

History of the Malpighiaceae in the Light of Pollination Ecology

by

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Abstract

VOGEL, S. (Institut für Spezielle Botanik der Universität Mainz, D-6500 Mainz, Federal Republic of Germany). History of the Malpighiaceae in the Light of Pollination Ecology. *Memoirs of the New York Botanical Garden* 55: 130-142. 1990. The pantropical disjunction of the Malpighiaceae reflects their taxonomy: no genus is shared by the Old and New World (except for two large American genera each with a single West African species). Most New World genera are distinguished by their possession of calyx-borne elaiophores (E), an adaptation to oil-collecting bees. These glands have been claimed as a basic family character, and the family is believed to have arisen in already isolated South America, co-evolving with the endemic pollinators from the very start. In consequence, the palaeotropical genera are said to be American decendants, once displaced by transatlantic drift, which reduced or lost their E, since the appropriate bees were absent. Gland morphology contradicts this hypothesis. The calyx glands found in some Old World genera are not vestigial E, but are extranuptial nectaries of the vegetative (extrafloral) type widespread in the family. From calyx nectaries E evolved. The Malpighiaceae are therefore supposed to have originated in Cretaceous West Gondwanaland; their palaeotropical members still represent the ancient

pollen flower state from which the New World phyla emerged, acquiring E as an apomorphy during post-Gondwanian time.

Zusammenfassung

Die Vergangenheit der Malpighiaceen im Lichte der Blütenbiologie. Die pantropisch-disjunkte Verbreitung der Malpighiaceen spiegelt sich in ihrer Systematik: Keine Gattung ist der Alten und Neuen Welt gemeinsam (ausgenommen zwei große amerikanische Gattungen mit je einer westafrikanischen Art). Die meisten Neuwelt-Genera sind durch den Besitz kelchbürtiger Elaiophoren (E) ausgezeichnet, einer Anpassung an ölsammelnde Bienen. Diese Drüsen sind neuerdings als basale Apomorphie der Familie gewertet worden, und letztere soll als solche von Anfang an in Coevolution mit den endemischen Bestäubern im bereits isolierten Südamerika entstanden sein. Ihre paläotropischen Gattungen werden demnach als amerikanische, durch Fernverbreitung dislozierte Abkömmlinge angesehen, die in Ermangelung der angestammten Bestäuber sekundär ihre E reduzierten oder verloren. - Dieser Ansicht widerspricht die Struktur und Morphologie der Drüsen. Die bei einigen Altwelt-Gattungen vorkommenden Kelchdrüsen sind nicht Rudimente von E, sondern extranuptiale Nektarien jenes vegetativen (extrafloralen) Typs, der in der Familie weit verbreitet ist. E entwickelten sich vielmehr aus solchen Kelchnektarien. Es wird hier die Ansicht vertreten, daß die Malpighiaceen schon im Westgondwanaland der Kreidezeit ihren Ursprung genommen haben; ihre paläotropischen Vertreter zeigen noch den ursprünglichen Typ der Pollenblume; aus ihnen gingen die Neuweltstämme hervor, indem sie zwar früh, aber erst in postgondwanischer Zeit das Ölblumensyndrom als Apomorphie erwarben.

Key Words: Malpighiaceae; oil flowers; elaiophores; extrafloral nectaries; Centridini; oil-collecting bees.

Introduction

Comprising over 1000 species, the Malpighiaceae constitute an important element in the forests and savannas of both the Old and New World tropics. Almost all of them are woody, with the majority of genera and species consisting of lianas. Typical features of importance in the following context are: The occurrence of disc-shaped epithelial glands on their leaves, bracts, and sepals, and the floral organization, which is rather uniform: Five sepals; five separate, clawed, often fringed petals; two basically pentamerous, obdiplostemonous whorls of stamens and a three-merous superior or semiinferior ovary. The arrangement is regular or zygomorphic, with an oblique plane of symmetry at least in the bud stage (Fig. 1B). The flowers, predominantly yellow, are notoriously bee-pollinated, although they have no nectar.

Based on these and many other characters, the

family appears to be a natural and monophyletic entity usually assigned to the order Polygalales. The taxonomy within the family is less clear and is nowadays discussed mainly on the basis of palynology and floral adaptations (Anderson, 1979; Lobreau-Callen, 1984).

Taxonomy and Phylogeny; Recent Geographical Distribution

The Malpighiaceae were divided by Niedenzu, in "Das Pflanzenreich" (1928), into two subfamilies: One with mostly samaroid, anemochorous fruits, now named Gaudichaudioideae, which has a pantropical distribution; the second subfamily was characterized by drupes or wingless nuts and is confined to the Neotropics (Fig. 2). The system of Niedenzu has basically been used to date, although it has undergone nomenclatorial changes by Arènes (1959) and Morton (1968). W. Anderson (1978) has also now claimed Niedenzu's

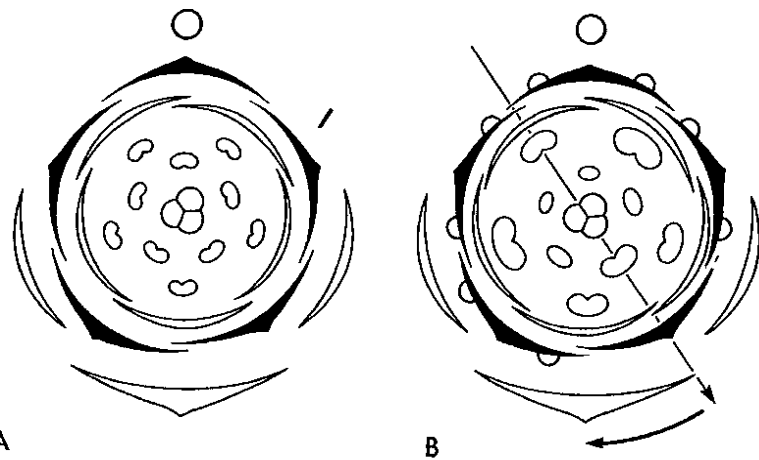


Fig. 1. Floral diagrams of Malpighiaceae. A. *Aspidopterys*, B. *Stigmaphyllon*. Modified after Niedenzu. In the zygomorphic flower (B), the oblique symmetry plane is turned to vertical position before anthesis (lower arrow).

second subfamily to be pleiophyletic. One part only, separated as Byrsonimoideae, is regarded as a natural phyletic line. The remaining genera, including the drupaceous genus *Malpighia*, have so far been left in an uncertain position by Anderson. This question, however, can be disregarded here.

The Gaudichaudioideae comprise four tribes, one of which is strictly neotropical, one is only paleotropical, and two are pantropical. Thus the tribe Hiptageae has nine Old World and seven New World genera. The former constitute Niedenzu's subtribe Aspidopteridinae, the latter (including one paleotropical genus) the subtribe Mascagniinae. Arènes (1959) considered the relationships within the Hiptageae as more intricate insofar as three generic groups revealed independent phyletic affinities: the Old World *Hiptage*, *Tristellateia* and *Digoniopterys* are linked with New World *Tetrapterys*; Old World *Aspidopterys* with New World *Mascagnia*; and Old World *Triaspis*, *Caucanthus*, *Flabellaria* and relatives with New World *Hiraea*. In short, the transatlantic relationships within the Hiptageae appear to be rather close.

The tribe Banisterieae also consists of a paleotropical subtribe, the Sphedannocarpinae (seven genera), and a neotropical subtribe Banisteriinae (more than 14 genera), two species of which,

however, are found in West Africa, a case we shall discuss later on.

The Problem of Disjunction: The Theory of Gondwanian Origin

Earlier authors have already attempted to explain the disjunctive area of the Malpighiaceae historically, and to bring it into line with taxonomy.

Niedenzu did not comment on the problem explicitly, but by placing the Old World subtribe of the Hiptageae and that of the Banisterieae each ahead of the respective New World subtribes, he implied that the Old World members were the more primitive.

Arènes, on the other hand, stressing the relative preponderance of recent Malpighiaceae in the Neotropics in terms of numbers of species (70%) and genera, suggested that northern Brazil was the cradle of the family. On the basis of land bridge theory, he supposed that from there the Malpighiaceae were able to spread at early times (Upper Cretaceous) to the eastern part of the Old World, where they later became largely extinct. During the Paleogene, at the time recent neotropical genera already existed, a second wave starting from South America reached Europe via

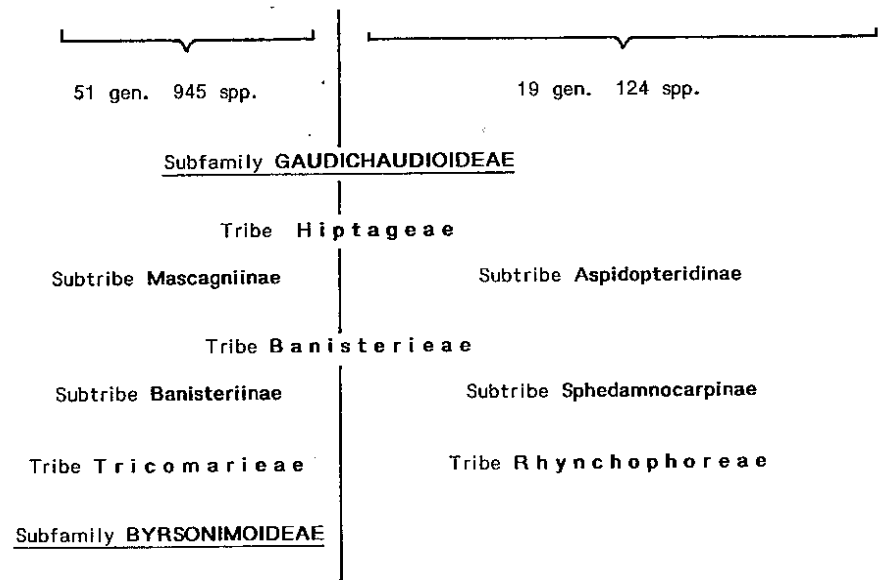
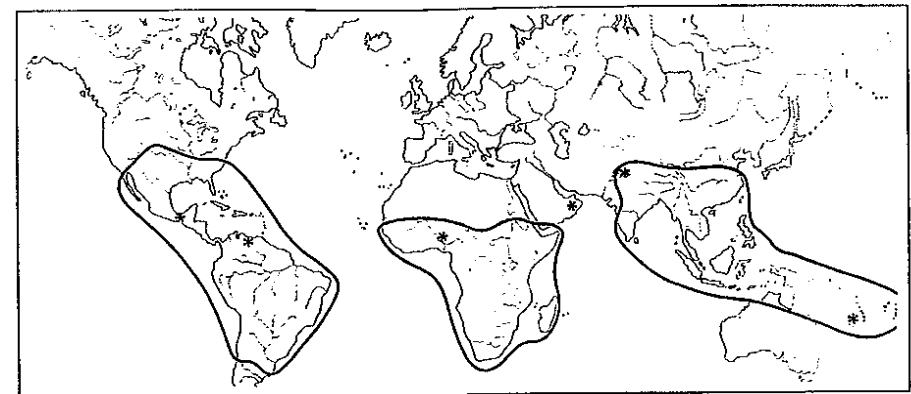


Fig. 2. Distribution map of the Malpighiaceae and corresponding outline of their higher taxa. Asterisks mark fossil pollen records after Lobreau-Callen, 1974.

North America. Arènes was led to this opinion by European macrofossils attributed to neotropical genera of that family, but their identification is now open to doubt: according to Lobreau-Callen (1984), no fossil Malpighian pollen has been found so far in Europe. Malpighian pollen fossils confidently document only an early (Paleogene) presence in Africa, South and North America. Recently, Taylor and Crepet (1985) have described an unequivocal Malpighian flow-

er from the Middle Eocene of Tennessee, giving evidence that a migration from South to North America was possible long before the Panamanian land connection arose. Principally then, the family appears to be of Southern Hemisphere origin.

Irmscher (1922) had been the first to reconcile the disjunction of the Malpighiaceae (as well as that of many other pantropical families) with Wegener's theory of continental drift. Their first

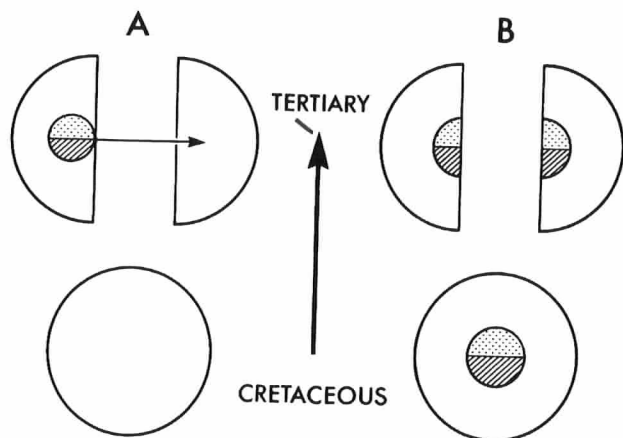


Fig. 3. Two versions of explanation for the recent distribution of the Malpighiaceae, roughly schematized. The circles (bottom) stand for West Gondwanaland, the halves (top) for the respective neotropical and paleotropical succession areas. The small circles signify the ancestral stock of the family (already differentiated into two entities.) A. Postgondwanian origin, secondary immigration, B. Gondwanian origin, autochthonous descent.

radiation took place, he said, under the different position of land masses in the Cretaceous; he thus presumed a considerable age of the Malpighiaceae, as did Arènes. Lobreau-Callen (1974, 1984) has developed this hypothesis further, using modern palynology. Also the level of floral organization is not at variance with this view. Starting from the presumed center of origin, western West Gondwanaland, ancestral lines could have spread with ease to the East when the South American and African continents were still united or close together. If the gross taxonomy of Nienhüser is correct, the tribes Banisterieae and Hipptageae at least should have been in existence at that time, each one subsequently splitting into New and Old World paraphyletic sister lines (Fig. 3B). Following Lobreau-Callen (1984), the Byrsonimoid tribes Galphimieae and Byrsonimeae have minute pollen grains of a primitive type. They thus appear to have branched off very early but without leaving descendants in the Old World.

The Colonist Theory

Several American authors take quite a different view of the history of the Malpighiaceae. In the opinion of Anderson (1979), joined by Raven and Axelrod (1974), Neff and Simpson (1981),

and Taylor and Crepet (1985), the family is not so old, but arose in South America only during Postgondwanian time. The living neotropical genera, they suggest, represent the plesiomorphic, and the paleotropical the derived, apomorphic condition: The winged fruits of South American Malpighiaceae may once have crossed the Atlantic ocean and the family became established in Africa, forming secondary centers of evolution and giving rise to the paleotropical genera (Fig. 3A).

Sepal Glands as a Criterion

Anderson's argumentation rests upon the distribution of a certain morphological structure, the sepal glands (Fig. 4). These glands, borne on the abaxial (outer) surface of the calyx, occur in not less than 873 species of 37 American genera belonging to both subfamilies (92% of all New World species), whereas in the Old World only 64 species of four genera (52% of all Old World genera) bear them. Anderson regards the sepal glands as apomorphic for the whole family, and symplesiomorphic for all neotropical genera. He interprets their absence in the majority of the Old World taxa (the supposed immigrants) as being derived and secondary.

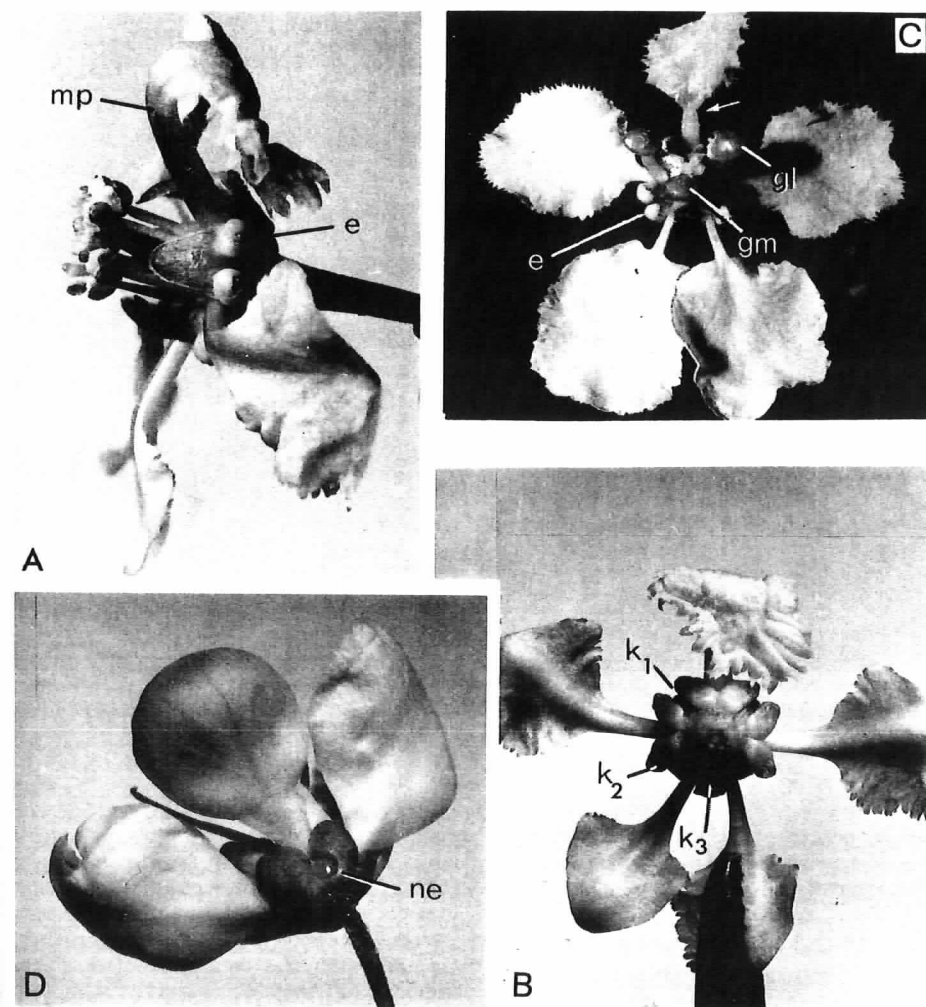


Fig. 4. Flowers of Malpighiaceae, showing sepal glands. A-C. Elaiophores (e): A. *Malpighia glabra* L., lateral view, B. the same, seen from the rear. C. *Stigmaphyllon littorale* Juss., frontal view. D. *Acridocarpus smeathmannii*(DC)Guill. et Perr. with calyx nectary (ne). mp = banner petal, in C with constriction (arrow), gm, gl = median and lateral stigmata, k_1 , k_2 = lateral posterior sepals bearing elaiophores, k_3 = median glandless sepal ($\times 2.4$).

Anderson relies on my finding that the sepal glands (of the American taxa) are oil-producing floral attractants, i.e. elaiophores (Vogel, 1974)¹. These glands are almost exclusively exploited by

specialized bees belonging to the Anthophorine tribe Centridini. As these pollinators are neotropical endemics, the Malpighiaceae are said to have co-evolved with them from the very start and only after South America became isolated. Most of their paleotropical descendants, newcomers in Africa, are said to have lost their

¹ For the oil-flower syndrome in general, see Buchmann, 1987; Vogel, 1988.

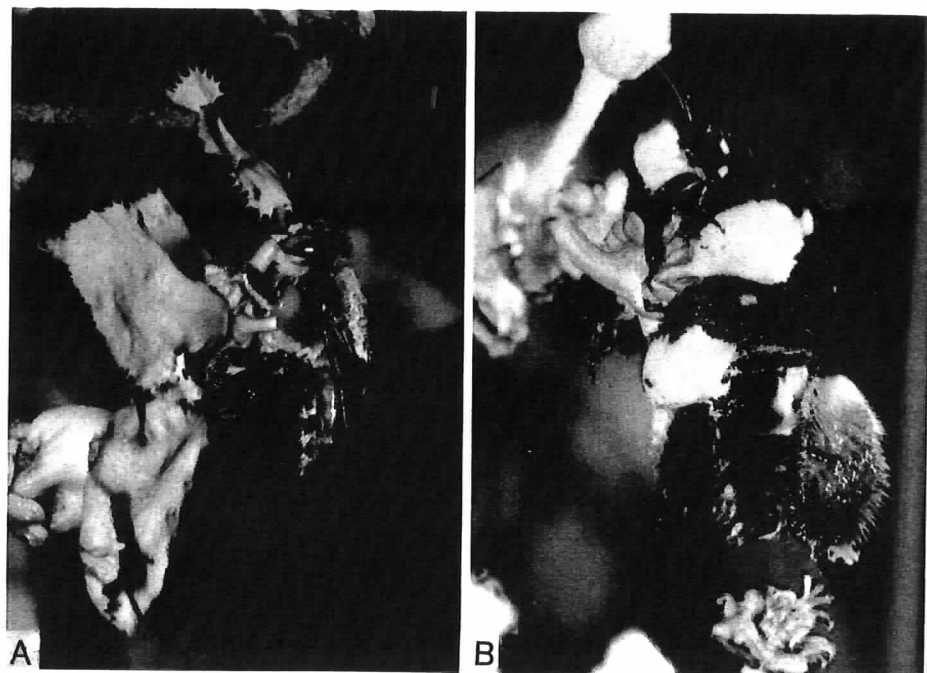


Fig. 5. Oil-collecting Centridine bees, pollinating flowers of Malpighiaceae. A. *Centris trigonoides* on *Stigmaphyllon littorale*, B. *Epicharis rustica* on *Banisteriopsis laevifolia* (Juss.) Gates. Although very different in body size, the bees behave in the same manner (see Fig. 6).

elaiophores as they failed to encounter their appropriate pollinators and had to adjust to vectors of another kind.

True American Colonists in Africa: An Exception

Hence, there are currently two contrary views of the paleotropical Malpighiaceae. Are they "Gondwanian aborigines" or "American colonists"? Before approaching an answer we can easily exclude two species to which Anderson's colonist theory applies with certainty: The first, *Heteropterys leona* (Cav.) Exell (= *H. africana* Juss.), is the single West African member of a genus comprising 80 South American species. I was able to investigate it in Cameroon. Its calyx glands are clearly of the New World type but were not found secreting oil nor any other product. Their epithelium is vacuolized and degen-

erate; the small flowers are probably autogamous. As Niedenzu already suggested, the winged fruits of some ancestor may have been blown overseas to Africa during the Tertiary, but early enough to develop a distinct species. Apparently the oil syndrome was lost due to the lack of Centridine bees in Africa. The second outsider, *Brachypterys ovata* (Cav.) Small, occurs in the South and Central American littoral, as well as in Senegal. It still has showy flowers with sepal glands (of unknown properties). It may have crossed the sea more recently.

Origin of the Old World Malpighiaceae

Let us now examine whether the remaining bulk of paleotropical Malpighiaceae can also be explained that way or not. To this end, we must inspect the calyx glands more closely. As we said,

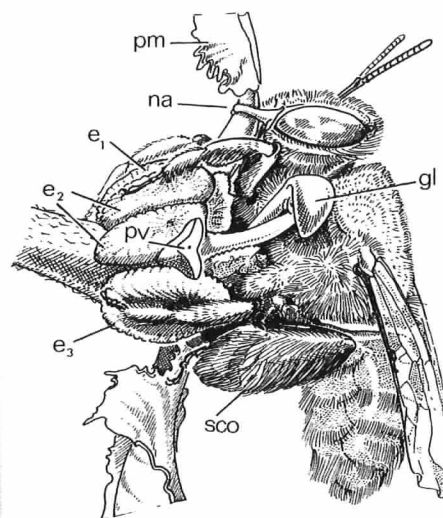


Fig. 6. *Centris* exploiting a zygomorphic malpighian flower. The bee clings to the banner petal (pm) at a preformed constriction (na) and scratches the elaiophores (e_1 - e_3) with her fore and mid legs. gl = one lateral stigma-stamen-complex, touching the shoulder of the bee. pv = petal (cut off), sco = scopa. From Vogel, 1974.

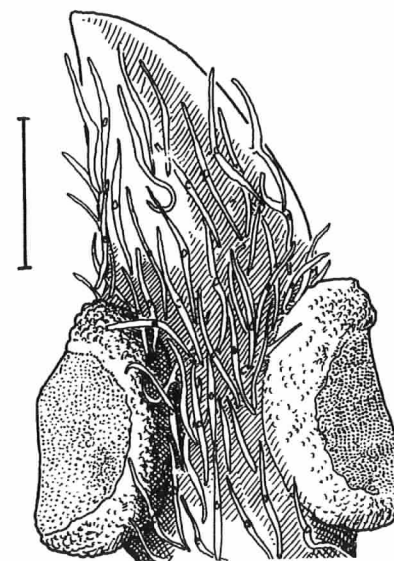


Fig. 7. *Stigmaphyllon littorale*. Bract with paired extrafloral nectaries. Scale: 1.0 mm. From Vogel, 1974.

Evolutionary Provenance of Elaiophores

But from what did the sepaline elaiophores evolve? Their anatomy reveals that they are basically of the same type as the glands that occur on the green leaves and bracts in most New and Old World Malpighiaceae and often have a similar paired arrangement. These vegetative glands, N.B., produce true nectar, as has been known long since. They are typical extrafloral nectaries (Figs. 7, 8A). The nectar penetrates the cuticle which may or may not separate as a blister. It is often licked by ants and wasps which may provide some protection against herbivorous insects. As these organs are so widespread in the family it is apparent that they are the general plesiomorphic structure from which elaiophores evolved. The supposed homology of extrafloral nectaries and elaiophores is paralleled by glandular trichomes of other oil flowers such as those of the Scrophulariaceae, the Cucurbitaceae, and Iridaceae (Vogel, 1974).

their American type produces fatty oil. The oil is stored below a cuticular blister which finally bursts. The secretion is gathered exclusively by female bees which have special collectors on their legs (Neff & Simpson, 1981; Vogel, 1974). They scratch the glands, reaching them from the front between the slender petal stalks (Figs. 5, 6). By these movements, they become ventrally dusted with pollen that, in the next flower, is transferred to the stigmas. The surplus pollen is combed from her body while on the wing, mixed with the oil and carried to the nest as larval provision; possibly purely collected oil (perhaps chemically altered by some bodily secretion) also serves for waterproofing the earthen brood cell walls. The bees are thus obligatorily dependent on these oil sources but always obtain nectar and additional pollen from a variety of non-malpighian flowers. The mutual adaptations, however, leave no doubt that the American floral syndrome of the Malpighiaceae has evolved under the selective impact of oil-collecting bees.

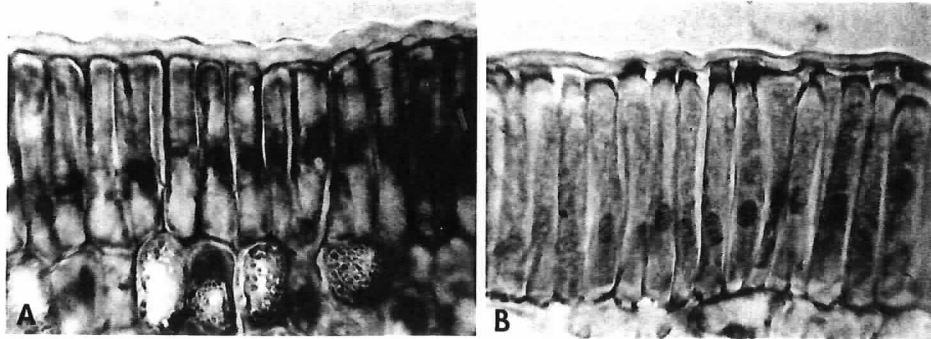


Fig. 8. Nectar- and oil-producing epithelial glands of Malpighiaceae compared. A. Extrafloral nectary of the bract of *Stigmaphyllon littorale*, B. Calyx elaiophore of *Malpighia glabra*. From Vogel, 1974.

The Sepal Glands of the Old World Members

Now what about the glands of the Old World members? The majority of these lack calyx glands. As to the four genera possessing floral glands (*Acridocarpus*, *Rhinopterys*, *Hiptage*, and *Tristellateia*, Fig. 4D). The present author has demonstrated (Vogel, 1974: 65) that these are not elaiophores but plainly resemble the extrafloral nectaries shared by the same plant and a multitude of other genera. They are often smaller and have an intersepaline position, possibly resulting from fusion of two neighboring twin glands, and hence are located behind the petals (Fig. 9). Most species of *Hiptage* have a single large gland between the two posterior sepals.

Unfortunately, there are very few data on the pollination of Old World Malpighiaceae. One can extrapolate from various members inspected in the field that "pollen flowers" prevail through-

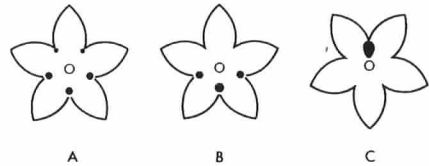


Fig. 9. Position of sepal glands in Old World malpighs, schematically; calyx seen from the rear. A. *Tristellateia bojerana* Juss.; B. *Acridocarpus smeathmannii*; C. *Hiptage benghalensis* (L.) Kurz.

out. Heteranthy occurs in *Hiptage*, a typical progression of pollen flowers (Fig. 10A). In accordance with their using only pollen as an attractant, Old World Malpighiaceae always have the complete set of stamens and often enlarged, poricidal anthers with dry, dusty pollen available by buzzing, as in *Tristellateia* (Fig. 10B) and *Acridocarpus* (Fig. 11).

As the Malpighiaceae are devoid of intrafloral, nuptial nectaries such as a disc, pollen was initially their only reward. This condition has been maintained in the Old World. Surely the calyx nectaries, where present, are not nuptial attractants. Because they are placed behind the petals they cannot be reached from the front. Their function, if any, is extranuptial, as is also found, for instance, in the calyx of certain Bignoniaceae.

Apparently, an evolutionary propensity for the calyx to acquire these vegetative glands also existed, a conceivable process considering the vegetative provenance of the sepal whorl. But this was not obligatory. Other groups failed to do so, and their lack of glands on the sepals appears to be primary. There is no need to derive Old World glandless or gland-bearing flowers from those that bore elaiophores. The evolutionary sequence was opposite, but the paleotropical Malpighiaceae did not share this development and thence represent the ancestral stage (Vogel, 1974; Lobreau-Callen, 1984).

Provided the current system of the Malpighiaceae is correct, the New World branches of the tribes Hiptageae and Banisterieae, as well as the Byrsonimoideae and the *Malpighia* affinity, have

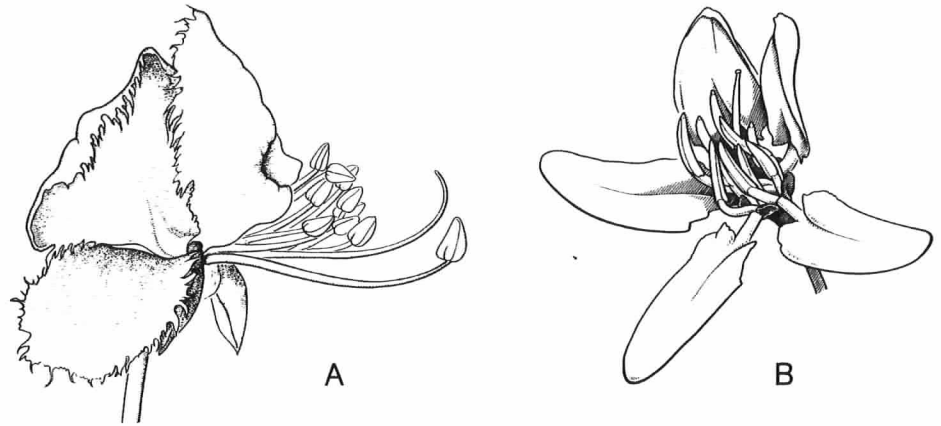


Fig. 10. Pollen-flowers of Old World malpighs (tribe Hiptageae). A. *Hiptage benghalensis* showing heteranthy: one big fertilization stamen and a bunch of fodder stamens. B. *Tristellateia bojerana*.

acquired elaiophores in independent parallel lines, as repeated apomorphies that commenced to develop soon after the isolation from the Old World stock. Taylor and Crepet's (1985) *Eoglandulosa* flower from the Middle Eocene, of unclear taxonomic position, already shows twin sepal glands of the American type, apparently elaiophores.

If the alternative possibility is true, namely that the advent of elaiophores was a single evolutionary occurrence, reflecting monophyly of the American portion of genera, it renders the assumption of intra-tribal connections between these and the paleotropical subtribes (as expressed in the current system) no longer tenable, and their (mainly carpological) coincidences would be a matter of convergence.

Co-evolution with Oil Bees

Accordingly, the endemic Centridini began to evolve soon after the isolation of the continent, passing a long period of their history in close interaction with the Malpighiaceae. It has been co-evolution in a broader sense because these are hardly species-specific interrelationships, since many Centridine taxa are compatible with many host taxa, as Gottsberger recently has shown (1986: 32). This bee family later also extended its oil sources to (mostly herbaceous) genera outside the Malpighiaceae. But certainly its presence was decisive for the great success the latter family

enjoyed in America (945 species) compared to its Old World members (124 species).

How can one imagine the first steps that finally led to the perfect mutual adaptation of oil flowers and their bees? Neff & Simpson (1981: 116) suggest that the calyx glands became floral attractants when they were still nectaries; that their nectar was first taken with the mouth parts, and in the further course of evolution was absorbed with the legs in the way the bees collect oil today. Because nectar is never taken up with the extremities by modern bees, this idea does not seem very convincing. My own speculation is

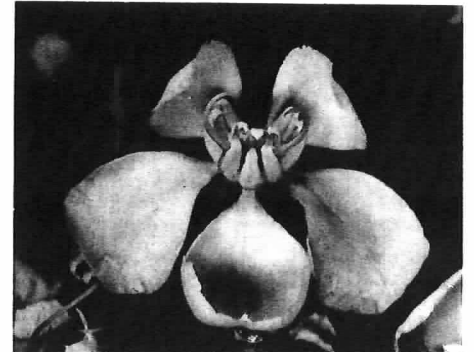


Fig. 11. Pollen-flower of *Acridocarpus smeathmannii* (tribe Hiptageae).

that initially the visitors gathered the pollen only and in doing so they unintentionally also touched the glands with their legs. When the nectar secretion transformed to oil, the bees learned to make use of it. As a matter of fact, their handling and transport of the oil resembles the manipulation of pollen rather than that of nectar.

Why, and how, the transition of nectaria to oil glands came about physiologically, is still open to debate. The occurrence in some nectars of small amounts of lipids on the one hand, and that of sugar traces in some floral oils on the other, suggests at least that such a change was feasible.

Reduction of Elaiophores in American Genera

Six American genera and a few scattered species of mainly oil-producing groups lack elaiophores. Contrary to the Old World members this is not primitive, except perhaps in the genus *Galphimia*, where it may be primary. Most of them appear to have reduced their attractant. They have acquired a deception strategy, maintaining a relationship to Centridine bees but now luring them by cheat. Certain species of *Banisteriopsis* and *Heteropterys* even have an intraspecific morph that lacks sepal glands which occurs alongside normally rewarding individuals (Sazima & Sazima, 1987). Also the cleistogamous flowers found in some genera lack elaiophores, while the pertinent chasmogamous ones produce oil.

Progressions of Oil Flowers

Once bound to the Centridini, with their particular way of exploitation, the American Malpighiaceae were prevented from undergoing any adaptive radiation towards other types of pollinators (Vogel, 1974: 241). Anderson (1979) has called this phenomenon 'Floral Conservatism' and compared it to the opposite behavior of nectariferous families. However, some progression has taken place within the oil flower syndrome.

The more primitive flowers are almost actinomorphic, and bear twin glands on all five sepals (*Byrsonima*, some species of *Bunchosia*; Fig. 12A). The bees probably circle round the flower to reach them all. The surplus pollen these flowers still produce in abundance is dusty and is

actively accumulated by brushing or buzzing, especially by the primitive genus *Epicharis*, but also by large, non-oil bees such as the Euglossini, which do not pay attention to the oil sources.

The more advanced, zygomorphic oil flowers have smaller amounts of fodder pollen, and the pollen grains are large and sticky. The bee is only passively dusted. Her activity is exclusively directed to the elaiophores. To this end, she assumes a rigid position dictated by the flower's symmetry (Figs. 5, 6). By clasping with her mandibles along the claw of the posterior petal (banner petal), she gets a hold on the flower, thus leaving her legs completely free for oil harvesting.

The necessary mid position of the banner petal is not congenital but results from the axial torsion of the flower bud through thirty-six degrees. As mentioned above and as already recognized by Eichler (1878), the flower's original symmetry plane is oblique and its functional orientation is acquired secondarily (Fig. 1B). This is another apomorphy compared to the Old World Malpighiaceae in which (except *Hiptage*) the flowers preserve their original orientation and where, in the case of zygomorphy, a pair of petals form the upper lip (Figs. 10B, 11).

The American oil-collecting bees, when clinging to the banner petal, can only manipulate four lateral twin glands: two of them with their forelegs, and two with their middle legs. The median-anterior pair of glands remains outside the reach of these extremities. Accordingly, many genera have lost their glands on the foremost sepal (Fig. 12B).

Although the Centridini usually collect oil with both their front and mid legs, advanced groups of the genus *Centris* tend to concentrate their effort on the front legs. Again in accordance with this behavior, the lateral-anterior twin glands are also often reduced to one single gland each (Fig. 12C). The secretory capacity of the remaining elaiophores is compensatorily increased.

The banner petal became the most specialized. It serves to support the pollinator as well as to guide its close-up approach. It often stands out by having longer, distinctly ciliate borders and contrasting colors, which sometimes change with age (Anderson 1979). The claw is reinforced by greater thickness and may even bear a preformed constriction where the bees' mandibles cling to it (Figs. 4C, 5, 6). In *Mascagnia anisopetala* (Juss.)

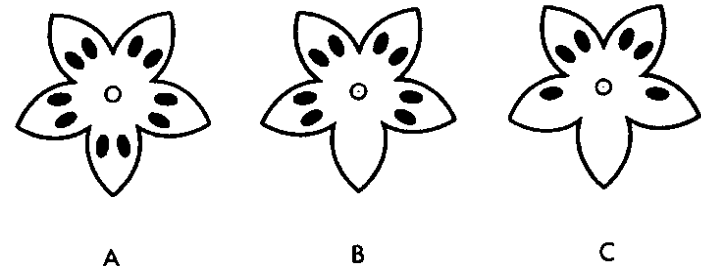


Fig. 12. Position of sepal glands (elaiophores) in New World malpighs, schematically, calyx seen from the rear. A. *Byrsonima*, some *Bunchosia*; B. *Stigmaphyllon*; C. *Malpighia*.

Griseb. and some *Byrsonima* species the remaining petals are much reduced in size or reflexed, while the glands advertise themselves by their bright cream color. In some taxa the banner petal and in others staminodial connectives are glandular and take part in oil secretion, the ecological significance of which is still unclear.

The Rôle of Non-Centridine Bees

Apart from the Centridini, two other Anthophorine tribes endemic in South America collect oil: The Exomalopsini and the Tetrapediini. Whether they also have influenced the evolution of the New World Malpighiaceae is doubtful. Equipped with pad-like collectors, they preferentially exploit trichomatous, soft elaiophores of other families. Some species are found on the Malpighiaceae as illegitimate guests that steal oil from the rear side (Neff & Simpson, 1981: 117; Sazima & Vogel, unpubl.). However, as certain of these bees in question have rigid oil collectors, well fitting the hard gland epithelia of the Malpighiaceae, they might be legitimate pollinators of some of their small-flowered genera.

Lobreaux-Callen (1984: 136) mentions that one species of *Paratetrapedia* (Exomalopsini) reportedly has been collected in West Africa. This remarkable circumstance demands confirmation. Because of their small body sizes, the bees in question would not be likely pollinators of the African populations of *Brachypterys ovata*.

Conclusion

To summarize, we conclude that, contrary to current opinions, the Old World Malpighiaceae

do not represent apomorphic branches of an original neotropical stock. It is the New World genera, at least with regard to the features discussed here, that appear derived. Both groups of the family evolved from a common ancestor probably already existing in Gondwanaland which bore unspecialized pollen flowers. This original condition is still conserved in the paleotropical descendants whereas the neotropical ones acquired elaiophores as an apomorphy after the separation of the continent.

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