

Floral Conservatism in Neotropical Malpighiaceae

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ABSTRACT

Over 950 species of Malpighiaceae grow in a variety of neotropical habitats and have evolved great diversity in habit, fruit, pollen, and chromosome number. Their flowers, in contrast, tend to be very similar in general architecture, especially in those aspects concerned with the attraction, orientation, and reward of pollinators. The flowers are visited only by Hymenoptera, principally female anthophorid bees and trigonid bees. The anthophorids collect oil from the calyx glands, mix it with pollen, and use the mixture as food for their larvae. The trigonids collect pollen. The usual character-syndrome of the flower seems to be related to and maintained by pollination by oil-bees, and was probably ancestral in the family. Pollination by pollen-collecting bees is probably secondary in many genera and has shifted to primary importance in groups that have lost the calyx glands. Other families such as Polemoniaceae, which have evolved very diverse flowers, reward pollinators with a sugary nectar that attracts a variety of secondary pollinators. This faunal diversity provides a bridge between one character-syndrome in the flowers and another. The specialized rewards and resulting lack of diversity in pollinators in neotropical Malpighiaceae explain why the flowers have remained so conservative in spite of the evolution of great diversity in other aspects of the phenotype. Calyx glands seem to have been lost in most paleotropical lines in the absence of oil-bees, but field observations on the pollination of those plants are practically nonexistent.

THE MALPIGHIACEAE are a family of mostly tropical flowering plants, currently classified in approximately 60 genera comprising at least 1100 species. Of these, 950 species in 47 genera grow only in the New World (Niedenzu 1928, plus since-discovered taxa, many of them still undescribed). The neotropical Malpighiaceae occupy a variety of habitats from southwestern United States to temperate Argentina, with the great majority of the species between the tropics. They are most commonly found in relatively open habitats, from woodlands through dense and sparse savannas (in the broad sense, including *cerados*), to open grasslands. Margins of rivers and forests are also common habitats, and some grow in tall forests. A few species have become adapted to xeric habitats; none has succeeded in breaching the barrier of cold weather that apparently bars the family from more "temperate" latitudes and from the high Andes in South America. As in most large groups of plants with such wide ecological and geographical amplitude, the Malpighiaceae have evolved great diversity in many respects, most notably their habit and fruits (Niedenzu 1928), their pollen (Lobreau 1967), and chromosome numbers (Anderson 1977, Fouët 1966). Habit varies from large trees in lowland wet forests, to medium-sized trees to shrubs to perennial herbs, and from large woody lianas to small herbaceous (but perennial) vines. Various groups produce bird-dispersed drupes, which I believe to have originated three times in the family, a great variety of wind-dispersed schizocarpic samaroid fruits, fruits adapted for dispersal by water, and diverse schizocarpic or indehiscent nutlet-like

fruits without obvious adaptations for dispersal (Anderson 1977)

While the Malpighiaceae show great diversity in other respects, their flowers are at least superficially very similar. Figure 1 is a comparison of three genera with very different habits and fruits but similar flowers. It is the purpose of this paper to consider why the flowers of this family have remained so similar while great changes were occurring in many other structures.

First, it is necessary to describe the structure and variation of the flowers, in order to decide in which respects they are actually conservative. The calyx comprises five free or basally connate sepals; four or all five sepals usually bear two large multicellular glands ("elaiophors") on the abaxial side, which produce fatty oils (Vogel 1974). These glands are reduced or absent in diverse populations or species of many genera and in most species of *Galpimia*, and completely absent in all species of five small genera (*Coleostachys*, *Echinopterys*, *Lasiocarpus*, *Ptilochaeta*, and *Thryallis*). The five free petals are conspicuously clawed, and often reflex between the sepals, so that the calyx glands are readily accessible to an insect that has landed in the middle of the flower. The petals are most often carrot-yellow, lemon-yellow, pink, or white. Blue petals are exceedingly rare, being found in a few species of *Mascagnia*, and petals that are dark red at anthesis are also very rare, although pink or white or even yellow petals may turn red with age, presumably an adaptation that prevents pollinated flowers from diverting the attention of insects from younger flowers. The limb

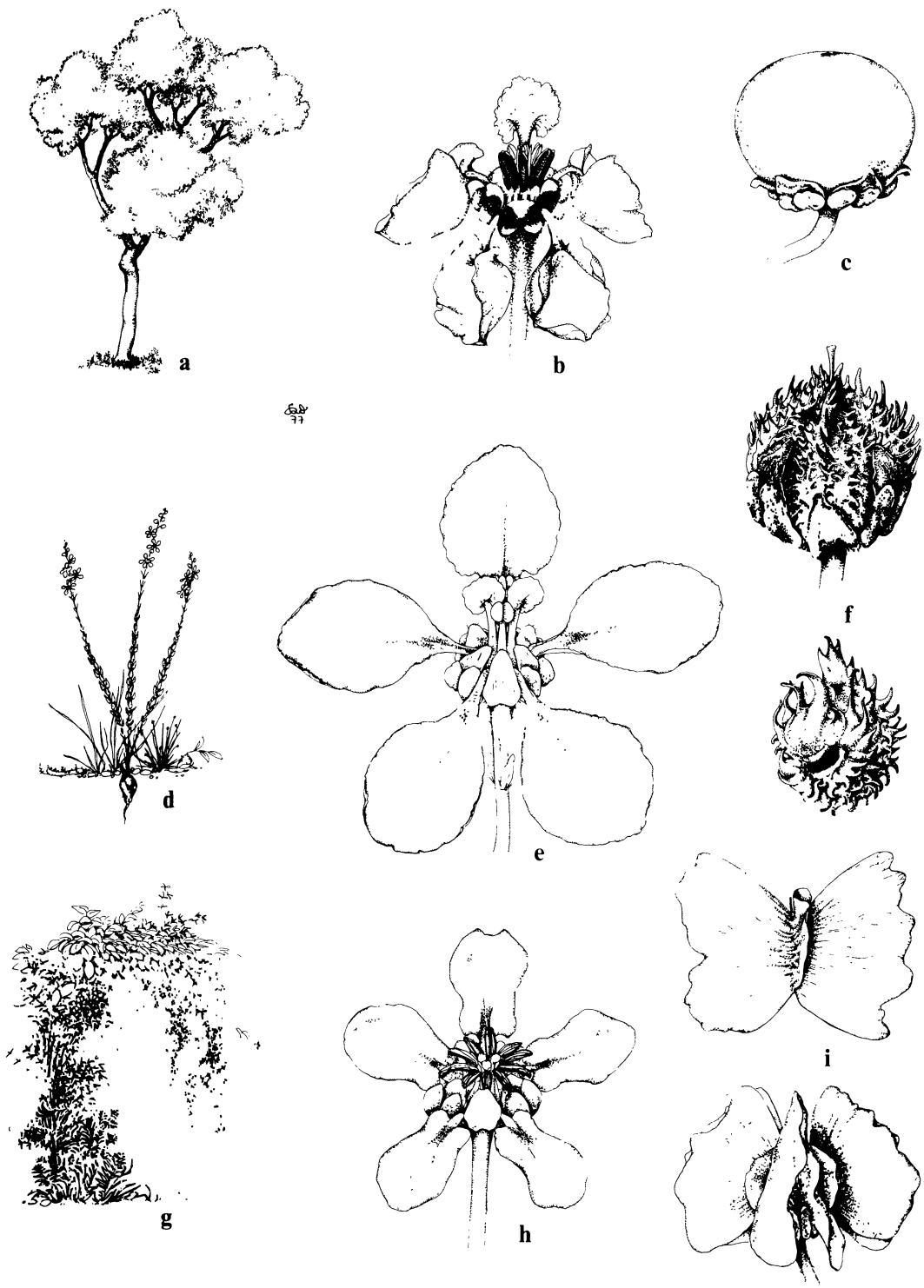


FIGURE 1. Comparison of three genera of Malpigiaceae. a-c, *Byrsonima*: a tree, 12 m tall; b, flower, X 3.5; c, drupaceous fruit, X 3.5. d-f, *Camarea*: d, perennial herb, 40 cm tall; e, flower, X 3.5; f, dry fruit breaking apart into three aculeate nutlets, X 7. g-i, *Mascagnia*: g, vine in shrub, 2 m high; h, flower, X 3.5; i, dry fruit breaking apart into three samaras, X 2. Drawn by Karin Douthit.

of the petals varies from flat to deeply concave, and the petals vary from 2 to 20 mm long; smaller flowers tend to be borne in greater numbers in dense inflorescences. The claw of the posterior "flag" petal is often conspicuously thicker than in the lateral petals. There is no disc, nor are there any other structures producing the sugary nectar usually found in animal-pollinated flowers. Aside from the calyx glands, the only secretory structures in the flower are small glands often present on the margin of the petals, especially the flag petal, which also secrete oils (Vogel 1974: 65), and possibly the glandular connectives of the anthers in some species (see discussion below). The androecium comprises basically 10 free stamens, which have undergone considerable modification in different evolutionary lines: the filaments are often partially connate, the anthers are often of different shapes and sizes in the same flower, the connectives of the anthers may become enlarged and glandular, and some stamens are reduced to staminodes or completely lost. The gynoecium comprises three superior uniovulate carpels, which may be free to connate in the ovary and free to connate in the styles, with reduction in fertile locules and/or styles to two or one in some lines. The stigmas vary from minute to fairly large and from terminal to internal; when they are internal, the styles may bear apical-dorsal extensions or appendages. The flower as a whole has a bilateral symmetry that may be subtle to developed (compare e and h to b in fig. 1); the flag petal stands at the back of the flower on the plane of symmetry, the eglandular sepal (if present) lies at the front of the flower on the plane of symmetry, and when the stamens or styles are heteromorphic they tend to remain symmetrical with respect to that front-to-back axis.

As this brief description attempts to show, there is actually considerable diversity in the flowers of Malpighiaceae, especially in the androecium and gynoecium. The basis for the above statement that the flowers are very similar is that the general architecture of the flower is so consistent—five sepals with paired abaxial glands, five free clawed petals zygomorphic with respect to a front-to-back axis, and a cluster of stamens and styles in the center of the flower which, although they vary greatly in details, preserve the same general orientation from a gross point of view. In other words, these flowers tend to be conservative in those aspects concerned with attracting, orienting, and rewarding pollinators.

The data on pollination of neotropical Malpighiaceae are meager, with observations available for only about 30 species, but all observers seem to agree that

the only visitors to these flowers are Hymenoptera belonging to a few families. Vogel (1974: 245-246) lists his own and previous workers' observations of visits by female bees belonging to the anthophorid tribes Centridini (*Centris* and *Epicharis*) and Exomalopsini (*Paratetrapedia*), with the great majority of visits by Centridini. He lists visits to species of *Banisteriopsis* (as *Banisteria*), *Bunchosia*, *Byrsonima*, *Heteropterys*, *Malpighia*, *Stigmaphyllon*, and *Tricomaria*. S. L. Buchmann (pers. comm.) has collected female oil-collecting *Centris* pollinating *Aspicarpa* (*C. atripes* and *C. neomexicana*) and *Janusia gracilis* (*C. atripes*) in Arizona. K. S. Bawa (pers. comm.) saw *Byrsonima crassifolia* in Costa Rica visited by several species of *Centris* and several species of *Trigona*. Gates (1977) reported large anthophorid bees taking oil and small trigonid bees collecting pollen in four species of *Banisteriopsis*. I have observed the same two groups of bees on diverse species of *Banisteriopsis* (including *Centris collaris* Lepeletier on "*Banisteria*" *oxyclada* Jussieu), *Byrsonima*, *Heteropterys*, and *Schwannia*; in addition, vespid wasps seem to collect pollen from the flowers of *Lasiocarpus* and occasionally *Banisteriopsis*.

The behavior of the anthophorid bees is as follows: The bee lands on the center of the flower with her head toward the flag petal and often grasps the thickened claw of that petal with her mandibles. Then she reaches between the claws of the lateral petals and scrapes the oil from the calyx glands with her front legs or front and middle legs. Pollen adheres to the underside of the bee and is presumably transferred to the stigmas of subsequently visited flowers. Given this behavior, it is not surprising that many genera have lost the glands from the anterior sepal, since the orientation of the bee and the restriction of oil-gathering to the front or front and middle legs (Vogel 1974) make the glands of the anterior sepal inaccessible unless the bee turns around. According to Vogel, the female bee transfers the oil and pollen to the hairy hind legs and takes the mixture to her nest, where it serves as food for her larvae. The adult bees of both sexes are nourished by sugary nectar obtained from other bee-plants.

The trigonid bees do not preserve any particular orientation with respect to the flag petal, and seem to collect only pollen. As mentioned above, the connectives are enlarged and apparently glandular in some Malpighiaceae, and it is possible that vectors collecting pollen also collect some secretion from such connectives. No one has determined what, if any, secretion is produced by these connectives.

From these limited observations it appears that

oil and pollen are the only rewards offered to pollinators of neotropical Malpighiaceae, and that their flowers attract an extremely limited clientele, principally female anthophorid bees collecting oil and/or pollen and *Trigona* spp. collecting pollen. The features of the flower that were described above as being especially constant all seem to be related to pollination by oil-bees—the calyx glands, the clawed petals that give most convenient access to the external glands from a landing-place in the center of the flower, and the zygomorphic corolla with a thickened posterior claw that can withstand clasping by the mandibles of the bee. The ubiquity of this syndrome of characters suggests that this peculiar flower with its mode of rewarding one group of very specialized pollinators characterized the ancestor of the Malpighiaceae and that its origin launched the group as a distinct entity. Other lines of evidence from my studies of comparative morphology and phylogenetic taxonomy in the family support that conclusion. Pollination by pollen-collecting bees (or perhaps wasps) was probably a secondary development in many groups, but in those relatively few cases where the calyx glands have been lost pollination has probably shifted wholly to such bees or wasps. For instance, *Lasiocarpus*, mentioned above as being visited by wasps, is one of the genera that lack calyx glands. In most groups that lack glands (e.g., *Galphimia* spp., *Lasiocarpus*, *Thryallis*) there is a tendency for the flower to be less zygomorphic, which supports the idea that the usual syndrome of characters is maintained through selection by oil-bees. In some of the more advanced eglandular species of *Galphimia* the anthers have become much larger, probably in response to selection by pollen-collecting pollinators (Anderson 1977, MacBryde 1970, Niedenzu 1928).

Compare this situation to that in the Polemoniaceae, described by Grant and Grant (1965) and discussed by Stebbins (1974). Starting from bee flowers, different evolutionary lines of Polemoniaceae have evolved adaptations for pollination by hummingbirds, butterflies, hawk moths, noctuid moths, beetles, bombylid flies, cyrtid flies, and bats. Polemoniaceae are ecologically no more diverse than Malpighiaceae, or not enough to explain the diversity of the flowers of one family versus the conservatism of the flowers of the other. However, the principal reward for pollinators of Polemoniaceae is a sugary nectar produced by a disc inside the base of the corolla, which, like most nectars (and unlike the oil of Malpighiaceae), can be used by diverse animals. Stebbins (1974: 64-65) points out that the shift from one kind of vector to another, and the con-

comitant evolution of a new character-syndrome, is only possible "via an intermediate stage during which both vectors are capable of pollinating the flowers." Plants that produce nectar, like Polemoniaceae, are often visited by a diverse assemblage of vectors, even if only one of them is the principal pollinator, so the stage is set for a shift to a radically different floral morphology in response to selection by a new principal vector, as might be expected with major changes in habit, habitat, or geographic range. The neotropical Malpighiaceae, however, have not had the diversity in their pollinating fauna that could have served as a bridge from one class of vectors to another and subsequent adaptive radiation in the flowers. Aside from oil-bees, the only secondary pollinators have apparently been pollen-collecting Hymenoptera, and the only major change that has occurred (and it has happened several times) is a shift to dependence on those vectors as primary pollinators. Even that change has been accompanied by only subtle changes in the flowers, presumably because the new vectors were attracted by the same general architecture as the old and did not favor major structural changes in the flower. Indeed, the pollen-collecting vectors may prove in some cases to belong to the same anthophorid genera as the oil-collecting bees. In two subgenera of *Centris* (*Xerocentris* and *Wagenknechtia*) the oil-collecting habit has been lost (S. L. Buchmann, pers. comm.). It is not yet known, however, whether any of these species pollinate Malpighiaceae.

My conclusion is that the floral conservatism of neotropical Malpighiaceae results from the early evolution of an almost obligate relationship with one group of very specialized pollinators. Grant and Grant (1965) collected a wealth of observations to support the thesis that floral morphology in the Polemoniaceae is the result of natural selection for adaptation to animal pollinators. The data from neotropical Malpighiaceae support the same thesis, but in this case the result has been conservatism instead of diversity.

Finally, a few comments about the paleotropical Malpighiaceae are in order. There are a modest number of species (ca. 150) scattered through the Old World tropics, all but two of them assignable to genera not found in the New World. The paleotropical genera were probably all derived from a few glanduliferous progenitors that reached Africa from South America when the two continents were still close enough to make dispersal of samaroid fruits between them feasible. A few of these genera still have calyx glands, at least in some species, but most

are eglandular (Niedenzu 1928). Since the oil-bees that pollinate neotropical Malpighiaceae are apparently not known from the Old World (Vogel 1974), it is tempting to speculate that the glands have been lost from most paleotropical lines in the absence of selection for their retention. However, the near absence of data on their pollination biology suggests caution. Vogel (1974: 175-176) cites only two references describing such observations in the Old World. It would be most interesting if someone working in the paleotropics would study the pol-

ination of glandular and eglandular Malpighiaceae there, with special attention to whether or not the glands secrete, what the vectors are, how they behave on the flowers, and what they collect as their reward.

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