

THE DISPERSAL OF PLANTS BY BATS (CHIROPTEROCHORY)

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A. THE ZOOLOGICAL ASPECT

The bats which play a role in the dispersal of plants belong to two different groups, a) the *Phyllostomidae*, a family of the *Microchiroptera* of which three subfamilies deviated from the general habits of this suborder and specialized in this direction and b) the whole suborder of the *Megachiroptera*. The first group lives in the warmer parts of the New World, the second in those of the Old World.

The ecology of the *Megachiroptera* has recently been reviewed by EISENTRAUT (1945) from the zoological point of view, so that I may refer to his compilation for this aspect. Of special importance for our purpose is his distributional map, reproduced here in part as Fig. 1. It embraces the group of the *Macroglossinae* (nectar feeders), which is here of no interest, and the *Pteropinae*, on the whole true fruit-eaters, though some of its members also have a tendency towards nectar feeding. The distributional area of the *Pteropinae* is larger than that of the *Macroglossinae*.

The biology of the vegetarian members of the above mentioned three sub-families of the *Microchiroptera* (the *Stenoderminae*, *Phyllonycterinae* and *Glossophaginae*, which seem to be independent lines of evolution), is less clear and contains many debatable points, which should further be studied. I refer to ALLEN (1940) (p. 100–105). The distribution includes the tropical mainland and the West-Indies.

Allen mentions transitional forms, which consume fruits as well as insects, and speculates on the way the diet may have changed.

Just as the nectarivorous bats from the Old and the New World, the fruit bats from the two regions have the same taste. That fruits serving as food for one group are also suitable to the other appears from observations on plants introduced from one area into the other.

The influence of bats on fruits (c.f. p. 300) may be a rather ancient one that has brought about fundamental changes. The oldest known megachiropteran seems to date from the Upper Oligocene.

Further remarks on the biology of fruit bats will be reserved for the following chapters in which they will be discussed in relation to the fruits on which they feed.

B. THE ROLE OF BATS IN DISSEMINATION

In botanical literature some appreciation of the significance of bats for dissemination is found in the writings of authors with tropical experience. Botanists with Europe-centric concepts, however, tend to neglect the interdependence.

The work of SERNANDER (1927) though in other respects so thorough may be quoted as an example of this onesidedness. He mentions under "Synzoic seed dispersal" only glirochory and myrmecochory i.e.

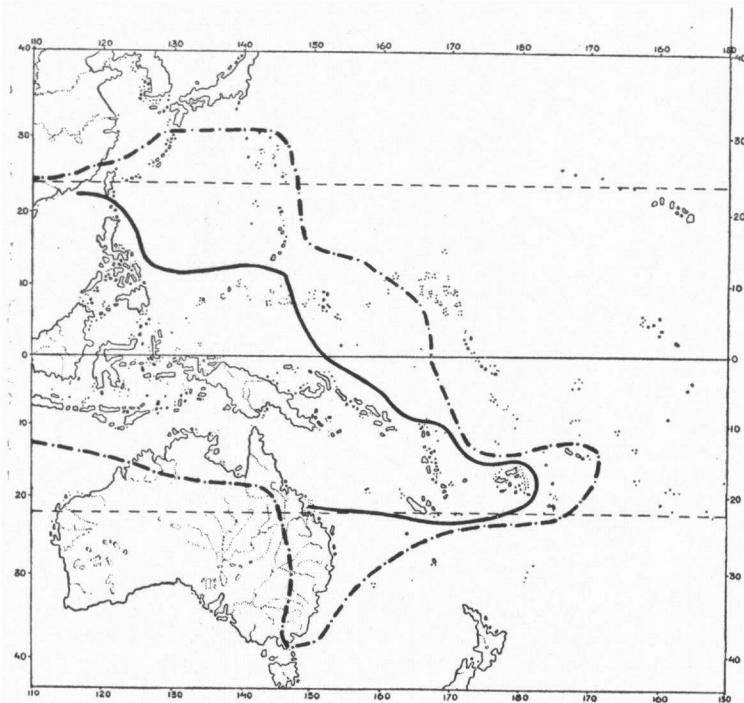


Fig. 1. Distribution in the Western Pacific Area of the Pteropinae (broken line) and of the Macroglossinae (heavy line).

dissemination by resp. squirrels and ants. The recently published general work of MÜLLER (1955) on seed dispersal entirely ignores bats and tropical relations. Even Guppy, a field botanist with a life-long interest in tropical seed dispersal, shows a peculiar disregard of bats, as we shall see (p. 310).

In his "Herbarium Amboinense" Rumphius already described the dissemination by bats of some plants in the Moluccas. This was already mentioned by RIDLEY (1930, p. 349), but after comparing Rumphius' text I see that the names cited by Ridley will have to be changed as referring to: *Artocarpus champeden* (I:109), *Annona reticulata* (I:136), *Mangifera indica* and related wild species as *M. foetida*, *M. odorata* and *M. caesia* (I:95).

OSBURN (1865) described how some American bats transported seeds of *Brosimum alicastrum*, *Cordia collococca* and *Eugenia jambos* to their caves, and that one of them carried internally seeds of *Morus* (*Maclura*) *tinctoria*.

ULE (1900) drew the attention of botanists to the question in a short article in which he mentioned some American Moraceae as bat-dispersed. He referred to an unnamed publication by Fritz Müller, also cited without further indication in Ludwig's *Lehrbuch der Biologie* (1985), which apparently mentioned *Billbergia zebrina* and *B. speciosa* as dispersed by bats.

HUBER (1910) went further and said that in the Amazonian forests of Brazil fruit bats are the most important of all agents of seed dispersal. This important ecological study seems to have been overlooked by most phytogeographers, though its remarks on bats have been quoted in Brehm's "Tierleben".

Huber mentioned some categories of fruits which seemed specially suited for this transport, in the first place the fleshy pods of some *Dalbergieae*, especially those of the genera *Dipteryx* and *Andira*. (The name *Andira* means bat in an Indian language and the Brazilian name of *Andira inermis* is "morceguiera"). Further he mentioned as bat-dispersed plants whose fruits are provided with large and hard kernels species of *Licania*, *Couepia*, *Parinarium*, *Saccoglottis*, *Vantanea* and *Poraquebia*. He gave detailed observations on this dispersal in the palm *Iriarteia exorrhiza*. An other important group is according to him formed by the *Sapotaceae* and *Annonaceae* with soft pericarp and relatively large seeds, which separate easily from the flesh. Finally he distinguished a group of fruits, with small seeds that pass the intestines of bats; they are found especially in *Moraceae* like *Cecropia*, *Ficus*, *Bagassa*, etc.

In his extensive handbook RIDLEY (1930) collected data from many sources, but from the authors mentioned above only Rumphius and Osburn were quoted. The data on *Anacardium* and *Psidium*, marked with his name in table I, refer to observations made in America, the other ones were collected in the Old World. He gave as his opinion (p. 347) that "bats are the most important seed dispersers of any mammals" and adds that they are very voracious and can fly long distances.

Ridley shows an aversion of classificatory terminology, but his comments help in the elucidation of class-characteristics. He draws the attention to a group of fruits that seem to offer no attraction to other mammals and to birds, viz. many hard-fleshed, green drupes. On page 392 he distinguishes (in *Eugenia*) bird-fruits (small, juicy, coloured, produced on low branches) and bat-fruits (large, greenish, provided with a firm pericarp). On page 435-436 a similar distinction is made in the genus *Ficus*, where cauliflorous species with large, dull-coloured fruits are regarded as bat-dispersed (outspoken in *F. polysyce* and *F. fistulosa*), whereas small, coloured figs point to bird-dispersal. Species like *F. benjamina* are suited for both birds and bats.

The data collected by Ridley are mentioned in table I under

his name as it does not seem necessary to refer to the original sources. The names of the diverse authors mentioned in this chapter and in later ones can be recognised in column 3.

In his book on carpobiology ULBRICH (1928) occasionally mentions bats, viz. in the discussion of the many juicy, large-seeded fruits in the tropics (p. 79–84). He differentiates but poorly between the many tropical fruit eaters, but mentions (mostly as a surmise) on page 84–85 some fruits as bat-fruits, e.g. *Achras sapota*, *Chrysophyllum cainito*, *Lucuma nervosa*, *Pouteria cainito* and *Mammea americana*. He also tries to give a characterisation of this type of fruit, in which he mentions the presence of long fruit stalks which would protect the fruits against the attacks of animals that do not fly.

The present author published two studies (1935, 1936a) in which lists of bat-fruits from Java were given but wherein also a characterization of the class was attempted. As both studies were published in Dutch in a semi-popular periodical, the contents are incorporated in the present paper together with some later finds.

DOCTERS VAN LEEUWEN (1935) gave an enumeration of the seeds found underneath the resting places of fruit-bats.

Misled by some confusion in my popular paper he erroneously cited some plants as being considered by me as proven chiropterochorous, viz. *Zalacca edulis*, *Ceiba pentandra*, *Sechium edule*, *Nephelium lappaceum*, *Phyllanthus emblica*, *Ph. acidus*, and *Garcinia mangostana*.

In his book on Krakatau (1936) this author gave many data on the dispersal of shore plants by bats.

The data from the latter four studies are comparable and refer to Javanese bats, mostly *Cynopterus* species.

BAKER and BAKER (1936) (B.a.B. in table I column 3) mentioned a number of fruits eaten by *Pteropus* on an island belonging to the New Hebrides.

Dr. H. Felten from the Senckenberg Institute in Frankfurt a.M. wrote me that he had regularly found remnants of fruits underneath the colonies of bats in caves in El Salvador. The fruits belonged to *Spondias purpurea* L. and *Ficus* species. The bat species concerned were *Phyllostomus discolor verrucosus* Elliot (*Spondias*), *Artibeus jamaicensis* Leach (*Spondias*) and *Artibeus lituratus palmarum* Allen and Chapman (*Ficus*).

In 1954 EISENTRAUT published an emended compilation by H. Jansen on the biology of the *Megachiroptera* (from the Old World). Being a zoölogist he is in the first place interested in the zoölogical aspect of the problem. He collects data from zoölogists and gives in the chapter on food-habits a list of the fruits eaten (p. 374–377). Data on *Microchiroptera* from America are naturally not included, but many data published by botanists on the activity of *Megachiroptera* (almost all those mentioned above) are also missing. The case of *Borassus* mentioned by Eisentraut, is not taken over in our table I, as the bat exercised here a merely dystrophic activity. The case of *Areca catechu* (improbable after my experience from Java) is left out as not present in the source mentioned by Eisentraut. I include his other data in so far as they have not been mentioned here before.

For the kind of bat and the country involved I refer to the original sources.

Mr. A. M. Greenhall, zoölogist of the Department of Agriculture in Trinidad, allowed me the use of the manuscript of a study about to be published (GREENHALL, 1956). This important paper gives details on ± 50 fruits eaten by the three principal fruit-bats of Trinidad and Tobago, viz. *Artibeus jamaicensis*, *Artibeus lituratus* and *Carollia perspicillata*.

Mr. Greenhall started from the zoölogical angle, investigating the food of the bats in all seasons, but he shows a clear understanding for the botanical side of the question. He mentions some fruits as greedily attacked, but too heavy to be carried off by the local bats, e.g. those of the *Mangifera*, *Annona*, *Mammea* and *Persea* species, and *Eugenia malaccensis*, all marked by his name in column 3 of table 1.

TABLE I
List of plants, described as being dispersed by bats

Name	Family	Author
<i>Achras sapota</i>	Sapotac.	Ule, Hub., Rid., v. d. P., Eis., Greenh.
<i>Acrocomia</i> sp.	Palmae	Allen
<i>Actinophloeas angustifolius</i> .	Palmae	D. v. L.
<i>Adinandra</i> sp.	Theac.	Rid.
<i>Aglaia</i> sp.	Meliac.	D. v. L.
<i>Anacardium occidentale</i> . .	Anacard.	Rid.
<i>Anacardium rhinocarpus</i> .	Anacard.	Pietri
<i>Ananomis umbellulifera</i> . .	Myrtac.	Greenh.
<i>Andira inermis</i>	Legumin.	Hub., Greenh.
<i>Annona muricata</i>	Annonac.	Hub., D. v. L., Eis., v. d. P., Greenh.
„ <i>reticulata</i>	„	Rumph.
„ <i>squamosa</i>	„	Greenh.
<i>Anthocephalus cadamba</i> . .	Rubiace.	Rid.
? <i>Antidesma bunius</i>	Euphorbiac.	D. v. L.
<i>Areca glandiformis</i>	Palmae	Rumph.
<i>Arenga pinnata</i>	„	D. v. L.
<i>Artocarpus communis</i> (<i>incisa</i>)	Morac.	D. v. L., Rid., B. a. B., Rumph., Eis.
„ <i>elastica</i>	„	D. v. L.
„ <i>champeden</i>	„	Rumph.
„ <i>integra</i>	„	D. v. L.
<i>Attalea</i> sp.	Palmae	Rid.
<i>Azadirachta indica</i>	Meliac.	Eis., Hall
<i>Baccaurea racemosa</i>	Euphorb.	D. v. L.
<i>Bactris speciosa</i>	Palmae	D. v. L., v. d. P., Greenh.
<i>Bagassa</i> sp.	Morac.	Hub.
<i>Bassia latifolia</i>	Sapotac.	Rid.
<i>Billbergia speciosa</i>	Bromeliac.	Müller
„ <i>zebrina</i>	„	Müller
<i>Brosimum alicastrum</i>	Morac.	Osb.
<i>Bouea macrophylla</i>	Anacard.	v. d. P.
<i>Byrsonima spicata</i>	Malpighiac.	Greenh.
<i>Calocarpum mammosum</i> . .	Sapotac.	Greenh.
<i>Calophyllum inophyllum</i> .	Guttifer.	Rid., D. v. L., v. d. P.
„ <i>pulcherrimum</i>	„	Rid.
? <i>Canarium commune</i>	Burserac.	D. v. L., v. d. P.

Name	Family	Author
<i>Carica papaya</i>	Caricac.	Rid., D. v. L., v. d. P., B. a. B., Greenh., Eis.
<i>Caryota rumphiana</i>	Palmae	D. v. L.
<i>Cecropia</i> sp. (incl. <i>peltata</i>) .	Morac.	Ule, Hub., Greenh.
<i>Ceratonia siliqua</i>	Legumin	Ulbr.
? <i>Cereus hexagonus</i>	Cactac.	Greenh.
<i>Chrysalidocarpus</i> sp.	Palmae	v. d. P.
<i>Chrysophyllum cainito</i>	Sapotac.	Greenh.
<i>Chrysobalanus icaco</i>	Chrysobal.	Greenh.
? <i>Citrus</i> sp.	Rutac.	Eis.
? <i>Clibadium surinamense</i> . . .	Compos.	D. v. L.
? <i>Coffea</i> sp.	Rubiace.	Greenh., Pietri
<i>Coccoloba uvifera</i>	Polygonac.	Greenh.
<i>Cordia bicolor</i>	Borragin.	Greenh.
„ <i>collococca</i>	„	Osbr., Greenh.
„ <i>abyssinica</i>	„	Eis.
<i>Corypha utan</i>	Palmae	D. v. L.
<i>Couepia</i> sp.	Chrysobal.	Hub.
<i>Coussapoa</i> sp.	Morac.	Ule
<i>Curtisia faginea</i>	Cornac.	Rid.
<i>Cycas rumphii</i>	Cycadac.	D. v. L.
<i>Cynometra cauliflora</i>	Legumin	D. v. L., v. d. P.
<i>Cyrtandra sulcata</i>	Gesner	D. v. L.
<i>Diospyros mabola</i>	Ebenac.	Greenh.
„ <i>melanoxylon</i>	„	Rid.
„ <i>embryopteris</i>	„	Rid.
<i>Dipteryx</i> spp.	Legumin.	Hub.
„ <i>odorata</i>	„	Greenh.
<i>Dracontomelum mangiferum</i> . .	Anacard.	B. a. B.
? <i>Durio zibethinus</i>	Bombac.	D. v. L.
<i>Dysoxylum</i> sp.	Meliac.	D. v. L.
<i>Elaeocarpus parvifolius</i>	Elaeoc.	Rid.
? <i>Elaeocarpus ganitrus</i>	„	v. d. P., Eis.
? <i>Epiphyllum hookeri</i>	Cactac.	Greenh.
<i>Eriobotrya japonica</i>	Rosac.	Rid., Eis.
<i>Eugenia aquea</i>	Myrtac.	D. v. L.
„ <i>cumini</i>	„	Eis.
„ <i>densiflora</i>	„	v. d. P.
„ <i>grandis</i>	„	Rid.
„ <i>javanica</i>	„	Rid., v. d. P.
„ <i>jambolana</i>	„	Rid.
„ <i>jambos</i>	„	Osbr., Eis., Greenh.
„ <i>polyantha</i>	„	D. v. L., v. d. P.
„ <i>malaccensis</i>	„	D. v. L., v. d. P., Eis., Greenh.
„ <i>striata</i>	„	v. d. P.
<i>Evodea</i> sp.	Rutac.	D. v. L.
<i>Fagraea</i> (<i>Cyrtophyllum</i>) sp. .	Loganiac.	D. v. L.
„ <i>peregrinum</i>	„	Rid.
„ <i>fragrans</i>	„	Rid., D. v. L., Corner.
? <i>Ficus ampelas</i>	Morac.	D. v. L.
<i>Ficus benjamina</i>	„	Rid., D. v. L., Greenh.
„ <i>bengalensis</i>	„	Rid.
„ <i>copiosa</i>	„	B. a. B.
„ <i>elastica</i>	„	D. v. L.
„ <i>callosa</i>	„	D. v. L.
„ <i>fistulosa</i>	„	D. v. L., v. d. P.
„ <i>fulva</i>	„	D. v. L.
„ <i>glomerata</i>	„	Rid., D. v. L., v. d. P.

Name	Family	Author
„ hispida	„	D. v. L.
„ religiosa	„	Rid.
„ ribes	„	D. v. L., v. d. P.
„ polysyce	„	Rid.
„ retusa	„	D. v. L.
„ umbellata	„	Baker
„ variegata	„	D. v. L., v. d. P.
„ sycomorus	„	Eis.
? Flacourtia rukam	Flacourt.	D. v. L.
? „ indica	„	Greenh.
Freycinetia sp.	Pandan.	Baumann
Glochidion ramiflorum	Euphorb.	B. a. B.
Gluta reinghas	Anacard.	D. v. L.
Guettarda speciosa	Rubiace.	D. v. L.
Hernandia peltata	Hernand.	D. v. L., v. d. P.
Hippomane mancinella	Euphorb.	Lasser
Hyphaene thebaica	Palmae	Eis.
? Hylocereus lemairii	Cactac.	Greenh.
Inocarpus edulis	Legumin.	Rid., D. v. L.
Iriarteia exorhiza	Palmae	Hub.
Irvingia barteri	Simarub.	Eis.
Lansium domesticum	Meliac.	D. v. L., Eis., v. d. P.
Licania sp.	Chrysobal.	Hub.
Litsea polyantha	Laurac.	D. v. L.
Livistona australis	Palmae	Rid.
? Livistona rotundifolia	„	D. v. L., v. d. P.
Livistona chinensis	„	Rid.
Malpighia glabra	Malpighiac.	Greenh.
Mammea americana	Guttif.	Greenh.
Mangifera indica	Anacard.	Rid., D. v. L., v. d. P., Greenh., Eis.
„ foetida	„	Rumph.
„ odorata	„	Rumph.
Maniltoa gemmipara	Legumin.	D. v. L.
? Melastoma malabathricum	Melastom.	D. v. L.
Melia azedarach	Meliac.	Rid., D. v. L.
Melicocca bijuga	Sapindac.	Greenh.
Mimusops elengi	Sapotac.	v. d. P., Greenh.
„ (Manilkara)		
bidentata	„	Greenh.
Morinda citrifolia	Rubiace.	D. v. L.
Morus (Maclura) sp.	Morac.	Eis.
„ (Chlorophora)		
tinctoria	„	Osb., Greenh.
? Morus nigra	„	Eis.
? Muntingia calabura	Elaeocarp.	D. v. L.
Musa spp. div.	Musac.	Rid., D. v. L., v. d. P., Greenh., Eis.
Nauclea elegans	Rubiace.	? Rumph.
Nephelium spp.	Sapindac.	Rid.
„ lappaceum	„	D. v. L.
Ochrocarpus congregatus	Guttif.	D. v. L.
Olea laurifolia	Oleac.	Rid.
Oncosperma filamentosa	Palmae	D. v. L.
Oreodoxa oleracea	„	Greenh.
Palaquium gutta	Sapotac.	Rid., v. d. P.
Pandanus tectorius	Pandanac.	Rid., D. v. L.
„ odoratissimus	„	Eis.
Parinarium sp.	Chrysobal.	Hub.

Name	Family	Author
? <i>Passiflora foetida</i>	Passiflor.	D. v. L.
<i>Passiflora quadrangularis</i>	"	Greenh.
<i>Persea gratissima</i>	Laurac.	Eis., Greenh.
<i>Phoenix dactylifera</i>	Palmae	Rid.
<i>Pimenta racemosa</i>	Myrtac.	Greenh.
<i>Piper aduncum</i>	Piperac.	D. v. L., v. d. P.
" <i>retrofactum</i>	"	D. v. L.
<i>Pipturus incanus</i>	Urticac.	D. v. L.
<i>Polyalthia</i> sp.	Annonac.	Rid.
" <i>longifolia</i>	"	Eis.
<i>Poraquebia</i> sp.	Icacinac.	Hub.
<i>Pouteria multiflora</i>	Sapotac.	Greenh.
<i>Prunus persica</i>	Rosac.	Eis.
<i>Psidium guajava</i>	Myrtac.	Rid., D. v. L., v. d. P., Greenh., Eis., B. a. B.
<i>Putranjiva roxburghii</i>	Euphorb.	Greenh.
<i>Saccoglottis</i> sp.	Humiriac.	Hub.
<i>Sandoricum koetjape</i>	Meliac.	D. v. L.
<i>Sapindus rarak</i>	Sapindac.	D. v. L., Greenh.
<i>Sideroxylon sundaicum</i>	Sapotac.	Rid.
" <i>quadriloculare</i>	"	Greenh.
<i>Sonneratia caseolaris</i>	Sonneratiac.	v. d. P.
<i>Spondias dulcis</i> (cytherea)	Anacard.	D. v. L., Rid., Eis., Greenh.
" <i>lutea</i>	"	D. v. L.
" <i>purpurea</i> (mombin)	"	Felten, Greenh.
<i>Strychnos nux vomica</i>	Loganiac.	Eis.
<i>Symplocos</i> sp.	Symploc.	Rid.
<i>Terminalia catappa</i>	Combretac.	Rid., D. v. L., v. d. P., Greenh., Eis., B. a. B.
<i>Thevetia neriifolia</i>	Apocynac.	v. d. P.
<i>Vantanea</i> sp.	Humiriac.	Hub.
<i>Xerospermum</i> sp.	Sapindac.	Rid.
<i>Zizyphus</i> sp.	Rhammac.	Rid.

I included these data in the list because the plants concerned had already been mentioned as dispersed by other, larger fruit-bats and because the observations in America confirm the universal preference of bats for these fruits.

Though there was no effort to distinguish between true bat-fruits and those that are incidentally eaten by bats, Mr. Greenhall noted that in the three *Cactaceae* mentioned (*Cereus*, *Epiphyllum*, *Hylocereus*) the bats did for some reason or other not contribute to the dispersal. I marked these names (and *Coffea*) in table I with a question mark, as I fear an incidental "derailment" of the bats here towards these purple bird-fruits.

The families that dominate in the list are resp. the *Moraceae*, *Palmae*, *Anacardiaceae*, *Sapotaceae* and *Meliaceae*, but chiropterochory has—apparently independently—developed in many other families.

A list like table I will always remain to some extent unsafe. It may include data given by zoölogists who tend to pay more attention to the plants as providing nutrition to bats than to the actual dispersal of seeds (cf. *Borassus* on p. 294). When I saw a *Cynopterus* bite off pieces of the fruits of *Sechium edule* without dispersing the seeds I did of course not include this species in the list.

Of course not all the items of the list have the same biological importance. A complete investigation should also consider the negative side, viz. the degree to which other dispersers are excluded; this point is discussed in chapter C.

I put a question mark before some names of doubtful importance. Some data evidently refer to incidental and abnormal visits due to special circumstances, as bats in a hunger period, the presence of cultivated temperate fruits in tropical mountains (cf. the introduction to chapter C).

A drawback of the list, obscuring the importance of bat-dispersal of wild fruits in natural vegetations, is that most observers paid excessive attention to plants cultivated in gardens. The fruits of the genus *Citrus*, for instance, though mentioned in some isolated instances, are quite atypical, and are in some other studies especially mentioned as being refused by bats.

GREENHALL (1956) who included many Asiatic plants grown in gardens, also made remarks in this direction. He expects that many cases could be uncovered in the forest, like the discovered one of the high balata trees (*Mimusops* or *Manilkara*) in the virginal forests of Trinidad. His (and Pietri's) find of *Coffea* seeds underneath roosts and in caves is clearly a derailment of the bat—for these fruits are neither in Africa nor in Asia, dispersed by bats.

In some cases from DOCTERS VAN LEEUWEN (1935) I fear contamination with bird droppings as the fruits in question, often borne on low plants are unfit for bats and are mostly ornithochorous. This refers to *Passiflora*, *Clibadium*, *Melastoma*, *Antidesma* and probably to *Flacourtia*. In a former study, on seeds dropped by the bird *Aplonis panayensis* underneath its nest, this author mentioned seeds of the above *Clibadium* and *Melastoma* species. The case of *Durio zibethinus* is enigmatic, as this fruit can obviously be handled only by very large mammals. The finds of kernels of *Canarium* gnawed off by bats in Java are incidental. In the home country of the plant the seeds are spread by fruit-pigeons. For parallel cases of ornithochorous fruits eaten by bats I refer to *Muntingia calabura* (cf. p. 304), *Livistona rotundifolia* and *Elaeocarpus ganitrus* (cf. p. 301).

C. CHARACTERISTICS OF BAT FRUITS

Of course fruit-bats eat whatever they can find and like, irrespective of the question whether the food is endemic in their habitat or not, and whether their activity is required for maintaining the natural composition of the vegetation by seed dispersal. In inhabited regions with many cultivated plants this will be very obvious (cf. *Livistona* and *Elaeocarpus* on p. 301). In Java they chew soft, new leaves of *Sechium edule*, in Trinidad those of *Ficus religiosa*,—a purely dystrophic activity. In the rare cases that nectar is taken from intact flowers or that parts of flowers and inflorescences are eaten, there may occur pollination. Sometimes whole flowers are squashed. Dystrophic activity of the latter kind was rarely found in Java (*Parkia*, *Durio zeylanicus* in the Botanical Garden), but occurs on a larger scale in Eastern

Indonesia and especially in the border regions in Australia (c.f. RATCLIFFE, 1931). Destruction of seeds is also rare (cf. *Calophyllum*, *Sechium* and *Borassus* on p. 298, 303 and p. 297). On the whole, fruit "destined" for bats seem to possess an efficient protection for their seeds. In a region like sub-tropical Australia, where many foreign fruits are cultivated and where *Pteropus* is met with as a migrator, the connection between bats and fruits will be more or less incidental. There too we find, nevertheless, a preference for native and introduced bat fruits, with mangoes and custard-apples at the top of the food list and with pome-fruits and especially *Citrus* at the bottom (cf. RATCLIFFE, 1931).

We have to recognise that bonds with bats may be a secondary deviation from more ancient bonds with birds and that the boundary line between the two classes may be unsharp.

All this, however, should not prevent us from looking in tropical fruits for features, which might bring them into the special sphere of interest of the fruit-eating bats. The stamp of the bat! As the fruit is a part with an outspoken ecological function it seems plausible to assume that local ecological factors (in casu the dispersing animals) may have had a profound influence on the evolution of its characteristics. We may leave aside the question whether this was a purely selective influence but, though we have no clear understanding of the way the influence may have acted, it seems unsatisfactory to assume that a special type of fruit would develop incidentally and without regard to the presence of agents fit to disperse such a fruit. A taxonomous group with fruits mainly fit for dispersal by bats would certainly be handicapped in a region without fruit-bats.

Of course when a general picture has been developed of the characteristic features of an ecological class, it will always be possible to discover cases where one of the features is missing. This is just as in the classes of floral biology, to whose acceptance only negativists object on the futile ground that there are transitional and non-classifiable forms. In this connection I would draw the attention to a quotation from Whewell in Arber's "Natural Philosophy of Plant Form" (p. 67): "A natural class of objects is determined, not by a boundary line without, but by a central point within; not by what it strictly excludes, but by what it eminently includes".

After some tropical ecological experience it is quite well possible to recognize a typical bat fruit, even if it were only because transport by other agents appears to be excluded.

A second step in the research is the recognition of the sociological importance of the bonds in the natural community.

A short characterisation of the class was given in my discussion of the ecological classification of leguminous fruits (1956a). It is as follows:

- 1) Edible part soft or hard, 2) dimensions of fruit and seed large, up till those of a manggo, 3) dull colour, 4) unfresh odour, 5) attached to the tree till after maturity, 6) tough skin (indehiscence) possible, 7) exposure outside the foliage.

For a full discussion I will follow my study of 1935.

For a comparison with the class of bat-flowers, which shows parallel adaptations, I refer to my monograph on this subject (1936*b*).

1. Colour

It has many times been mentioned that the typical bat-fruit is visually not conspicuous, being greenish or brownish.

I may refer here to the green drupes and figs mentioned by Ridley (cf. p. 293) and to FRITZ MÜLLER (cf. p. 293) who was struck by the fact that the fruits of the chiropterochorous *Billbergia* species are dull coloured in contrast to those of the mostly gaudy ornithochorous relatives.

In chapter E this point will be stressed for tropical table fruits and in chapter D 2 for a number of sea-shore fruits. It will be confirmed by a perusal of the tables I and II, especially when the incidentally bat-dispersed fruits, discussed on p. 299 are left out of consideration. The pigeon plum *Eleaocarpus ganitrus* (a bird fruit) and *Livistona rotundifolia* have blue fruits, which are rather small and without smell. The fruits of both species are nevertheless eagerly sought after by bats in Java, where the trees have been introduced into gardens. This transition is facilitated by the open structure of their crowns—so favourable to bats.

For a colourblind bat the absence of colour is no handicap, but it may be so for birds. Sometimes a lighter shade of colour may offer some help to bats in the night.

2. Odour

Fruit bats have a keen sense of smell as already indicated by the structure of the nasal cavity. No wonder therefore that the presence of a distinct odour is a character of the chiropterochorous fruits, which differentiates them from the ornithochorous ones.

There is even a slight differential characteristic in this respect with fruits eaten by other mammals, arboreal as well as terrestrial ones. Bats have a taste which differs from the one of other mammals, who, like man, seem to prefer, a fresh "fruit odour". Fruit-bats themselves often spread an unfresh, rancid or musty odour often emanating from special glands and seem to like fruits with a similar smell, often reminding of fermentation. Nectarivorous bats have a preference for flowers emitting a similar odour (cf. VAN DER PIJL, 1936*b*).

One day we may be able to define this characteristic in chemical terms. The very rancid fruits of *Morinda citrifolia* might be analysed in order to find out whether they contain butyric acids or related substances. At an earlier occasion I mentioned that the fruits of the cauliflorous *Ceratonia siliqua*, sought after by the Egyptian bat *Cynonycteris Geoffroyi* (according to ULBRICH (1928)), were actually found to contain butyric acid. The comparison with mouse urin, so often made in regard to the odour of bat flowers and bat fruits, also suggests a chemical investigation in this direction.

In the genus *Ficus* it is remarkable that large, dull coloured, and stem-borne figs, spread an odour of fermentation.

The smell of wild manggoes is notorious. For table fruits see chapter E.

As in bat flowers the typical smell arises after sunset, I tried to find out whether there is a similar rhythm in the odour production in a typical bat fruit, viz. that of *Psidium guajava*. No indication of this was found. The odour persisted for some days, also during daytime. CORNER (1940, p. 111) cited an opinion that the fruits of a *Mangifera* species ripen during the night.

3. *The dimensions of the fruits*

Generally speaking, a large size may also be a differential characteristic. It gives sense to the often mentioned fact that there are in the tropics so many large, juicy fruits with large seeds.

Bat fruits may be just some cm large, but also so large, that they cannot be swallowed or transported by birds. Some large fruits are also fit for bird food because they can easily be picked into pieces, as those of *Carica papaya*, liked by many animals. Typical bat fruits are not so readily broken up into smaller parts. Large birds like hornbills, some pigeons, crows and cassowaries (cf. p. 310) remain in this respect not so far behind bats, (with nutmegs, *Canarium* and palms), but the fruits of *Mangifera* (100–200 gr) and others are too large for them. Bats even can tear off pieces from the gigantic compound fruits of *Artocarpus* species.

The possible large dimensions have a relation to the way of transport, which is rarely endozoic, but usually synzoic. The fruits are (as many observers since Huber have reported) transported in the mouth to a quiet spot, sometimes hundreds of meters off. Osburn found half a mile and Greenhall some hundreds of yards. This spot may be the roosting place, but it is not necessarily so, certainly not in the case of *Pteropus*. In forests one often finds heaps of fresh debris under branches where no bats are sleeping. In Javanese crater regions heaps of *Eugenia striata* seeds are common. Greenhall distinguished in America too such fixed "digesting places" from the roosts.

In the case of cave dwellers transport of the fruits to the caves would be fatal to the seeds and what is actually found in the caves may be the remnants of only the last meal, taken home.

This kind of behaviour on the other hand makes that the distance of dispersal is less impressive than one might be inclined to deduce from the tens of kilometers *Pteropus* can fly. For small seeds the situation is different as we shall see.

The accumulation of many seeds on one spot in the forest, later on to be recognised by dense groups of seedlings, is another drawback.

Undoubtedly there is in the dimensions of the fruits some differentiation between those suitable for the large *Megachiroptera* like *Pteropus* and those for the smaller ones, for instance of the genus *Cynopterus*. *Pteropus* may carry fruits weighing up to ± 200 g, whereas *Cynopterus* as an average is fully loaded with a fruit of *Psidium* or of *Achras sapota*

of 75 g. I observed that *Cynopterus* had to gnaw the large fruits of a mango on the tree. *Pteropus*, however, takes small figs too.

I already cited from GREENHALL (1957) that the three Trinidad fruit-eating *Microchiroptera* were unable to transport some recognised bat-fruits as a whole or in parts, as these fruits were too large for them. Some other fruits (e.g. those of *Terminalia catappa*) could be carried off only by the larger local bats (the *Artibeus* species).

4. Size of seeds and kernels

This runs parallel with that of the fruits, but is sometimes decisive, viz. in smallish fruits, as is to be seen in ULBRICH (1927) Figs. 13 and 16, where a number of bat fruits are figured with the strikingly large seeds that are left behind after the meal.

In the centre of Javanese cities one may find heaps of bat's debris under the protruding part of a roof. Systematic collecting of such remains in tropical botanical gardens would yield useful results. The writer would gladly receive reports of seeds found.

It has been related by many observers (cf. RATCLIFFE (1931), VAN DER PIJL (1935), BAKER and BAKER (1936), and GREENHALL (1956) that neither *Megachiroptera* nor *Microchiroptera* swallow the substance of the fruits as such. Sometimes the pericarp is gnawed off separately, sometimes (with smaller seeds) the flesh and the seeds are squashed and pressed out together, but always the solid matter is ejected as dry pellets. Only the juice is swallowed. In the stomach one finds no solid substance but only a jelly. The excreta, which I collected for years, contain as a rule no seeds. The gullet is narrow and the intestine remarkably short.

EISENTRAUT (1945) already remarked that this way of feeding on vegetable matter is most fitting to the organization of a bat. A large abdomen such as would be required for the digestion of material full of cellulose might impair its power of flight.

It does not seem to be strictly necessary for the seeds that are gnawed off, to be protected by a very hard coat—another difference with the endozoic bird fruits. Some disagreeable property of the seed seems sufficient to prevent damage. In many *Sapotaceae* and *Annonaceae* we see that the seeds are so slippery that they escape as soon as the transported fruit is attacked.

The opinion that *Pteropus* sometimes also chews and eats the seeds themselves (e.g. those of *Calophyllum inophyllum*) has been recorded, though with some doubt, by EISENTRAUT (1945). In my observations of this plant I never saw anything of the kind.

Perhaps the situation is different with some transitional fruit eaters among the American *Microchiroptera*. Ridley cites old reports in which it is said that seeds and insects were found together in the stomach of *Vampyrus spectrum*. The available data about such American tropical bats are very unsatisfactory. Recently FELTEN (1956) reported that even *Glossophaga soricina leachii* (Gray), which is known as a flower visitor, prefers during the rainy season insects and soft fruit flesh to nectar.

The large size of the seeds is especially striking in the group of more or less certainly chiropterochorous *Leguminosae* which I discussed in a previous article (1956)*a*. They are often cauliflorous and have usually one-seeded, drupe-like pods. The fruits of one of them (*Cordyla*) are said to possess the typical colour and smell as of *Mangifera* fruits; in others representing this group colour and position of the fruits are typical for bat fruits, but more details are wanted. The group includes *Cordyla pinnata*, *Swartzia fistulosa*, *Cynometra cauliflora*, *Inocarpus edulis*, *Detarium senegalense*, *Angylocalyx* spp., *Andira inermis*, *Maniltoa gemmipara*, *Dipteryx odorata*.

I said that the excreta contain as a rule no seeds.

An exception should be made for some very small, smooth seeds, which were found to be swallowed accidentally. I already cited some cases from Huber and Osburn (*Maclura*, *Cecropia*, *Ficus*, *Bagassa*). In Java I found in the excreta seeds of *Piper aduncum* of which the green catkins acquire just before ripeness the consistency of a sweet jelly. Several kinds of animals eat them. At night they are plucked by bats and transported, after which the bats strip the sweet layer with the small seeds from the axis, squash this mass and leave the dry press cakes on the axis tip. Many seeds are swallowed and may later be found in the excreta, which are often spurt against walls when the bats alight on gutters. The same happens with the seeds of the introduced garden tree *Muntingia calabura*, which is ornithochorous, but readily accepted by bats. DOCTERS VAN LEEUWEN (1936) found seeds of *Cyrtandra sulcata* in excreta. GREENHALL (1957) found that *Artibeus lituratus* swallowed part of the seeds of *Psidium*.

The genus *Ficus* takes a somewhat intermediary position. After feedings on *Ficus* fruits *Pteropus* and *Cynopterus* were usually found to have no "seeds" in the intestines. Others reported the same find from India and Africa. From time to time, however, Docters van Leeuwen and I found some seeds in *Pteropus* and *Cynopterus*, a.o. of *F. fistulosa* and of *F. glomerata*. These exceptions may be ecologically important for transport over greater distances, though the evacuation is probably very fast. *F. fistulosa* was found in Krakatau as early as 1905. The presence of *Ficus* in clefts of walls therefore may not always be due to birds.

Sometimes the chewed pulp with small seeds is thrown as a sticky lump against trees and walls.

Prof. H. G. Baker wrote me that the walls of the Botany Department in Achimota (Gold Coast) become in this way streaked with the expectorates of the bats *Epomophorus gambianus* and *Nanonycteris veldkampii*. They contain many seeds of *Ficus umbellata*.

5. Consistency and morphology of the edible parts

Bats like a soft, sweet fruit flesh as that of many *Sapotaceae*, *Annonaceae* and *Moraceae*. They accept, however, also hard and sour flesh, present in a thin layer—as in the fruits of wild *Eugenia* and *Elaeocarpus* species.

Averrhoa, *Phyllanthus*, many palms and especially in the many diplochorous fruits found near the seashore, which are discussed in chapter D.

An unedible tough peel, which does not dehisce, is no obstacle, as it is torn off (c.f. *Lansium*, *Baccaurea*, *Nephelium* and *Artocarpus*). This point again is somewhat a differential characteristic with bird fruits, which when large and tough are dehiscent, so that the interior becomes accessible. This happens especially in fruits of "low standing", where the pericarp is protective only and the sarcotesta or aril edible.

In my study on the hierarchy of edible layers in fruits (1956a) I composed a scala of what in this respect is to be regarded as primitive and progressive. The range is: A. the nude, edible sarcotesta, B. the covered sarcotesta, C. the arillode (partial sarcotesta), E. the aril, F2. the endocarp pulpa, F3, the mesocarp.

My impression is that bird fruits dominate in the phases A and B, but that many fruits in phase B already became chiropterochorous, as illustrated by *Baccaurea*, *Lansium* and many *Sapindaceae*. It is even possible, that *Cycas rumphii* in phase A is truly chiropterochorous, though Gymnosperms as a rule rely on other animals. *Musa* is a good instance of phase F2.

In the *Leguminosae* (c.f. my study of 1956a) there is certainly a priority of ornithochory in phase B, though probably *Inga* in this phase already developed indehiscent, chiropterochorous pods. *Parkia* did this in phase F2.

Most chiropterochorous fruits (also in the *Leguminosae*) are in phase F3.

6. Position of the fruits on the tree

Bat fruits and bird fruits have one feature in common, by which they differ from fruits spread by ground mammals, viz. that the mature fruits remain attached to the tree.

In one other respect there is, however, a strong contrast between the two former classes, viz. that bat-fruits occupy a peculiar position on the tree, one that enables the bats to fly to them without inconvenience from the foliage.

This position may be:

a) on the surface of the crown, at the ends of the twigs (as in *Achras*, *Psidium*).

b) on pendulous branches or peduncles; in this case the fruits dangle in open spaces in or underneath the crown. This "flagelliflory" or "penduliflory" can be seen in all degrees of development in *Melia*, *Mangifera*, *Musa*, *Spondias*, *Morinda*, etc.,

c) on the old branches of an open crown, or on the trunk (cauliflory), (Sometimes b) and c) are combined, as in many *Ficus* species, *Lansium*, *Baccaurea*, *Phyllanthus* and many palms),

d) in pagoda-shaped trees, as is very striking in *Terminalia catappa*. In a general discussion of the construction of the crown of many tropical trees BREMEKAMP (1936) described the curious construction of this tree and others with the foliage in tiers. For a special reason I refer also to the analysis of CORNER (1940), who coined the terms "pagoda-tree" and "Terminalia-branching".

The two phenomena were there described for Malaya as occurring in: *Alstonia*, *Ochrosia*, *Terminalia*, *Endospermum*, *Salmalia*, *Achras*, *Palaquium*, *Manilkara*, *Sterculia*, *Archytaea* and *Elaeocarpus*. I might add *Ceiba* as an introduced tree.

To find an ecological interpretation of the latter construction I beg to compare this enumeration with our tables I and II, wherein we find the names of *Ochrosia*, *Terminalia*, *Achras*, *Palaquium*, *Manilkara* and *Elaeocarpus*.

Of *Salmalia* (*Bombax Valetonii*) and *Ceiba* I have already reported (1936) that they are pollinated by bats.

Of the 12 genera only *Alstonia*, *Endospermum*, *Archytaea* and probably *Sterculia* have no intimate connections with bats.

In CORNER's book (1940)—a goldmine for ecological details—the crowns of some other trees are especially described because of their curious, open structure. One is *Duabanga sonneratioides* Buch.-Ham. (*D. grandiflora* Walp.), which is certainly chiropterophilous (c.f. Corner's data on the flowers of this species and my own (1956*b*) on those of *D. moluccana*). The others belong to the genus *Fagraea*. *F. crenulata* has the pure pagoda-shape (c.f. his plate 121), and *F. fragrans* has this structure combined with flagelliflory, the tops of the branches being pendulous—as in *Duabanga*. In this genus we find pronounced chiropterochory—as described by Corner himself for *F. fragrans*.

I shall not discuss here, whether form or function is primary in this respect but the typical position is sometimes an easy criterium to decide from a description or from a figure whether a plant might be chiropterophilous or chiropterochorous. The stamp of the bat even on the vegetative system!

In many species the special position of the flowers, and consequently of the fruits, is important for both pollination and seed dispersal, so that they are in two ways bat plants. I mean some *Sapotaceae* like *Bassia latifolia* and probably some *Palaquium* and *Madhuca* (*Payena*) species, further to *Musa* spp., *Sonneratia caseolaris*, *Eugenia cauliflora*, *Freycinetia insignis* and perhaps *Kigelia*, *Adansonia*, *Parmentiera*, *Duabanga* and *Parkia* species.

The rise of bat flowers in a group can sometimes been seen as following an earlier development of chiropterochory.

Let us add some remarks on flagelliflory and cauliflory.

The significance and the actual importance of these positions in relation to the physiology of *Megachiroptera* has been fully discussed by me in previous articles (1936, 1941, 1956*a*). These papers dealt principally with the parallel case of pollination by bats, but fruits were sometimes used for comparison. Flagelliflory and cauliflory, considered by many earlier writers from many angles as peculiarities of the tropics, were recognised by me as mostly adaptations to the visits of bats. The almost complete absence of the two phenomena in Europe often considered as normal is the peculiarity,—to be explained by the lack of *Megachiroptera*.

ULBRICH (1928) was the only one who had somewhat the correct, though vague, understanding in regard to cauliflorous fruits, as

quoted before. On p. 93 he also cited incidentally, without expressing its significance in this connection, the dispersal by bats of *Ceratonia siliqua*, the typical "European" cauliflorous plant. This date regards Egypt, in the curious Northern offshoot of the area of distribution of the *Megachiroptera*, which terminates in Cyprus.

Although I admit anew that cauliflory may sometimes be ecologically meaningless, I maintain that it is mostly ecologically important. This sometimes concerns the pollination of the flowers but mostly the dispersal of the seeds, the feature which interests us here.

For the other cauliflorous *Leguminosae* (cf. the chiropterochorous group mentioned on p. 304) this connection has already been demonstrated in my special study (1956a). A strikingly large part of the group shows cauliflory (*Cordyla*, *Swartzia*, *Cynometra*, *Angylocalyx*). Further it is very rare in the family.

Among the plants mentioned in table I cauliflory is found in species of *Ficus*, *Annona*, *Lansium*, *Baccaurea*, *Eugenia*, *Artocarpus*, etc. In the palms the cauliflorous position of the flowerstands, due to the organization type of the family, in combination with the pendulous stalks (flagelliflory), brings the fruits into a favourable position underneath the crown.

For many other cauliflorous, juicy fruits the actual bat-dispersal remains to be proven. Especially observations in tropical America should fill the gaps in our knowledge. I remind of the several cauliflorous, edible melastomataceous, sapotaceous and myrtaceous fruits occurring in America. Think of *Marlieria edulis* and *Myrciaria* discussed and figured together with the African *Anacardiaceae* *Trichoscypha ferruginea* in ULBRICH (1928) (Fig. 16). This author already remarked (p. 82) that it is striking how markedly species with juicy fruits dominate amongst cauliflorous trees. To prove this, he analysed the list of African cauliflorous species given by MILDBRAED (1922).

A list of all known cauliflorous plants, stating the accompanying characters of their fruits, was prepared by me before the war. It was lost, but would anyhow have taken too much space here.

In some cases of cauliflory a bond with a special way of pollination is clearly excluded, so that the special position can be of importance only in connection with the fruits. *Artocarpus integra* bears its male inflorescences in the crown near the tips of branchlets, whereas the female inflorescences are found near the base of the larger branches or on the trunk. In *Stelechocarpus burahol*, with certainly chiropterochorous, large, juicy, large-seeded and greyish fruits, the arrangement is the same.

D. BAT-DISPERSAL IN SPECIAL AREAS

1. General remarks

It may prove important, to study not only the general significance of bat-dispersal, but also its quantitative influence in special vegetations.

The usual "biological spectrum" covers the diverse "life forms"

and may serve to characterize temperate and arid floras in their relation with the climatic periodicity in their region. We are, however, still badly in need of other biological spectra, which could express the relation with factors, climatic as well as biotic, which are of importance for the reproduction of the plants. A pollination spectrum and a dissemination spectrum would doubtless help us to obtain a better understanding of tropical floras.

Bat-dispersal might then prove to be of unequal importance in diverse tropical and subtropical vegetations. The first phases in the succession, when trees are as yet absent, are, of course, unable to harbour fruit-bats.

Most of the species enumerated in table I belong to open vegetations in sub-optimal condition, to sub-climaxes, secondary forests and the like, in tropical and adjacent subtropical regions. The trees mentioned have mostly a maximum-height of 25 m. The impression created by the table may be somewhat onesided owing to an as yet unsufficient analysis of the rain forest proper. However, many of the trees from earlier stages in the succession will persist in the lower stories of the forest. Many of the moraceous, meliaceous and sapotaceous trees from the higher stories may also be bat-dispersed (cf. Huber's remarks on p. 293 and those of Greenhall on *Manilkara*, on p. 299). Fruit bats do live in the rain forest up till high altitudes.

We are not yet in a position to extend these considerations very far, and will have to limit ourselves to some special cases.

2. *Diplochory on pacific shores*

Chiropterochores are especially abundant in the vegetation near the sea. The principal species from the Western Pacific have been collected in table II. The chiropterochory of most of them is a well-established fact, but of some it is, though probable, not yet proven.

TABLE II

<i>Calophyllum inophyllum</i>	<i>Morinda citrifolia</i>
<i>Cerbera manghas</i>	<i>Ochrosia parviflora</i>
<i>Cordia subcordata</i>	<i>Pandanus</i> spp.
<i>Cycas rumphii</i>	<i>Sonneratia</i> spp.
<i>Guettarda speciosa</i>	<i>Spondias lutea</i>
<i>Hernandia peltata</i>	<i>Terminalia catappa</i>
<i>Inocarpus edulis</i>	<i>Ximenia americana</i>

From American shores I could add many species from the "tropical littoral woodland" as *Coccoloba uvifera*, *Chrysobalanus icaco* and *Hippomane mancinella*. As Dr. Tobias Lasser from Caracas wrote me, the latter is spread on the Venezuelan beach by microchiropterous fruit bats. Ridley mentioned the apple-like, greenish yellow fruits as typical drift-fruits that are also eaten by goats and tortoises.

Phoenix paludosa from Malayan coastal swamps is probably another asiatic case of dispersal by both sea and bats. If this is true it would be ecologically intermediate between the majority of palm fruits and those of *Nipa* and *Cocos*, which are entirely sea-dispersed.

Perhaps the presence of so many chiropterochores near the Pacific

shore explains the fact that *Pteropus* species are so common in this region. Most colonies of *Pteropus* in Malesia are situated near the sea, and when they are situated inland the animals travel every night to the sea, unless there is a more attractive crop in the interior.

Such a migration (for the sake of the fruits of *Fagraea fragrans*) has been described by CORNER (1940, p. 425).

I possess no data on migrations of other fruit-bats from S.-Asia. We know that *Cynopterus* was already numerous on Krakatau in 1919. In tropical America such migrations seem possible as they have already been described there for flower-bats (cf. VAN DER PIJL, 1956*b*). In Africa the bat *Eidolon helvum* (feeding partly on flower-nectar, partly on fruits) migrates over an unknown distance. Mr. J. B. Hall from Cape Coast (Gold Coast) wrote me on the periodical appearance (medio August—medio October) of large flocks when there was maximum fruiting in the extensive plantations of *Azadirachta indica*.

As has been set forth (VAN DER PIJL, 1956*b*) for flowers and nectar-bats, a stable association between plants and fruit-bats can be reached only when all the year round suitable fruits are available. This should be checked up on islands with a bat population that does not migrate.

BAKER and BAKER (1936) gave a dietary calendar for *Pteropus* in the New Hebrides. This is, however, not an analysis of a natural vegetation as but few wild plants, especially few from the seashore, are included. Many plants mentioned by them are introduced ones.

The plants mentioned in Table II are of old known as sea-dispersed by means of floating seeds or kernels, which partly explains their occurrence near the sea. They have, however, bonds both with the sea and with fruit bats, being diplochorous. We may say that their distant dispersal over larger stretches is brought about by sea currents, but their inland colonization by bats.

The question which mode of dispersal is the original one can be answered definitely that zoöchory developed first. Their taxonomic affinity with true zoöchores, as well as the presence of hard layers, as a primarily zoöchorous character, and the structure of their crown (cf. p. 305) favour this conception. One might be inclined to assume that transport by sea-currents would be one of the oldest forms of dispersal, but the fact that sea-dispersed plants form taxonomically a heterogenous group (cf. RIDLEY, p. 250) makes this very improbable. Pacific floras show few signs of speciation from immigrants arrived by sea. This stands somewhat in contrast to the opinion which GUPPY (1906, p. 134) brought forward, with regard to islands floras. He thought that in islands the littoral species would have given rise to part of the inland species or that both are of independant origin. According to him two thirds of the genera of beach plants would have no inland species at all. To this group he reckons even genera like *Vigna*, *Calophyllum*, *Morinda*, *Cordia*, *Ipomoea*, *Casuarina*, *Erythrina* and *Ochrosia*.

In *Hernandia* the loose, inflated calyx that is edible, is a most remarkable adaptation.

Ridley knew the bat-dispersal of *Terminalia catappa* and of *Calophyl-*

lum inophyllum and mentioned (p. 265) also *Ximenia* as diplochorous (birds and sea-currents).

It is, however, remarkable that the presence in our group of fruits provided with a fleshy cover that is thin, green and hard, but edible for bats, has as a rule been overlooked. Schimper mentioned it in 1891 in his classical study: "Die Indo-malayische Strandflora" (p. 75). He observed the regular disappearance of this layer before the fruits were dropped, but could not find any function for it.

GUPPY (1890, 1917), who paid in his classical researches so much attention to those seeds and their sea dispersal, only says (1890) that the *Morinda* fruit is eaten by sheep, deer and fowl. He ignores the fleshy calyx of *Hernandia*. For the group as a whole he thought that the fleshy covering was functionless and that there was only dispersal by sea, when the fleshy layer had decayed after the fall. In this way he explained the lack of the flesh in most of the floating fruits.

In his study of 1906 GUPPY (p. 122) pointed out that a number of sea-dispersed fruits still have bonds with birds. Though he described (p. 152) that a captive cassowary dispersed the externally juicy, large fruits of the undoubtedly diplochorous *Ochrosia parviflora*, he thought, that any other agency of dispersal but that of the sea currents was here out of the question. Strange as it sounds, he practically ignored the role of bats and expressed only some queer ideas, viz. (p. 321) that when visiting the flowers of *Freycinetia* they might carry off the seeds in their fur whilst brushing past a ripe-fruit-head, a misconception repeated (p. 343) in his remarks on *Metrosideros polymorpha*.

Some of the fruits for which he accepts only sea dispersal are very palatable, pure bat fruits, like *Mammea americana*, *Andira inermis* and *Chrysobalanus*.

I described (1936) the diplochory of some of these plants (*Terminalia*, *Morinda*, *Calophyllum*, *Hernandia*) after a visit to a small island in Street Sunda, where I saw actual dispersal by bats.

DOCTERS VAN LEEUWEN described these and other cases from Krakatau (*Cycas*, *Guettarda*, *Pandanus*, *Spondias* and probably *Ximenia*) in his important book on this island (1936). In Krakatau the quick inward spread of *Terminalia* after 1919, following the arrival of *Cynopterus* was very striking.

The diplochory of *Pandanus* is especially well expressed in the structure of its fruits. It has been clearly described and figured in the study of BROWN (1931) on the Marquesas. The basal part of the mesocarp is edible flesh containing pectine, sugar and starch (also eaten by man), whereas the apical part of the mesocarp forms the dry floating tissue. Brown even saw that in the shore species the floating part is dominant, whereas in inland species the fleshy part is better developed.

In the older literature the inland dispersal of such plants was often ascribed to crabs and rats, whose activity is mostly destructive, but may play a role (cf. Ridley). Introduced ruminants and pigs may also play a part.

3. *Pacific islands and fruit bats*

The conclusions arrived at in the preceding chapters can be checked up in Hawaii—a tropical island without fruit-bats. In the vegetative sphere it is tropical, but it has a biotically not completely tropical environment. At a former occasion (1936b) I already pointed to the scarcity of cauliflory in Hawaii.

Though the total number of indigenes is limited, so that the value of negative finds should not be over-estimated, it is nevertheless remarkable that the Hawaiians had not developed a single table fruit that is native to the region. Their famous *Eugenia malaccensis* is an introduced species. There are no large fruits edible for man in the islands. Of the diplochores discussed in chapter E. *Morinda* is mentioned as growing spontaneously only near the sea. How the spontaneous dispersal of the inland *Pandanus* species takes place is not clear.

The S.-Polynesian region too has no or but few fruits edible for man, and has no fruit-bats.

This becomes the more clear by the simultaneous disappearance of the fruit-pigeons, which obscure the issue elsewhere in many large seeded species of *Sterculia*, *Elaeocarpus*, *Myristica*, *Canarium*, *Sideroxylon*.

It seems attractive to look for a further relation between the eastern limits of resp. the *Megachiroptera* in the Pacific (see map) and the chiropterochorous plants in the islands—just as I did (1956b) for bat flowers.

The area of the *Pteropinae*, especially of the genus *Pteropus*, is wider than that of the nectar-bats belonging to the *Macroglossinae*. The latter area agrees fairly well with the tropical part of the generally accepted ancient continental boundary.

It is not satisfactory to consider the distribution only statically, i.e. as a remnant of old continental boundaries. For the *Macroglossinae* such a static concept might still seem more or less acceptable, as their presence is firmly connected with that of specific flowers (and vice-versa), so that colonization is, despite their capacity of flight, only imaginable together with that of the plant species they rely on for food. Moreover, there is no information, even from tropical continents, with regard to any migratory capacity of these flower-bats. In this regard they differ from the American flower-bats, the nectarivorous *Microchiroptera*, which do migrate and surpass the limits of the tropics (cf. VAN DER PIJL, 1956b).

For the *Pteropinae* a more dynamic view is indicated. Migrations are known for the genus *Pteropus*, not only over land but also over the sea. In this way the genus seems in Australia to have surpassed the limits of the tropics.

This partly temporary, partly permanent, expansion is facilitated by the adaptability of these fruit-bats, viz. their change to some non-tropical fruits and to the squashing of subtropical flowerers (cf. RATCLIFFE 1931). Moreover, (and this refers to the eastward expansion of the area), *Pteropus* could follow an eastward migration of those

food-plants whose seeds were not only spread by it, but also by sea-currents.

The genus *Ficus* becomes less and less dominant towards the East and only some small-fruited (ornithochorous) species reach the Polynesian Islands. In Tonga and Fidji (within the limit) there are still cauliflorous species. The group of typical cauliflorous species found in Malesia (*F. fistulosa*, *F. glomerata*, *F. miquelli*, *F. variegata*) remain (as Dr. Corner kindly wrote me) west of the line Formosa, Philippines, N. Guinea, North Queensland.

Of course the distribution of *Ficus* is also influenced by the distribution of the gall-insects, and this might even be the most limiting factor.

The existence of the whole family it belongs to (*Moraceae*) is narrowly linked with that of the fruit bats as demonstrated in the table. Its other large genus, *Artocarpus*, seems also to be limited in its distribution in this way. The breadfruit is everywhere one of the best liked foods of the fruit bats. Though wild forms are abundant in Malesia and the genus is essentially Melanesian, it is sometimes considered to be native to Polynesia, where it forms one of the main foods of man. Apart from other arguments this seems improbable because of the absence of fruit-bats in the region.

For *Musa Fehi*, so popular in Hawaii and Tahiti, the same holds true.

The genus *Spondias* and the whole tribe of the *Spondieae*, with representatives in Asia and America, is markedly chiropterochorous. *Spondias dulcis*, so popular in Tahiti and known as Polynesian plum or Tahiti-apple, is probably introduced in early times or may have come there by sea-currents from Malesia; it has no means of dispersal on land outside the bat area.

The same relates to *Inocarpus edulis*, the Tahitian Chestnut.

The exposition given by DRAKE DEL CASTILLO (1893) creates the impression that *Spondias*, *Inocarpus* and other diplochores have spread spontaneously into the interior of Tahiti, and are maintaining themselves there. This seems strange, the more as later authors as Setchell and Merrill denied that these plants are native to Polynesia. Therefore I was glad to receive information on this point from Mr. J. Lehaire (Service de l'Agriculture of Tahiti). Apart from dispersal by water, *Spondias*, *Inocarpus*, *Hernandia peltata* and *Terminalia catappa* do not grow and spread spontaneously in the interior. Their eventual presence there is always due to human agency.

To the contrary a number of chiropterochores, including *Spondias dulcis*, seem to be indigenous or at least to be spread spontaneously in Tonga, Samoa and Fiji, which are inside the area of the fruit bats. Many representatives, especially of the diplochores, live in Guam, which is also inside this area. It may be said that typically bat-linked taxa with few adaptations to other disseminators, show a decrease towards the boundary-line.

The occurrence of fruit-bats, which itself, of course, depends on historico-geographical factors, is at the present time still a factor

of importance in the maintainance and change of phytogeographical boundaries in the Pacific. The often mentioned decrease in number of large-seeded plants towards the East is usually interpreted as a consequence of the absence or inadequacy of land bridges. Besides the fruit-pigeons the fruit-bats may be the main realisers in this connection.

I refer here to the study of SMITH (1955), where the chiropterochorous *Cynometra cauliflora* is mentioned as one of the *Leguminosae* and *Polyalthia* as one of the *Annonaceae* terminating in Fiji.

For the geographical relations between certain flowers and nectarivorous bats I gave (1956b) some considerations in the same direction. The chiropterophilous genus *Sonneratia* was mentioned there as remaining within the area of the *Macroglossinae*.

As we dispose here of a map I can elaborate this point in one detail, viz. their curious common limit above the deep trough between the Carolines and the Mariannes. This line does not correspond with clear edaphic or climatic differences or with different possibilities in the seed dispersal of *Sonneratia*. The extension into the Carolines seems strange when we see that many zoögeographers consider the Carolines as oceanic islands, outside the ancient continent. The occurrence of macroglossine bats, however, together with native plants from the chiropterophilous genera *Sonneratia*, *Parkia* and *Musa* suggests that these islands may be continental. It is therefore, interesting that other zoögeographers leave the possibility open, that the scarcity of insects, one of the main arguments for the oceanic character, may be secondary and due to the small size of the islands.

Geological evidence shows that the Carolines West of Truk lie within the andesite-line, and may belong to the ancient Australasian continent. The eastern islands (Ponape and Kusaie) were in this connection seen as probably formed near the continental line in eocene times, and may then in early times have obtained continental plants and animals.

An other supposed geological boundary, the sial-line (cf. STEARNS, 1945) lies a little east of the andesite-line and includes all the Carolines.

The occurrence of *Sonneratia* on Iriomote (Riu Kiu Islands), outside the *Macroglossus* area, remains to be investigated. Do we find there a settled community or a loose collection of sterile immigrants?

E. THE STAMP OF THE BAT ON TROPICAL TABLE FRUITS

A short side trip into the field of human relations may be allowed here.

A visit to a tropical fruit stall results in an impression entirely different from the one in a temperate country. Instead of coloured fruits like berries and cherries, that are naturally ornithochorous, one sees there greenish and brownish fruits, that are in nature chiropterochorous. Fruits of *Mangifera*, *Achras*, *Psidium*, *Annona*, *Spondias*, *Artocarpus*, *Musa*, *Lansium*, *Baccaurea*, *Bouea*, *Dracontomelum*, *Stelecho-carpus*, *Diospyros*, *Phyllanthus*, *Mammea*, *Persea*, *Cynometra*, *Detarium*, *Averrhoa*, *Aegle*, *Feronia* and *Manilkara* may be quoted as examples.

Colour pictures of fruits from "the colourful tropics" mostly give a false impression by giving undue preference to the few edible ornithochorous fruits, like *Capsicum* and some *Eugenia* species, to non-tropical tangerines and tomatoes and to the exceptional case (of an ecologically questionable character) of *Nephelium*.

Instead of emitting the fresh scent of strawberries, apples, plums, melons and other fruits "designed" for ordinary mammals, it reeks (with the exception of pine-apples) faintly or strongly unfresh.

The stamp of the bat!

This is very typical in the semi-wild *Mangifera foetida*.

We find a rather primitive condition in many tropical fruits; they are but little improved compared to their wild ancestors—this in contrast to European edible fruits that have far outgrown their forefathers. Nevertheless tropical table fruits are strikingly large. Tropical man could base his fruit menu on large bat-fruits, that were already present in a serviceable form.

Europeans new to the tropics, have to leave behind their accustomed preferences and to follow the taste of bats, though in the cultivated forms of, for instance, the manggo and the banana this taste is not, what it used to be in native species, which smell too strongly. Even in the smell of *Psidium*, *Achras*, *Annona*, *Spondias* and tropical *Diospyros* species something has to be overcome at first, not to speak of *Artocarpus champeden* and *A. integra*. The durian and the mangosteen may remain outside our present discussion, as they are suited respectively for elephants and monkeys. No wonder the newcomer starts to prefer a mangosteen, to finish his career with *Artocarpus*, *Durio*, *Morinda* and a semi-wild manggo.

The bat may even be the solution to some of the "witchcraft and mysteries of the East". The explanation of the mysterious "spitting of beteljuice" on a set table may often be simple when we have an open window, a gutter with bats alighting on it and a red fruited *Ficus* in the neighbourhood.

The not less notorious "stone-throwing" when no outsider can be made responsible, can often be explained in the same way, when the "stones" are kernels of *Spondias* or of *Elaeocarpus*. When the "stones" are said to fall vertically through an undamaged roof it is time to look at the beams for bats.

Fruit-bats have long been known as important to mankind, being a pest to fruit-trees. The damage done by them is immeasurable (cf. RATCLIFFE, 1931). Accurate knowledge of the food of fruit-bats has also become important since we know that a bat population may be a reservoir of pathogenous microbes and viri. Direct transmission regularly occurs in America by bites of bats whose diet consists partly of fruits. It seems worth while giving more attention to the question whether a virus may be transmitted by means of fruits. Fruits on tropical markets often show imprints of bats' dentures, obviously from trial-bites.

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