ECOLOGICAL ASPECTS OF FLOWER EVOLUTION.
II. ZOOPHILOUS FLOWER CLASSES

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For a century botanists have tried to construct schemes to classify flowers apart from taxonomy. As quite a number of parameters (forms, diverse functions, visitors) had to be reckoned with, all the systems are more or less one-sided.

Werth (1915, 1956) objected to the vagueness of Delpino's ecological classes (according to pollinators), which "only comprise the extremes" and pointed to their structural diversity. He therefore promoted the use of structural types (Bautypen) of a supposed autonomous, morphological nature and showed the emerging of higher types during geological periods.

What is pure form to one man is, however, crystallized function to another. The structural types are not independent of pollination, as shown above (cf. Leppik), and as admitted incidentally by Werth.

The exclusive use of "morphological" types, according to the way of pollen deposition, splits natural entities and leaves some clear and natural ecological classes in the cold. Therefore, Werth has to discuss hydrophiles, anemophiles, pollen flowers, saprophyophilous traps, etc., separately in a large part of the book. The convergence in saprophyophilous flowers is ascribed (p. 92, 123) to "einem zielgerichteten Schöpfungswillen" (finalistic creation).

Here I will try to revive interest in the classes according to the visitors—classes with bad boundaries, but with a clear center, foci of differentiation in different substrata but leading to convergence, a style. Acquaintance with them may shed light on evolutionary processes in the past and peculiar forms in the present. I shall, of course, not try to give a complete review but shall make a selection in the direction of dynamics.


Canthanaphily (Pollination by Beetles)

The main points (mostly negative) have been discussed already: often pollen or food bodies or traps for attraction; nectar (when present) open; few optical attractions; no special shape; no depth effect; no nectar-guides; the strong odor sometimes fruity, sometimes aminoid. Sometimes we find large single flowers (class 5 of Delpino), sometimes cylindric or flat complexes of small flowers fit for poor flyers (class 6 of Delpino).

Jaeger (1957) wrote in his review (p. 394), obviously acquainted with European mixed cases only: "There are no beetle flowers." One might rather say: The flower is fundamentally a beetle flower and many have remained so or have become so.

We may dispute whether in the canthanaphilous flower-complexes of Cornus, Spiraea, Viburnum, Sambucus, Umbelliferae, Proteaceae, etc., the canthanaphily is primary or secondary. That flies are often found on them is no wonder—as I said before.

The flat complex of Compositae, dating from early Cretaceous, later became ecologically backward, but is now in progress. Some of them (Brachyglossitis-Adenocystis-Cenia and Wyethia species and many others in South Africa), and to a lesser degree Tanacetum and Achillea are still canthanaphilous. Vogel (1959) paid little attention to beetles (no Stil?) but said (p. 77) that beetles are important on the masses of annual Compositae in South Africa.

In some Proteaceae we also find open complexes with beetles (Leucadendron decorum, Protea scolymocephala and Pr. mundtii, all more or less canthanaphilous according to Marloth (1913–1925).

In New Zealand, beetles (together with flies) are the dominant flower insects, as
described by Thomson (1927) and Heine (1938). There may be depauperization as well as primitivity in this condition.

Dr. Grant wrote me that in California all *Calochortus* species, all Cactaceae, *Escholtzia* and some other Papaveraceae and some *Rosa* spp. are pollinated by Nitidulidae and Melyridae. *Cuscuta* there is also beetle-pollinated (weevils).

A promising field exists in the tropics for studies of beetle pollination.

**Sapromyophily (Pollination by Carrion and Dung Flies)**

A general class of fly-flowers would be poorly distinguished as some of the higher Diptera are as specialized as the Apidae. I should like to consider the flies that are not eutropous pollinators and have coprophilous tendencies. Though this group is very heterogeneous, with transitions to flower preference, it seems to have evoked the origin of a distinct flower class. It is now a peripheral, convergent group of the most divergent taxonomic origins. Just as in beetle-traps the connection with allotropic flies still means irregular pollination. I have found strong variations in the numbers of visitors, apparently dependent on the presence of breeding-substrata for the flies.

The ecological, recent nature of sapromyophilous adaptations is especially clear in the orchids. There an organization built strictly for bee pollination had to use the strangest detours and reorganizations (to be described below) to make the flowers fit to deceive much lower pollinators.

In the Asclepiadaceae there exists, perhaps, some bond with a pre-existing or even persistent organization fitted for flies, since here the sapromyophilous type occurs in many different genera. Good presents this as “autonomous repetition.” He even points to the “repetition” of such character combinations inside this family in the Araceae and in *Aristolochia*—where they represent sapromyophilous characters and are clearly parallel adaptations.

The angiospermous families strongly affected by sapromyophily are: Asclepiadae, Aristolochiaceae, Sterculiaceae, Rafflesiaceae, Hydnoraceae, in the Monocotyledons the Taccaceae, Araceae, Burmanniaceae, and, of course, the versatile Orchidaceae as a regression. For the curious case of *Theobroma* (pollinated by a *Forcipomyia*) see Soetardi (1950) and Posnette (1950).

It is curious and perhaps a mark against myophily as generally primitive that in the Ranales sapromyophilous flowers are rare. Perhaps cadavers and dung (of reptiles) and also ancestral flies were different. Some Annonaceae show it: thus species of *Polyalthia*, *Sapranthus*, *Asimina*, and *Duguetia* (see also *Mitrephora*, discussed below). The primitive lantern-construction (see below) of some annonaceous flowers points perhaps to a more general trap design for beetles and non-coprophilous flies. See also the lantern-type of *Hydnora* in Vogel (1954, pp. 78, 191).

In the Rafflesiaceae, Hydnoraceae, and Aristolochiaceae the trapping of flies and beetles may nevertheless perhaps be used as a flower-ecological aspect to confirm the bonds with ancestral Ranales. In the Araceae too fly-flowers are often separated only vaguely from beetle-flowers.

The differential characteristics of this class as shown by comparative morphological study (cf. van der Pijl, 1953, and Vogel, 1954) are: (1) radial shape without nectar-guide; (2) purple-brown or greenish color; (3) often no food, sometimes open nectar or pseudo-nectaries; (4) transparent parts to be designated as light windows; (5) smell of decaying substances; (6) often lantern type by fusion of petal tips, with lateral apertures between, to be designated as “slits”; (7) in traps a ventricose lower part (“kettle”) with arresting devices; (8) mobile appendages, the “Flimmerkörper” of Vogel, or fluttering petals; (9) filiform appendages, the so-called “tails.”

Any “Ausnutzung” (incidental utilization) of loose characters, though probable in the initial phases, is out of question for most cases. The syndrome is strongly correlated and the elaborative development well di-
rected. The type described as "Ekeibliiten" in Europe is mostly but a poor shadow.

The morphological nature of one character, the "tails," varies from case to case. We find: sterile bracts (Tacca), petal tips (Theobroma, Trichosacme, Cypripedium spp.), calyx- or perigone-tips (Aristolochia, Masdevallia, Sterculia), spathe tips (Arisaema spp.), appendix tip (Arisaema spp.). See Troll (1928) and van der Pijl (1953).

The strong convergence has struck many early authors. Goebel explained the lantern-construction as due merely to an arrest in bud-development and ridiculed the tails. Troll (1928) thought that this criticism and some incomplete experiments (mentioned before) had done away with any ecological explanation. It was all "Gestalt." He originally admitted significance for the odor (which he obviously could not place in his "Gestalt") and later for the light-windows.

The improbability of "Gestalt" becomes more obvious when we see that entirely different organs having connections with flies, like the pitcher-leaves of insectivorous plants, have the same convergent adaptations. Hallier (1897, p. 752) already pointed to this convergence, even in coprophilous and fly-dispersed mosses (Splachnum) and the fruit-bodies of Phallineae like Dictyophora. Vogel (p. 33), though refuting such likenesses as just "Ausnutzung" and recognizing the ecological significance, maintained it as "Stil."

The predominance of myophily in African desert plants is striking. In those regions flies are important. It is, however, also striking that in the Cactaceae there is no clear old or present fly-phase. Is this a consequence of differences in the fauna or structure or phase?

In sapromyophilous orchids like Bulbophyllum, Cypripedium, and Pterostylis the refined traps with irritability and a catapulting labellum, etc., are not to be considered as just catching traps comparable with Aristolochia, but as devices to guide unintelligent flies to the stigma of a precision flower. Sargent (1909) gave a fine analysis of Pterostylis and Werth (1956, pp. 81–92) also discussed this wonderful flower. Some orchids, like Stanhopea, even force bees (Euglossa) in this way (Pohl, 1927). In such traps there is no protogyny and no long imprisonment.

In these orchids the labellum has lost its original function. In Masdevallia it has mostly become functionless; here we have a flower returned to the radial shape of some Aristolochia species, often even with sympetaly.

A digression for taxonomists: Is the orchid Cryptophoranthus, otherwise a Masdevallia, to be considered as a separate genus just on account of its queer fused sepals? The answer seems to be no. The lantern of this fly-flower lies within the range of the syndrome, so well represented in Masdevallia.

The same relates to Cirrhopetalum as apart from Bulbophyllum. Its tails, fringes, slits between fused petals, its return to radial inflorescences, are just further myophilous refinements. This seems morphology in the making—just as in the beetle- and fly-era millions of years ago.

In some groups the general myophilous complex seems already suprageneric, though there is also narrow specialization. It is curious that in the orchids ecological barriers replace the sterility barriers so weakly developed here. The strong speciation in polymorphous giant genera like Cypripedium sens. lat., Masdevallia, Bulbophyllum and related genera may be correlated with a strong specificity of odors and of pollinators. The same may be true in the large genus Pterostylis, where each species has its own dipteran (Sargent, 1909). The convergence of this orchid with some Araceae is extremely striking; along with the case of Masdevallia—Aristolochia this is a warning against "Bautypen."

One more instance of the importance of ecological insight for taxonomists may be added to what has been said already on the Annonaceae. The instance is drawn from the study of Sinclair (1955). His figure 4 shows a nice range of development in the
direction of the lantern-flower of Mitrephorae. The functional aspect of these traps for beetles and flies is left aside. The coloring of some Pseuduvaria and Mitrephorae flowers, however, suggests sapromyophily. The early basal sympetaly of some species (of Papualthia, Hexalobus, Cardiopetalum, etc.), leading to a “kettle,” might be added to the picture. The strong convergence to Aristolochia, Ceropegia, and some Sterculiaceae then becomes interesting.

**Melittophilous Subclasses**  
(Pollination by Bees)

We have already discussed bee-flowers in general. The Papilionaceae, Labiatae, and Orchidaceae bear the imprint of the hymenoptera distinctly in their lack of red; in the frequency of color contrasts; their intricate, closed, zygomorphic flowers; the scarce nectar (hidden, but not deeply); the nectar-guide; and the alighting place.

To return to Darwin and his classical red clover, a trifling change has indeed appeared to be important in the switching over from Bombus to Apis. Modern races of the honey bee with slightly longer mouthparts are nowadays rather frequent on Trifolium pratense in Europe. In New Zealand too the introduced Bombus is no longer the all-important pollinator. Apis now pollinates 90% of the flowers there, perhaps for the same reason (Forster and Hadfield, 1958).

Vogel (1954, p. 44) confirmed for South Africa the class with micromelittophily, abundant in the heathes and savannas. The small flowers stand on stiff filiform stalks spreading horizontally. They remain hidden between the low vegetation but vibrate easily and seem in this way to attract small Hymenoptera in this biotope.

A contrasting group is that of the bumblebee flowers. As a later specialization with quantitative refinement of heterogenous forms they are morphologically badly demarcated. An extreme of this group are the tropical flowers more or less exclusively pollinated by Xylocopa spp., the big and rude carpenter bees, that make boreholes in wood with their strong mouthparts.

I found (1954) many instances among orchids and some large-flowered Papilionaceae (Canavalia, etc.). Besides the characteristics of very large nototribe bee-flowers we find firstly an extra strong lock-out, with mechanical reinforcement of the alighting place. In the Papilionaceae the latter feature is furnished by the resupinate thick standard. The significance of this specialization has been proved experimentally. The flowers obtain a striking convergence with the large Labiatae. This demonstrates that a “Fahnenblume” can easily be transformed into a “Rachenblume,” and that the morphological types are not as primary as Werth thinks.

Burkart (1937) described the opposite case, where a usually nototribe labiate changed into a sternotribe, explosive “Fahnenblume” imitating a member of the Papilionaceae.

The wonderful flower of Thunbergia grandiflora is narrowly adapted to the largest Xylocopas. Its extra-floral nectaries lure masses of ants, guiding them to the flower base. The flower is never visited by other insects and never robbed. In some Ipomoea spp. I could prove experimentally the protective value of the ant-guard against robbing.

The carpenter bees puncture the less adapted flowers easily, even more than Bombus does in Europe. This dangerous side-effect is, however, balanced in the adapted tropical flowers, sometimes by the ant-patrol, sometimes by mechanical reinforcement of the flower base. I point to this specially because of Melin’s remarks that selection has produced no protection against puncturing by hummingbirds. The situation involving Bombus in Europe is evidently still unbalanced.

**Sphingophilous (Pollination by Hawkmoths)**

The characteristics of the flowers are correlated with those of the Sphingidae. The plate of Vogel (1954, pl. III) shows this.
Odor heavy-sweet; color whitish or absent (green); form not necessarily zygomorphic; mostly with narrow tube or spur; rim often turned back, no place for alighting; nectar abundant; anthesis nocturnal; anthers often movable; deep dissection. The type is less frequent outside the tropics.

The odor is quite typical and seems to act directly, not just as a signal based on experience, whereas it is not interesting for other insects.

Though the type develops most easily in higher sympetalous families, it is found in a single Ranalian and frequently in Cactaceae and Capparidaceae. The differentiation in most families seems peripheral, mostly intrageneric, also in orchidaceous genera, perhaps deeper in the Cactaceae.

Sphingophily is essential in Capparidaceae, where it seems to have put a general stamp on the flowers, though there are many deviations. A simple, radial pollen-flower of the Papaver-type has become a nocturnal brush-flower with nectar and long filaments, fitted for sphingids (Capparis). Its stigma had to be brought into the outer, sexual plane. As the formation of a style seems to have encountered difficulties in this family with sessile commissural stigmas, the entire pistil was elevated by a gynophore. As demonstrated by Stebbins (1950, pp. 503–510) this single ecologism may have brought about reorganization by means of selection. The first change became a central family character. In more advanced types, like Cadaba, the stamens too were elevated and the petals turned upwards. The handicaps of the absence of a flower tube and the presence of basal nectar accessible to all insects were overcome by the development of long tubular nectaries. I believe that the stiped ovary in this group does not have a merely protective function (Grant, 1950a).

Good (p. 349, 552) found “senseless repetition” of this syndrome in Isotoma (Lobeliaceae), Clerodendron (Verbenaceae), Saponaria, Silene, Phlox. Of course the repetition is due to convergence.

Miscellaneous Pollination Classes

In phalenophily (pollination by small moths) the floral characters are like those in the preceding class but are less conspicuous in color and length.

With regard to psychophily (pollination by butterflies), plate II of Vogel (1954) shows the characters of this class. In his table of differential characteristics (p. 38–39) we find: (1) colors diverse, including, however, the scarlet of non-ornithophilous European flowers; (2) nectar-guide; (3) long narrow tube or spur with a flat wide margin; (4) margin not deeply dissected; (5) agreeable odor; (6) diurnal; (7) tender tissues.

Myrmecophily (pollination by ants), malacophily (by snails), and batrachophily (by frogs) are dubious classes, probably to be considered as outdated. I gave reasons for this in regard to ant pollination, considering the published cases as incidental (van der Pijl, 1955, p. 191). The batrachophily of the orchid Lisschilus roseus in Morocco sounds questionable (Guinea, 1946, read in abstract only). I have described cases where a frog (Rhacophorus) was regularly found on Alocasia inflorescences and a lizard (Hemidactylis) on Artocarpus inflorescences (van der Pijl, 1933, 1953). D'Ewes (1959) reported an “arum-frog” (Hyperolius horstocki) as a regular visitor to Zantedeschia. In all these cases the vertebrates were seeking insect visitors in the flowers.

Ornithophily (Pollination by Birds)

A long-lasting battle since the 1920's has led to the general recognition of ornithophily as a class (cf. Werth, 1915). The work of Porsch (1923, 1933, etc.) was largely responsible for this. Melin's book (1935) was a belated regression by a writing-desk critic with an interest in marginal, not harmonious relations. Vogel (1954), though anti-selectionistic himself, criticized Melin’s negativism extensively. The interest in demarcation and classification shall here be replaced by more positive elements.

Ornithophily has originated independently on different, older, eco-morphological
substrata. So the class has differently constructed flowers, a situation which has been used by Melin and Werth, followed by Kugler, to belittle its existence as a class. It is rare in the lower families, though appearing in Capparidaceae, Cactaceae, Proteaceae, etc., but is widespread in tropical Leguminosae and Tubiflorae. We can follow its emergence in groups with recent speciation, whereas it is supraspecific in other groups.

The adaptations in the birds also arose parallel in many groups and in many ways, perhaps via simple quenching of thirst in arid zones, via destructive eating of flowers, or via the catching of insects, even through boring for insects in tissues accompanied by a flow of sap. As to the latter I refer to some woodpeckers like the Asiatic Dryobates analis (Spennemann, 1932; Cammerloher, 1928; Docters van Leeuwen, 1931).

In regard to the catching of insects in flowers, it is necessary to remark that this is a rare exception, though the old stories about it are still repeated. Melin upholds (p. 104) the opinion, impossible to any real observer, that hummingbirds are not dependent on the nectar of flowers.

In a sense the flower birds have not become as narrow flower-animals as some bats (the Macroglossinae). The birds cover their needs of protein outside the flower. Data on pollen consumption are rare. Melin collected some old ones (pp. 76, 172, 196).

There exist, as already discussed, many transitional flower forms, interesting from an evolutionary viewpoint. Spennemann (1932) and others described cases where frugivorous birds are semidystrophic, plucking off flowerparts. In some instances unadapted birds are legitimate visitors and instrumental in pollination, when solid foodbodies are offered, whereas the sexual organs are protected. Porsch (1923) described how in Freycinetia funicularis edible bracts were eaten by bulbuls. The most curious one is the Boerlagiodendron (Osmoxylon) mentioned by Beccari (1877, p. 194), as attracting pigeons as pollinators by means of false fruits between the flowers. Lam (1945, p. 75) described the phases of false and true fruit-formation.

The old, often-repeated instance of edible petals in Feijoa (Orthostemon) has now to be discarded. Werth (1943a) reduced it to ordinary ornithophily with nectar. Schroeder (1947) even showed that it is a bee-flower. The still more famous case of Marcgravia is discussed below.

According to Melin a bird visits a certain flower “attracted” by some character which is present only incidentally. He cited many incidental visits to apparently non-adapted flowers—which seems not astonishing. Singh (1933) also recorded such visits as to the fragrant Morinda tinctoria, but was mistaken in thinking that scent might help; he also considered Strelitzia and other bird-flowers as not adapted for birds.

I might add many more instances like this, as of brooding sunbirds visiting flowers in the neighborhood which they otherwise neglect (van der Pijl, 1950, p. 147). Usually, however, the better adapted flowers are chosen by birds. In this context it should be related that though these birds show no flower constancy there is surely competition for birds between different flower species. Sometimes a much-visited species is left when another starts flowering. Docters van Leeuwen (1933, p. 102) described how a sunbird visited all kinds of flowers in the summit region of a volcano, in open competition with insects.

The excluding nature of some of the characters, giving the final touch to the syndrome, is especially clear in the oblique profile of some Cactaceae and in some Labiatae, which do away with their underlip in different ways. Docters van Leeuwen (1938) pointed to the shrivelled lip of Leonotis. I could demonstrate (1950, p. 150) how a bumblebee could, with some difficulty, still manage some intermediately ornithophilous Salvia spp., but not the well-adapted S. splendens.

The full syndrome of characters, as already stated by Porsch, Werth, and even by Delpino, is (in accordance with the physiology of birds): (1) diurnal anthesis; (2)
odorless; (3) visual flower with vivid colors, often scarlet or with contrasting parrot-colors; (4) honeyguide absent or simple; (5) rather deep nectar in large quantity; (6) reduction of corolla margin, leading to tubular corollas, even in Choripetalae; often brush type; (7) mechanical strengthening by fusion of flowerparts or by mechanical tissue; (8) often capillary systems for the nectar.

I could clearly demonstrate (1937b) a differential diagnostic character between American and Old-World bird flowers, already indicated before by Delpino (1875) and Porsch (1934) and others. In accordance with the different approach by their visitors (resp. hovering and sitting) there is a difference in position and perching possibility. The exceptional American plant with a perch (Puya) was again described by Gourlay (1952) as pollinated by exceptional birds. Vogel (1954, p. 44) denied this geographical difference, using my conclusion in the opposite sense. Disharmony of American plants in Java was answered by puncturing. Short-billed hummingbirds do so with more Andine bird-flowers.

Puncturing by birds is a dangerous side-effect of a labile interrelationship. Swynnerton (1915-1917) described it for plants in South Africa where sunbirds had no sufficient perch. There seems to be much puncturing by short-billed birds in the large-flowered Sesbania grandiflora (Tiwary, 1927). The general puncturing of Hibiscus rosa-sinensis (cf. Swynnerton, 1915-1917, and van der Pijl, 1937b) is mysterious if the plant is indigenous in the Old World. Werth relates in a chapter on ornithophily, full of long disproven conclusions, that a sunbird visited its flowers while hovering before them (1956, p. 132).

The dominance of scarlet flowers in ornithophiles and therefore in ornithophilous floras, has often been attacked as unreal. Melin did this, but his own table 1 A proves it statistically. Weevers (1951) thought he had disproven the phenomenon by statistical comparisons, but these seem too coarse, putting all shades of pink and red together and leaving out figures from Central America and the Andes. Pickins (1955) also gave a statistical elaboration on this point.

Good (p. 328) considered the queer color combination of yellow and red in many flowers as autonomous repetition. Needless to say, all his instances are bird-flowers, as is his pair Antholyza-Leonotis (p. 351).

When studying diversification in groups with growing ornithophilous tendencies, taxonomists should keep the co-adaptive syndrome in mind and not only consider the separate characters independently. Taxonomists analyzing the characters of a group statistically in the way recommended by Sporne and finding some correlation should not neglect the existence of such “adaptive peaks” of an ecological nature (cf. Stebbins, 1951).

We can follow the evolution of the syndrome in many families, as Porsch (1937) did for the Cactaceae. Ornithophily became dominant in the Andine genera, viz. in the suprageneric group of Loxanthocerei, where first a tube, later zygomorphy and reduction of ventral flower parts developed. Vogel pointed to the contrast of Cactaceae with the succulent Asclepiadaceae, where the pre-existing organization apparently did not lend itself to ornithophilous reconstruction. In the Andes even the Compositae have reached ornithophilically in Mutisia spp. which hang down like a Fuchsia.

The long-tubed, red Salvia splendens with reduced lower lip from the Andes is a nice contrast with blue temperate Salvias (bumblebee flowers), making another sudden change in organization type. This is still more obvious in andine Scutellaria spp. There is not enough space here to follow the reorganizations in tubiform choripetalous Malvaceae, or the improvising of tubes from flowerparts in Cuphea, Cadaba, Tropaeolum, Fuchsia, etc.

Grant (1950a) made the suggestion that the strong staminal tube of Papilionaceae might be a protective relic-condition of a formerly more completely ornithophilous, tropical family. The symmetry pleads against birds. A decision is difficult as the
family is old and we do not know the time of appearance of regular flower-birds. I made parallel suggestions as to its tropical origin, based on extrafloral nectaries near the flowers (1954) and on the testa of its seeds (1956a).

It is known that in the Loranthaceae the tribe Loranthoideae is strongly ornithophilous. Docters van Leeuwen (1954) collected many data and personal observations from Java, also on the curious Dicaeid birds which show double adaptation to the plants, viz. as pollinators and as seed-dispersers with specialized stomachs.

CHIROPTEROPHILY (POLLENATION BY BATS)

There are old, incidental observations on bats as flower visitors. Firstly Burck (1892) in Java saw fruit-eating bats visit the inflorescence of Freycinetia insignis, well adapted to them, in contrast to ornithophilous sister species (confirmed by van der Pijl, 1956b). Hart (published by Knuth 1897) saw bats on the flowers of Bauhinia megalandra and Eperua falcata in Trinidad, Cleghorn (1922) on Bassia latifolia in India, Heide (1927) on Markhamia stipulata and Kigelia in Java, Danser (1929) on Parkia in Java.

Since 1922 Porsch has been the prophet of chiropterophily as a flower class; he predicted its characters, pointed to many possible instances and published the first purposefully investigated case (of Crescentia) in 1931. He compiled afterwards (1934, 1935, 1936) many data on the subject, adding deductions on such Cactaceae as Carnegiea (1939), later more or less confirmed by Allen's observations on some "Cereus" and by the finding of its pollen in the stomach of the bat Leptonycteris nivalis.

The present author published some preliminary notes followed in 1936 by an extensive monograph in German, adding and ascertaining many instances (species of Agave, Musa, Adansonia, Ceiba, Durio, Sonneratia, Madhuca, Parmentiera, Oroxylum, and Gossampinus. Later additions were Mucuna spp. (1941) and Duabanga and Haplophragma spp. (1956b).

Vogel (1954) added as a possible case for South Africa Ipomoea albivenia and later (1958) in a surprisingly rich paper on South America added species of Enallagma, Trianaea, Drymonia, Campanea, Symbolanthus, Cobaea, Cayaponia, Cleome, Chelonanthus, Macrocarpaea, and Purpurella. It is most interesting that the famous "ornithophilous" Marcgravia species here proved to be chiropterophilous. Some instances are based on deductions, others on direct observations.

Jaeger (1954) gave a review of the field in French and added further details on Ceiba, also on Adansonia in its natural habitat, Africa.

The characters of the main class, where pollen and nectar are eaten, are in accordance with the physiology of the bats in question. Bats are color-blind, have a good sense of vision and smell and a less well-developed sonar-system. The colors of the flowers deserve experimental research. According to Vogel (1958) they are functionless and just "Stil." He bases this on the same arguments Melin used against the colors of bird-flowers.

The syndrome is: (1) nocturnal anthesis; (2) whitish or drab colors, sometimes pink or dark-reddish; (3) large and strong flowers or inflorescences; (4) exceedingly large quantities of nectar, up to 15 cc; (5) unfresh smell, reminiscent of fermentation; (6) large quantities of pollen (large or many anthers); (7) a peculiar position outside the foliage, enabling bats to alight and depart easily.

The position of the flower often takes the form of cauliflory or flagelliflory (penduflory), with the flowers dangling on long slack stalks. (A few ornithophiles also show some flagelliflory.) A pincushion-type, with projecting flower-stalks, also occurs. The "pagoda-tree" of Bombacaceae (cf. van der Pijl, 1957, p. 360) is also a favorable "bat structure."

The typical claw marks of the thumbnails on the flowers betray the nightly visits of bats.
The bats involved are all tropical though some migrate to the southern U.S.A.

In the Old World we meet with the Megachiroptera, known as fossils since the Eocene (Monte Bolca). The most primitive forms are the Pteropinae, true fruit-eaters. A more specialized group, the Macroglossinae, reduced in size, feeds on nectar and pollen only and has rudimentary teeth (except for the canines) and a very long tongue.

In the New World Megachiroptera belonging to the subfamily Glossophaginae evolved independently into fruit-eaters, and some more or less into nectar-eaters. This must have occurred more recently.

We may suppose that Pteropinae first acted on flowers as destructive eaters. An apparently recently immigrated *Pteropus* in Australia feeds on *Eucalyptus* flowers and already shows signs of degeneration of the teeth (Rathcliffe, 1931). In Java I found *Durio* flowers squashed by bats and this happens more in regions to the east (*Melaleuca, Eugenia*). Being also fond of bleeding sap (fermenting or not) *Pteropus* can incidentally lap up nectar, leaving the flowers intact and pollinating them, as reported by McCann (1931, 1934) for ornithophilous species of *Grevillea* and *Bombax*.

The smaller Asiatic fruit-bats of the genus *Cynopterus* behave in the same way but are more apt to become incidental pollinators (McCann, 1931, Hanelt, 1959). In Java they are sometimes semi-destructive on *Parkia* (van Heurn, 1929), but were never seen as real pollinators of normal bat-flowers. I never found pollen in the numerous intestines dissected. Only the Macroglossinae, eating pollen as a source of protein, are effective there, and bat-flowers often have a large quantity of pollen.

In Africa the macroglossine bat *Megaloglossus* seems to be rare, perhaps due to the lack of flowers throughout the year. Observers in Africa (Jaeger, 1954) found smaller Pteropinae on bat-flowers, one (*Eidolon*) even eating pollen. Baker and Harris (1957) reported them as the actual pollinators of *Parkia* and photographed them later also on *Kigelia* and *Ceiba*.

As the smell of typical bat-fruits and bat-flowers is the same and as Pteropinae only swallow the juice of fruits, the transition is easy and understandable. The smell, perhaps due to butyric acids, is not a signal as in bees, but acts directly on an innate sense (cf. the experiment in van der Pijl, 1936, p. 28). It seems related to the smells of bats themselves and has some stimulating effect.

In a small group of flowers, the subclass with solid food-bodies (containing *Bassia, Madhuca*, and *Freycinetia*), the fruit-bats remain the obligate pollinators (Cleghorn, 1922, van der Pijl, 1936, 1956b). It is uncertain whether the cases of *Pachira insignis* (Porsch, 1937) and *Eugenia cauliflora* (Porsch, 1941) can be included. The latter has the typically large anthers of the main class.

In the New World the differentiation of flower-bats seems more recent and less pronounced. The diets of the bats are often mixtures of insects, fruits, and nectar. It is, therefore, the more curious that the bat-flowers of the New World show the full type and fit perfectly to Asiatic Macroglossinae.

The relatively recent nature of chiropterophily is reflected in the distribution of bat-flowers among the plant families. The bat-flowers are loosely spread over many of the higher families, as changes from other classes. In the Ranales bat-fruits are known, but bat-flowers not. The complete list of known bat-flowers contains about 40 genera in 22 families, Monocotyledons and Dicotyledons from Capparidaceae and Cactaceae onwards. One can mention such families as the Bignoniaceae, Bombacaceae, Cactaceae, and Sapotaceae. Some cases stand more or less isolated (*Agave, Cobaea, Symbalanthus, Campanea, Freycinetia, Musa, Parkia*, etc.).

Vogel (1958) used this to fortify his anti-selectionistic concept, when discussing the remarkable case of *Purpurella* in the Melastomataceae, a family with pollen flowers. The case becomes less surprising when we see that flowers of sister species, though perhaps bumblebee flowers, secrete much nec-
tar, and that the related *Brachyotum* is ornithophilous.

In the Cactaceae (Porsch, 1939, p. 119–133) chiropterophily seems to have evolved in some separate species of *Cephalocereus* (*Pilocereus*), *Carnegiea*, *Pachycereus*, and *Lemaireocereus* on a common basis with sphingophily, together with cauliflory. Probably some species are transitional. Judging by the broad tube, the color, the nightly anthesis and the large anthers of the newly discovered *Cephalocereus machrisii* from Brazil I was able to predict to the discoverer (Dawson, 1957) that it would emit a sour smell at night. Later Dawson confirmed this.

The chiropterophilous *Cleome anomala* (Vogel, 1958) is also clearly derived from the sphingid flowers of other Capparidaceae. In *Frevcinetia* and other genera the basal type seems to be ornithophilous. This has also been presumed for *Musa*, but the true ornithophiles from the section (or genus) *Ensete* are subtropical and peripheral. In the remaining sections *Musa* proper apparently contains some ornithophilous species in addition to a majority of chiropterophiles. The oldest group (*Eumusa*) seems to be chiropterophilous. One of the ornithophilous *Musa* species (*M. sanguinea* Hook. f.) still gives off a chiropterophilous smell in the afternoon.

In the Bignoniaceae too sphingophily and ornithophily seem at first glance to be primary. On the other hand, there is in this old family chiropterophily in three different tribes, and some general tendency towards musty smells, which suggest old chiropterophily. *Spathodea campanulata* is certainly ornithophilous and of the Old World type with the sexual organs pointing toward the inner part of the inflorescence. It is, however, not fit for sunbirds, but attracts less specialized, larger birds (Cammerloher, 1928, van der Pijl, 1936, Ali, 1932, Docters, 1938). The whole plant and also the flowers possess the musty smell. The opinion of Vogel (1954, p. 256), that the smell (not conforming to the “Stil”!) is due to microbes in the nectar, is most improbable (cf. Winkler, 1907). The flowering plant has, moreover, the pincushion-form of *Markhania* spp., whereas the flowers, though rimless, thin-walled, diurnal and fiery red, are wide-mouthed. This is transitional to the the closely related complex of *Markhania-Haplophragma-Pajanelia*, with strong chiropterophily. Sprague (1919) split off from this complex (incl. *Spathodea*) the sphingophilous plants as *Dolichandrone*. A rare case of taxonomy on a flower-ecological basis!

In the Bombacaceae, we also find transitional types, in which the direction of the transition is not clear. *Bombax malabaricum* is certainly not specially nocturnal and is ornithophilous, though not conforming completely to the type, and it is popular with unspecialized birds such as starlings and crows (Spennemann, 1932). The large, open flowers, however, have the same musty smell as *B. valetonii*, a bat-flower. In Java I found no bat-visits, the bats preferring other trees in the neighborhood, but Hahnelt (1959) relates that the flowers are eaten by *Cynopterus* in southern China, and McCann (1934) saw *Pteropus* lapping nectar from them while still open at night.

The same transitional condition was reported by myself (1941) for the low climber *Macuna pruriens*. The flowers of the plant are dark-purple and smelly, but are ignored by bats and actually visited by birds (Docters, 1938). Many sister species—in the Old and New Worlds—are truly chiropterophilous, while others are beautifully ornithophilous (Docters, 1938).

In the Solanaceous tribe *Hyoscyaminae* there seems to be some pre-adaptation towards chiropterophily. The low Himalayan *Scopolia luridus* has clearly a part of the syndrome (pendulous, sour-smelling, lurid color, but probably not nocturnal). The American *Trianaea* spp. described as chiropterophilous by Vogel (1958) seem to be more related to the *Datureae*, in which on the other hand nocturnal anthesis of large hanging flowers is found as prerequisite. Some *Solandra* species may be, or may have been, chiropterophiles.
In the Sapotaceae (and perhaps Musa, Sonncratia, and Parkia) there is a pre-existing bat-smell which functions in seed-dispersal. Sometimes the smell is even emanated by the leaves (van der Pijl, 1936, p. 28). In the Bignoniaceae such relations are only possible in the Crescentiae. In the Bombacaceae such older relations are not probable, but Vogel (1958, p. 511) points to a pronounced bat-smell in the fruits of a Drymonia species (Gesneriaceae) whereas other species have bat-flowers.

(In my studies on seed-dispersal (1955a) I pointed out that there is a difference in phase between the dispersal of spores and of seeds by vertebrates. Though seeds are later developments than spores, the relations of herbivorous reptiles with seeds probably developed earlier than those of vertebrates (or even bees) with spores. Birds and mammals could easily take over dispersal when fruits had originated. Fruit-bats likewise existed before flower-bats, though flowers precede fruits historically and ontogenetically.)

Baker and Harris (1957) pointed to a discrepancy between three facts regarding the bat-pollinated genus Parkia. These are, (a) the pantropical distribution of Parkia, which can only have happened from America before the Eocene and via Beringia; (b) the absence of Megachiroptera in America; (c) the much later evolution of microchiropterous fruit-bats. This makes them suggest that the Parkia-type of inflorescence might be a fortuitous pre-adaptation. I agree that some basal requirements for parallel development may originally have been present, such as much nectar, large "flowers" with much pollen, nightly anthesis. I already pointed to a "pre-adapted" "bat structure" of the crown in chiropterochories (1957).

An analysis of the genus Mucuna with both American and Asiatic chiropterophiles might also be valuable. The most chiropterophilous families, the Bignoniaceae and the Bombacaceae evolved parallel genera in the Old and New World with bat-flowers. Most American cases of chiropterophily, however, have evolved de novo in world-wide families without parallels in the Old World, in the same way that Salvia species in the Old and the New World developed ornithophilous independently.

Chiropterophily and chiropterochory have implications in synecology, physiognomic changes and geographical distribution. The author published (1957) a map of the distribution of MacroGLOSSINEAE and Pteropinae in the Pacific area and found some bat-flowers or bat-fruits which have the same eastern limits as the bats. Nur (1958), confirming the chiropterophily of Musa textilis, brought the distribution of some sections of Musa into a map, together with the corresponding distribution of MacroGLOSSINEAE generis.

The author also pointed (1936, 1956b) to the synecological factor of common pollinators linking some chiropterophiles in a vegetation. A succession of flowering periods throughout the annual cycle make the life of both bats and plants possible. In single cultures of Ceiba only those trees near gardens with Musa, Parkia, etc., were visited. This interdependence deserves special research when but one chiropterophile is known from a region.

Chiropterophily (and chiropterochory) make clear why flagelliflory and cauliflory are confined to the tropics. There is no common taxonomical, morphological and anatomical basis for the cases of cauliflory. I gave in my articles (1936, 1941, 1956b) a review of all the old theories on this phenomenon, now almost entirely superfluous because the right ecological approach has been found. For the majority of cases, where the flower is not chiropterophilous, I found bonds with the dispersal of seeds by fruit-bats (van der Pijl, 1957). Fruit-bats have left an earlier but quite comparable stamp on many tropical fruits.

In the tropics many more mammals play a role in pollination than in temperate regions. Many squirrels there like nectar and are not as destructive as the temperate ones. The same is true of some insectivores and marsupials. Porsch (1934-1935) collected
many data on this point, so interesting for the Australian region.

At the end of this discussion of flower-classes from a dynamic angle it would be interesting to study the pollination-spectrum of some orders and families. There are old trials of this kind (Müller, 1873, p. 413). Porsch (1938–1939) made an attempt in this direction for the Cactaceae. Vogel (1954) did so for some genera and families in Africa. The Orchidaceae deserve such a special study. Vogel (1959) started it in a brilliant analysis of South African Ophrydeae. In the forthcoming Vol. II of his book on the Polemoniaceae, Grant promises a complete review of its pollination systems.

Up until now such classifications, as we saw, produced no grand reforms in taxonomy.

It might be interesting to study the relations between flowers and changes in climate and the importance of flower-ecological spectra for synecology, plant-formations, and local floras. Docters van Leeuwen (1933) gave a fine survey for a tropical mountain-region.

It is in agreement with our views that the direct influence of the climate on flowers is unimportant and more or less limited to anemophily and rain-pollination (Hagerup, 1951). Notwithstanding the opinions cited by Jaeger (1957, p. 308) the geographical variations in flower-characters seem to be influenced via the changes in pollinators (cf. also Weevers, 1951).

As a student of plant-dispersal I am also tempted to compare our finds with the evolution of fruits, which offers a parallel development of primitive and progressive classes, both crossed and influenced by the dispersing agents (cf. van der Pijl, 1956).

Admitting the heavy burden already placed on modern taxonomists, one should nevertheless state that flower-ecology (and seed-ecology) are important to them. The two fields do not deserve the neglect shown by the four pages out of 407 in Richards’ “The Tropical Rainforest,” nor the total omission of pollination in the chapter “Factors of Distribution” in Good’s “Geography of Flowering Plants.”

**Summary**

1. The study of flower-classes does not lead to delimitations of groups, but can supply the ecological background for evolutionary trends in such groups. The preference of visitors is not, as thought by Goebel, always just utilization of a loose incidental character.

2. In the class of sapromyophiles a complex of characters fitted for flies is demonstrated to be a convergence. This explains much in the Annonaceae. In some orchids regression to fly pollination leads to a return to radial symmetry. Knowledge of the character complex serves to revise the separation of genera for conspicuous structures, still inside the ecological complex (*Cryptophoranthus* and *Cirropetalum*).

3. In one of the melittophilous subclasses, viz. the *Xylocopa-*flowers, there evolved a new protection against “unwanted” activities of rude pollinators, an ant-guard. The failing of such contraptions in flowers for birds and bumblebees, used by anti-selectionists, seems an as yet unbalanced condition.

4. The study of the floral spectrum of some families has divulged that some “ecologisms” have already become suprageneric “morphologisms.” The parallelism of forms in distant groups is not undirected, kaleidoscopic morphological repetition as believed by Good, but is convergence.

5. In ornithophiles we also find a typical complex of characteristics though superimposed on different, older, “morphological” substrata. There are many transitional flowers, fitted for unspecialized birds. Independent development in the Old and New Worlds has led to differences in style.

6. In chiropterophily we find transitional cases, visited by transitional nectar-bats, still mainly destructive. Some families, as Bignoniaceae and Cactaceae, show a pre-adaptive basis, sometimes leading separately to bat-pollination in Old- and New-World forms. Some points of the syndrome
(flagelliflory and cauliflory) explain typically "tropical" characteristics. Seed-dispersal by bats may also provide a pre-adaptive basis.

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EVOLUTION OF FLOWERS


