

REMARKS ON POLLINATION BY BATS IN THE
GENERA FREYCINETIA, DUABANGA AND
HAPLOPHRAGMA, AND ON CHIROPTEROPHILY
IN GENERAL

BY

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This paper contains a collection of notes on chiropterophily. They form part of the material I intend to include in a general review of the subject, which will be published in book-form. As it may take some time before this work appears, it seemed worth while to issue a selection of this material beforehand.

Recently a concise review, stressing general points, has been published in French by JAEGER (1954). It includes some new observations on *Ceiba* and *Adansonia* made by Jaeger himself.

1. FREYCINETIA (*Pandanaceae*)

It seems to me a commendable procedure to start these notes with some remarks on the genus in which pollination by bats was first observed and described.

BURCK (1892) described in a work on the Botanical Gardens at Buitenzorg how bats feed on the juicy bracts by which the inflorescences of a *Freycinetia* are surrounded, but do not damage the flowers. He thought it likely that the bats effect pollination, and suggested that the plant might be dependent upon these animals for its survival. The bats that were responsible for this feat were held to be flying foxes (*Pteropus*), but the choice of his words suggests that this was a mere guess.

A still earlier observation made by Moseley and quoted by KNUTH-LOEW (1904) as possibly referring to *Freycinetia*, cannot apply to this genus, as the plant Moseley had in view, is said to be a tree, whereas *Freycinetia* is a liana.

During his stay in Java in 1899 Knuth observed in the Botanical Gardens at Buitenzorg, as described in KNUTH-LOEW (1904), bats visiting the "flowers" of a *Freycinetia* species, for which he uses the name *Fr. strobilacea* Bl. The bats observed by him, were not the large flying fox, but a small and a medium-sized species, which he thought might be resp. *Pteropus minimus* Geoff. and *Cynopterus marginatus* Geoff. He regarded both as fructivorous species, but we now know that the first (syn. *Macroglossus minimus*) feeds on nectar, and does not have the power to dissect the bracts.

Knuth noted that the juicy inner bracts and the erect „*Beköstigungskörper*” (food-bodies), which are metamorphosed bracts inserted between the spadices, serve as food for the bats.

For a long time the genus was passed on in the literature as the standard example of pollination by bats.

PORSCH (1915) doubted its chiropterophily, and correctly stated that the *Freycinetia* species which dominates in the famous *Canarium* avenue at Buitenzorg, is ornithophilous. He drew the attention to its diurnal flowering, its bright red colour and its lack of smell. It was for him the first instance of a flower provided with food-bodies that is pollinated by birds. According to him the bats were mere plunderers.

In a later paper PORSCH (1923) identified the species which he had studied as *Fr. funicularis* (Rumph) = *Fr. funicularis* Merr. He says that the plants were in 1914 labelled as *Fr. strobilacea* Bl., and that this was the reason why he had used this name in his first, preliminary publication. Porsch described in detail how the flowers are pollinated by the bird *Pycnonotus aurigaster* Vieill., and suggested that incidentally pollination may be brought about by a fructivorous bat.

Since that time the observations made by Burck and Knuth have fallen into discredit, although PORSCH (1935) maintained the genus in his list of plants in which bat visits have been observed. JAEGER (1954), however, absolutely denied the occurrence of chiropterophily in the genus.

Do we really have to discredit Burck's observations? Certainly not! In other fields of study I could already confirm some of the contested ideas of this former sub-director of the Gardens, who doubtless made mistakes, but who certainly deserves to be honoured as a pioneer in the field of tropical ecology.

When we carefully examine what he actually says on p. 67, we will see that he does not mention a species by name, and it will be clear that the plant to which he referred, was not *Fr. funicularis*, but probably *Fr. insignis* Bl., for he describes the flowers as pinkish. We may assume, therefore, that a specimen of this species grew in 1890 in the garden. At the present time *Fr. insignis* still occurs in the neighbourhood. A coloured plate is given by Blume (*Rumphia* I, tab. 42).

With regard to the description given by Knuth, I can only say that Knuth and Loew possibly confused the two species. Their fig. 3 agrees with *Fr. funicularis*.

Fr. insignis is undoubtedly chiropterophilous.

In a paper which appeared in 1941 I mentioned that I intended to publish an article on this matter, but during the war and revolution in Java my manuscripts and notes were lost. In August 1950 I could study the plant once more in a forest (alt. 1400 m) near Bandung.

On inflorescences that had flowered in the preceding night, I found in the morning on the hard outer bracts marks of bat claws. The erect white food-bodies and most of the pinkish or pale-lilac inner bracts had been removed. Of the more peripheral bracts, which are provided with harder tips, only the basal part had been bitten away. (c.f. fig. 1 and 2). The parts that were left clearly showed the imprints



Fig. 1. *Freycinetia insignis* Bl. from above. Male inflorescence in the morning following anthesis. Edible bracts consumed by bats. Top of half-edible bract spared.



Fig. 2. *Freycinetia insignis* Bl. The same inflorescence as in Fig. 1 from the side; some of the enveloping bracts and one spadix removed.

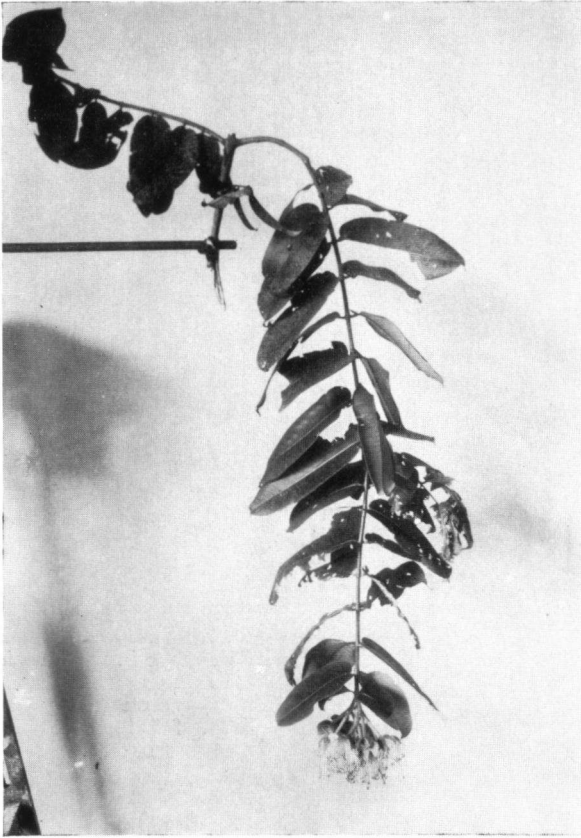


Fig. 3. Drooping branch of *Duabanga moluccana* Bl. with terminal flower cluster. Late evening.

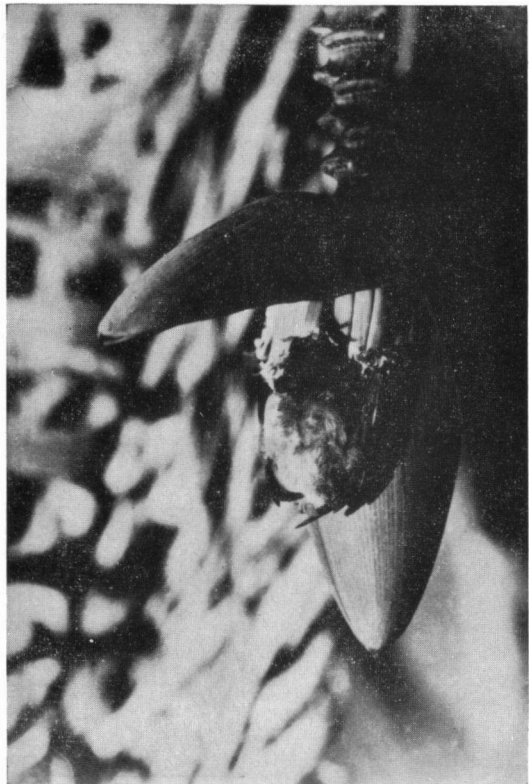


Fig. 4. Flowerstand of *Musa paradisiaca* with visiting *MacroGLOSSUS*. Late evening.

made by the teeth of the nightly visitors, which could in this way be identified as belonging to *Cynopterus*, a well-known genus of fruit-eating bats. From the Indonesians living in the neighbourhood we heard that fruit-bats were during the night regularly fighting round the inflorescences.

The spadices themselves are apparently unedible. I found no imprints of teeth on them.

At 13.— p.m. I took some inflorescences home. They were on the verge of opening but emitted as yet no fragrance.

At home I could make photographs and observe the process of anthesis. It is probable that it was accelerated by the transport in the dark luggage hold of the car.

Early in the afternoon the outer bracts began to separate, exposing the edible inner bracts. Pollen was set free and a sweet fruit odour, but mixed with a musty component, began to escape. Late in the evening the opening was completed and the odour became much stronger and also more pronouncedly musty.

It is possible that the inflorescences retain their attractiveness for a second night, although during the latter the female spadices become discoloured.

The pinkish to pale-lilac colour agrees with that observed in other bat-flowers, e.g. those of *Dombeya*. The position of the flowers, at the end of branches that stand away from the stem of the supporting tree, causes the free exposure that is so typical of flowers that are pollinated by bats.

The taste of the food-bodies and bracts is at first sweet, but afterwards it becomes disagreeable to us, viz. wry as of tannic acid.

As always when studying a flower belonging to a certain ecological class, we find that it fits the senses of the legitimate visitors and excludes others. Once the legitimate visitors know the place, they can often find flowers that are missing one of the usual signals. Fructivorous bats also take unripe fruits that emit as yet no smell. This happens also in *F. insignis*, where some inflorescences are robbed by bats the night before anthesis. This may also explain why bats may eventually shift their attention to the inflorescence of a neighbouring *F. funicularis* which emits no smell at all.

F. insignis does not belong to the large group of chiropterophilous plants (which consists of at least 25 genera), which offer nectar and pollen to strongly specialized bats that feed on nectar, such as *Macroglossus*. It belongs to the small group of plants, formed by *Madhuca*, *Bassia* (*Illipe*), and possibly *Pachira insignis*, which offer solid foodtissue to the less specialized fruit-bats, which occasionally may deviate from their ordinary line of fruit-eating, subs. flower-squashing.

In the class of flowers, that are pollinated by beetles, the use of solid tissues is often regarded as a primitive character, but this does not necessarily hold true for the chiropterophilous flowers just mentioned. They seem to follow a new line, parallel to that of the main group. I find as yet no reason to assume in the *Pandanaceae* former connections with beetles or primitive vertebrates.

It is possible that other Javanese *Freycinetia* species are chiropterophilous, as for some of them smelling flowers are mentioned.

It might also be of interest to study the pollination of the New-Zealand *F. Banksii* A. Cunn., of which the white or pale-lilac bracts are eaten by man. This happens also with the bracts of *F. marquisensis* and of *F. monticola* which occur in the Marquesas. The bracts of the latter are orange or red.

In 1927 HEIDE published observations made in Bogor (Buitenzorg) on *F. funicularis*. It is rather remarkable that he saw no nocturnal visits of bats, and said nothing on diurnal visits of birds. He observed squirrels (*Sciurus notatus* Bodd), visiting and destroying inflorescences in the afternoon. He supposed that these animals might incidentally cause pollination.

A relation to rodents (rats) seems lately to have been established in the Hawaiian *F. arborea* Gaud. The rats are not indigenous to the islands, and the inflorescences, though they spread an odour, look as if they might be ornithophilous. Observers have reported visits by native birds.

Sinclair reported already in 1885 the activity of rats on the bracts of this species, and DEGENER (1945), says that the inflorescences are provided with fragrant, bright orange, fleshy and sweet tasting bracts, which are eaten by rats, but he does not mention what happens to the spadices. The whiskers and fur of the rodent proved to be covered with pollen. As the plants fruit well, the visits seem to lead to regular pollination.

2. DUABANGA MOLUCCANA BL. (*Sonneratiaceae*)

The tree is indigenous in the Moluccas, but a specimen is cultivated in the Botanical Gardens Bogor (Buitenzorg). In 1941 I made observations on this tree, but the notes were lost during the war and revolution. The relationship with the chiropterophilous *Sonneratia acida* led to the discovery.

I do not remember whether actual visits of bats were observed, but I do remember that both species were at the time included in a list of plants that were proven to be chiropterophilous.

The flowers open at night, are creamy-white, spread a strong, sourish-sweet odour and produce the abundance of nectar that is typical of this class. The anthers are uncommonly large. The position of the flowers is also typical, for they are found at the end of drooping branches, well exposed and easily accessible. Here again the structure of the tree proves to be more or less adapted to bat-visits. The stem and main branches emit long horizontal side branches. The latter are rather far apart and their ends are drooping (c.f. fig. 3).

3. HAPLOPHRAGMA ADENOPHYLLUM (WALL.) DOP. (*Bignoniaceae*)

In my study "Fledermäuse und Blumen" (1936) I already pointed at the frequent occurrence of chiropterophily in the family *Bignoniaceae*,

especially in the *Markhamia*—*Dolichandrone*—*Heterophragma* group, to which the above-named species belongs (syn. *Heterophragma adenophyllum* Seem. ex Benth. et Hook., *Spathodea adenophylla* D.C.).

The species is indigenous to Birma and Malaya and has large, fleshy flowers of a dull-brown-yellow colour. They spread a typical bat-odour—as I could observe in May 1949 in a specimen cultivated in the Botanical Gardens in Bogor. The swellings on the lower lobes of the corolla make it easier for the bats to obtain a foothold.

The flowers are nocturnal and in the morning, when they are shed, they show the typical marks of bat claws.

The shape of the tree is identical to that of the chiropterophilous *Markhamia stipulata*. This means that it is of the "pincushion type" with the flowers borne on long, stiff stalks which project on all sides of the crown—a typical chiropterophilous position.

4. ADANSONIA GREGORII F. v. MUELL (*Bombacaceae*)

This Australian species is, like its better known relative from Africa, chiropterophilous.

I could observe a specimen in Bogor (Buitenzorg) in June 1952.

The yellowish-green flowers open in the night and are shed in the morning, showing at that time the claw marks of bats.

5. COMMENT ON NEW EXAMPLES RECENTLY RECORDED BY OTHER AUTHORS

a) *Ipomoea albivenia*

The communication by VOGEL (1954) deserves to be cited here. He mentions as characteristics of the flower: broadly campanulate shape, a nearly white colour set off with a dull-violet throat, nocturnal anthesis and a disagreeable odour reminding one of garden swedes. He thinks that the chiropterophily is questionable, as he found no traces of bat visits. He was, moreover, not sure whether flower-visiting bats occur in South-Africa.

As, however, the finding place (Zoutpansbergen) lies in or near the tropical region, either *Megaloglossus*, or the fructivorous *Eidolon*, which according to JAEGER (1954) has developed a taste for nectar, might be present. Vogel referred to another *Convolvulacea*, viz. *Erycibe ramiflora*, which I should have regarded as chiropterophilous, but I wish to point out that I (in 1936) merely suggested that it might be so.

b) *Eugenia cauliflora*

PORSCH (1941) thought it probable that this species was to be placed in the group of chiropterophilous plants provided with solid food-bodies for attracting visitors (from which group he omitted *Madhuca*). I think that the prophet and grandmaster of chiropterophily here too has correctly understood the chiropterophilous character. One point, which he does not mention, though it is easily discernable in

his photographs, is the large size of the anthers, which far surpasses that of its sister-species. For parallel cases in other genera I may point to *Bauhinia megalandra*, to *Duabanga moluccana*, to *Eperua falcata* and to the chiropterophilous Cactaceae (c.f. PORSCH, 1939).

This point, however, fits in (like the increase in the number of anthers elsewhere) with the character-complex of those chiropterophilous plants which offer nectar and pollen as food. It might be, therefore, that the flower does not belong to the group to which it has been assigned by Porsch, and that in its natural habitat it produces nectar. Fleshy petals are found in the main group also.

c) ***Mucuna monosperma***

As the short note on this flower by BÜNNING (1952) is hidden between considerations of a different nature, I wish to draw the attention to it.

Whereas most *Mucuna* species are flagelliflorous, this one is cauliflorous. The photographs clearly show claw marks, identical with the bat marks described and figured by me for *M. reticulata* (1941). This find too shows the relation existing between cauliflory, flagelliflory and bats.

6. PLANTS THAT HAVE ERRONEOUSLY BEEN REPORTED AS CHIROPTERO-
PHILOUS

I refer here in the first place to the list given by PORSCH (1935). Porsch himself stated that some cases were dubious. Unfortunately this list is sometimes used uncritically.

a) ***Piper aduncum***

The original statement by HEIDE (1927) was based on an oral communication by an observer who merely said that bats similar to those caught on *Kigelia* visited this plant, but this observer did not differentiate between fruit-bats and flower-bats.

There is in this case no question of chiropterophily. The ripe catkins are, however, eagerly sought after and consumed by *Cynopterus* species, as described by me (1935).

b) ***Eriobotrya japonica***

This example probably rests on a similar error, as a fruit-eating bat is mentioned as pollinator.

c) ***Cocos nucifera***

The old report of Moseley quoted by Porsch says that insect-eating bats were seen circling round the flowers. They undoubtedly prey upon the insects visiting the flowers, but this has nothing to do with pollination.

d) ***Areca catechu***

This statement must also rest on some error of the kind mentioned under a) or c).

Many data reported in the list in which *Pteropus* is mentioned are doubtful, as the activity of this animal consists nearly always in the destruction of flowers and young fruits. In kapok-plantations it is for this reason regarded as a pest.

7. *MUSA*

I present here the first photograph ever made of a *Macroglossus* in the act of visiting a flower (fig. 4). The animal is seen clinging to the still closed bracts of a male banana inflorescence and introducing its snout into an open flower, while forcing apart the perianth slips.

I have to thank Mr. J. Fersenaar (Bandung), who took this picture, for his cooperation.

The study of CHEESMAN (1947) shows that the classification of the species in the genus *Musa* according to the mode of pollination does not agree with the taxonomic groups in that paper. The section *Eumusa*, however, seems to be entirely chiropterophilous.

8. FLOWERBATS AS A FACTOR IN PLANT COMMUNITIES

At an earlier occasion (1935, p. 17) I have already pointed out that flower visiting bats can only subsist in plant communities where all the year round chiropterophilous flowers are present. The reverse is just as true.

When we find in a region a chiropterophilous plant species with a limited flowering period, we may be certain that other chiropterophilous plants will be present with a different flowering period. The species are bound together by means of the bat—and in the case of the cave-dwelling bats by the presence of suitable caves.

ALLEN (1940) already drew the attention to this necessity of overlapping flowering periods. It might be of interest to test this in a community with a limited number of plant species, e.g. in the African savannah-regions where *Kigelia* and *Adansonia* are present as nuclei of bat-pollination. Probably some *Markhamia*, *Spathodea* and *Parkia* species will fill up the gaps. For Australian regions in which *Adansonia gregorii* occurs, the study of these relations might be an attractive task for a local biologist.

PORSCH (1939) describes chiropterophilous *Cactaceae* (e.g. *Carnegiea* from Arizona) from regions with only some *Agave* species as possibly supplementary plants and with a winter period in which such flowers are entirely absent. If we cannot assume hibernation of the bats, we might, as the region borders on more tropical regions, think of migration (c.f. the humming birds).

It is of interest to note that, as Professor Chas T. Vorhies (Tucson) wrote to me, there is in Southern Arizona a species of nectar-feeding bat, viz. *Choeronycteris mexicana*. It probably migrates southward in the winter. According to Prof. E. Lendell Cockrum the same holds true for *Leptonycteris nivalis*.

I hope to describe elsewhere the role of fruit-eating bats in tropical

plant-communities, especially in those occurring near the sea. Their role is more conspicuous. In that study I shall include a distributional map.

9. FLOWEBATS AND PLANT AREAS

We know some instances where the distribution of a plant species is limited by the distribution of its pollinators (and vice-versa).

One day we may be able to reconstruct the repopulation of Europe after the last glacial period by immigrants from warmer regions by taking into account the speed with which their pollinators and seed dispersers could follow them. In a forthcoming study on the leguminous pods I made a first attempt in this direction, and I pointed out a.o. that it is not the presence of cauliflory in the tropics, but its absence in Europe, that has to be explained, and that this explanation is to be sought in the direction just mentioned.

The interdependence is demonstrable only when there is but a single pollinator, and when we may be sure that there is no autogamy.

I pointed already (1936) to the case of *Kigelia* which in Hawaii is sterile because of the absence of bats. Why the *Adansonia digitata* cultivated there is fertile, I do not know. In this connection it is useful to consider the old question whether *Musa Fehi* is native to Hawaii. Apart from other considerations it seems clear that this chiropterophilous and chiropterochorous species cannot be native to an island in which there are no bats. An introduction from New Caledonia is for this reason a more probable assumption.

The eastern limit reached by many *Phanerogamae* that penetrated into the Pacific region should not be considered only from a historical and geological point of view, but also in relation with the distribution of flower bats and fruit bats, though this factor may not be independent.

A detailed study would necessitate the cooperation of some botanists and a zoologist. I will confine myself to some of the basal points.

The chiropterophilous plants are, so far as we know, limited to the region west of Fiji.

The Macroglossine bats—the nectar-feeders—are in Africa represented by the genus *Megaloglossus*. It is accompanied there by transitional forms included in the *Pteropinae*, like *Eidolon*, of which JAEGER (1954) has shown that it can act as pollinator.

In S.-Asia there are several genera, viz. a) *Macroglossus*, which reaches Indonesia, New-Guinea and the Bismarck Archipelago, b) *Eonycteris*, known from Tonkin, Siam, Birma, Malaya, Indonesia and the Philippines, c) *Melonycteris* and d) *Nesonycteris* which occur in the Salomons and the Bismarck Archipelago, e) *Notopterus* found up to New-Caledonia, the New Hebrides and Fiji, f) *Syconycteris*, a native of New Guinea, the Bismarck Archipelago and North Australia.

Small *Pteropinae* may take over their role, incidentally with regard to the main class of chiropterophilous plants, and obligatory with regard to the class which attracts the bats by means of solid food.

A study of the genus *Parkia*, which reaches in Fiji its eastern limit might give interesting results.

The chiropterophilous *Sonneratia acida* L.f. (*S. caseolaris* (L.) Engl.) does not go so far eastwards as most of the other mangrove plants, and remains within the area occupied by *Macroglossinae*.

The fertility of *Ceiba* on many eastern Pacific islands (Makatea, Niue, Rarotonga, Samoa, Marquesas) is undoubtedly due to the introduction of self-fertile forms, like those cultivated in Java.

The fertility of introduced *Ochroma lagopus* and *Crescentia cujete* in the Marquesas (F. B. H. Brown) and of *Durio zibethinus* and *Crescentia cujete* in Rarotonga (Wilder) deserves further study. The omnipresence of *Mucuna gigantea* in the Pacific islands shows that this species is a transitional form in chiropterophily, just as *M. pruriens*, which I already recognized as such (1941).

10. BEHAVIOUR OF THE BATS AND CAULIFLORY

I already paid some attention (1936, p. 3) to the fact that *Macroglossinae* and *Pteropinae* are less dexterous in avoiding obstacles, which is due to their less efficient "radar"-system. The necessity of an exposed position of the chiropterophilous flowers therefore, is obvious.

Native hunters in Ambon (where bats are eaten) know that this kind of bat is more easily caught by means of nets and hooks than the other ones.

LAND and CHAPIN (1917) already said (p. 483) "contrary to the behaviour of insectivorous bats the larger fruitbats, when let loose in a room, fly against obstacles". TATE (1942) reported from New-Guinea that the nectar-eating *Syconycteris australis* was the only species of bat, which was readily trapped in fowling nets at night. This study also describes the gradual change in skull structure and the reduction of teeth in resp. *Eonycteris*, *Macroglossus*, *Nesonycteris* and *Notopteris*.

The specimen figured in fig. 4 when coming back after the flash, took fright when it approached the flower on its second round, made a right turn, and collided with the camera tripod. Its repeated refusal to land afterwards on this inflorescence seems to prove the existence of a memory for the position of objects.

Notwithstanding these facts and the frequency of cauliflory and flagelliflory in chiropterophilous and chiropterochorous plants, some authors hesitate to accept the importance of cauliflory as an adaptation to bat visits. Of course, when we call a structural modification an adaptation, this does not mean that it is regarded as developed entirely de novo. Every change of this kind starts with materials, tendencies, and relations that are already present. On the other hand it seems to be an over-sensitivity to the teleologic point of view to regard an adaptation merely as an "*Ausnützung*", and that e.g. bats simply make use of morphologically conditioned, but in relation to them accidentally present, cases of cauliflory.

PORSCH (1941) applies this reasoning to the cauliflory of *Eugenia cauliflora*, saying that it lies within the scope or variation of the genus. However, it seems to me that the cauliflory of many sister species may also be interpreted as ecologically conditioned by bonds between

themselves and bats. Such bonds doubtless exist, for these plants are chiropterochorous.

When we see how in myrmecochorous plants the whole organization may be changed in order to bring the ripe fruits and seeds nearer to the ground and within the grasp of the ants, it is strange that the changes in position of bat flowers resulting in an easier accessibility to these animals are not generally recognised as adaptations.

In this connection it has been argued that the fact that cauliflory is limited to the tropics, does not rest on an ecological cause, but that it merely is a remnant of a primitive morphological structure. This may be true in some cases, but cauliflorous chiropterophilous plants like *Kigelia*, *Crescentia*, *Parmentiera*, *Eugenia*, *Amphitecna*, *Durio*, *Mucuna* and many *Sapotaceae* seem to be far from primitive.

The investigations of MC LEAN THOMPSON (1946, 1951) with regard to the anatomical background in various cases of cauliflory have shown that the character can not be regarded as primitive and that there is no homology, but that to the contrary cauliflory is a secondary character; it is an example of a convergence obtained by the most divergent means.

REFERENCES

- ALLEN, G. M. 1940. Bats. Harv. Univ. Cambridge.
 BÜNNING, E. 1952. Ztschr. f. Bot. 40: 293-306.
 BURCK, W. 1892. Wandelingen door den Botanischen Tuin (in Treub, 's Lands Plantentuin te Buitenzorg), Batavia. (German edition 1893).
 CHEESMAN, E. 1947. Kew Bull. no. 2: 97-117.
 DEGENER, O. 1945. Plants of Hawaii National Park. Ann Arbor.
 HEIDE, F. F. R. 1927. Dansk Bot. Ark. 5.
 JAEGER, P. 1954. Bull. Inst. Afr. N. A. 16: 796-821.
 KNUTH, P. and LOEW, E. 1904. Handbuch der Blütenbiologie. III/1. Leipzig.
 LANG, H. and CHAPIN, J. P. 1917. Bull. Am. Mus. N. H. 37: 479-520.
 PIJL, L. VAN DER. 1936. Flora 31: 1-40.
 PIJL, L. VAN DER. 1941. Ann. Bot. Gard. Buitenz., 51: 83-93.
 PORSCH, O. 1915. Akad. Anzeiger 21. K. Akad. d. Wiss. Wien.
 PORSCH, O. 1923. Österr. Bot. Ztschr. 72: 125-149.
 PORSCH, O. 1931. Österr. Bot. Ztschr. 80: 31-44.
 PORSCH, O. 1935. Biol. Gener. 11: 171-188.
 PORSCH, O. 1939. Jahrb. D. Kakt. Ges., 1: 81-142.
 PORSCH, O. 1941. Biol. Gener. 15: 283-294.
 TATE, G. H. H. 1942. Bull. Am. Mus. Nat. Hist., 80: 331-347.
 THOMPSON, J. MC LEAN. 1946. Proc. Linn. Soc. London, Sess. 157: 72-91.
 THOMPSON, J. MC LEAN. 1951. Proc. Linn. Soc. London, Sess. 162: 212-222.
 VOGEL, S. 1954. Blütenbiologische Typen als Elemente der Sippengliederung. Fischer — Jena.