaeger, P.

Les aspects actuels de probleme de la Cheiropterogamie.
Bull. Inst. Franc. Afr. noire (Serie A), 16:796-821. 1945.

Knuth, P.

Handbook of Flower Pollination. (Translated by R. A. Davis).
Oxford, 3 vols. 1908.

McCann, C.

On the fertilization of the flowers of the Sausage Tree **(Kigelia pinnata,** DC.) **by bats.**
Journ. Bombay Nat. Hist. Soc., XXXV: 467-471. 1931.

Moseley, H.N.

Notes by a Naturalist on the "Challenger". London. 1879.

Porsch, O.

Crescentia-eine fledermausblume.
Osterr. Bot. Ztschr., 80:31-44. 1931.

Rosevear, D.R.

The Bats of West Africa. Brit. Mus. (Nat. Hist.), London. 1965.

Van Der Pijl, L.

Fledermause und blumen.
Flora, 131:1-40. 1936.

———————— .

Remarks on pollination by bats in the genera **Freycinetia, Duabanga,** and **Haplophragma,** and on chiropterophily in general.
Acta Botanica Neerlandica, 5(2): 135-144. 1956.

Vogel, S.

Fledermausblumen in Sudamerika : Ein Beitrag zur Kenntnis des chiropterophilen Stiltypus.
Ost. Bot. Z., 104:491-530, 1938.