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WILLIAM R. ANDERSON

Figures 115, 116; Plate 28

- *trees, shrubs, vines, and a few perennial herbs*
- *indument of unicellular hairs, usually 2-branched*
- *leaves usually opposite, simple, many with large multicellular glands on petiole, abaxial surface, or margins*
- *flowers mostly bilaterally symmetrical; 4 or all 5 sepals usually bearing 2 large abaxial glands; petals 5, mostly clawed; stamens mostly 10; ovary superior, mostly tricarpellate with the styles distinct; ovules 1 per locule*
- *fruits mostly schizocarpic and winged in vines, mostly unwinged and dry or fleshy in shrubs and trees*

Numbers of genera and species. Currently approximately 65 genera and 1,260 species of Malpighiaceae are recognized worldwide. Fifty genera and approximately 1,110 species occur only in the Western Hemisphere, except for two species found also in western Africa (*Heteropterys leona* and *Stigmaphyllon bannisterioides*). The largest genera, all of them mostly or entirely Neotropical, are *Banisteriopsis* (94 species), *Bunchosia* (68), *Byrsonima* (127), *Heteropterys* (136), *Stigmaphyllon* (92), and *Tetrapterys* (70). Sixteen genera have only one species.

Distribution and habitat. The Malpighiaceae have little tolerance for extreme cold and, therefore, show a typically tropical distribution. In the Western Hemisphere, a few species reach southern Florida, Texas, New Mexico, and Arizona, and in the south the family is moderately well represented to 35°S, the latitude of Buenos Aires; only a few species occur farther south, to about 39°S. A similar pattern exists in the paleotropics, but it is much less dramatic there because there are only about 150 species in the Eastern Hemisphere.

The great center of diversity of Malpighiaceae is South America north of the tropic of Capricorn. Except for Chile, which has only two species, all the countries in tropical South America have substantial numbers of species, Brazil having far more than any other. In the *cerrados* of Minas Gerais, Brazil, for example, there is an astonishing diversity of Malpighiaceae. Some species have extensive distributions (e.g., *Banisteriopsis muricata*, from Mexico to Argentina); but many more species are restricted to much smaller regions, and narrow local endemism is fairly common. Patterns of species richness differ from genus to genus; for example,

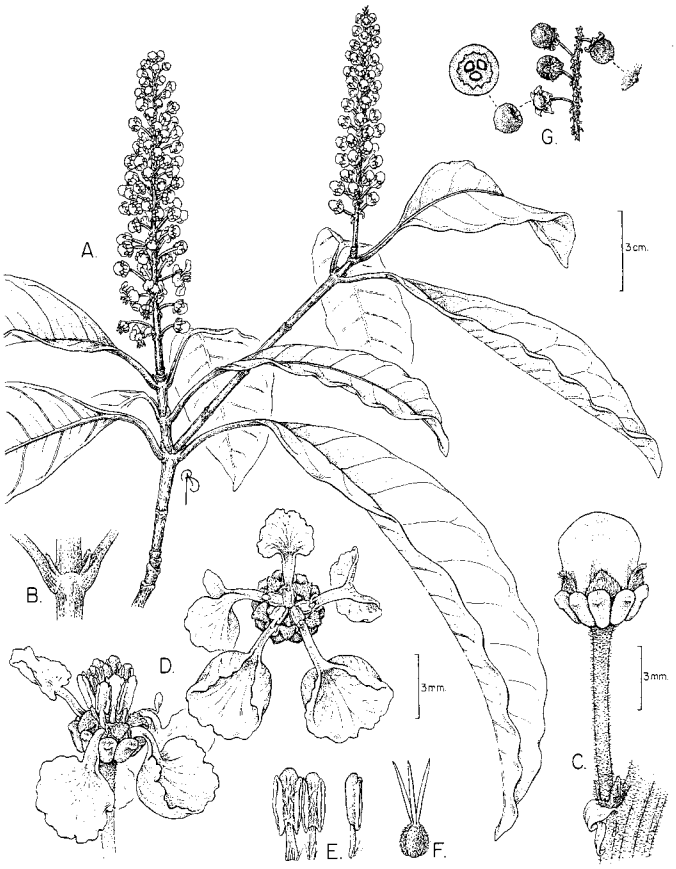

Figure 115. MALPIGHIACEAE. *Byrsonima aerugo*. **A.** Stem with leaves and inflorescences. **B.** Node showing petiole bases and connate intrapetiolar stipules. **C.** Lateral view of flower bud with sessile pedicel subtended by two short bracteoles and one long, reflexed bract; note oil glands on calyx. **D.** Lateral (left) and apical (right) views of flowers. **E.** Adaxial (left) and lateral (right) views of stamens. **F.** Lateral view of gynoecium. **G.** Part of infructescence with one fruit removed (center) and transverse section of fruit (left), showing three seeds in a common stony endocarp surrounded by fleshy mesocarp; detail of sericeous apex of fruit (above right). Reprinted with permission from Mori et al. (2002). Artist: Bobbi Angell.

Byrsonima has many species in southern Venezuela and the Guianas and rather few in Ecuador, while the reverse is true for *Stigmaphyllon*. The family is well represented in the tropical West Indies, but not in the extratropical Bahamas.

The Malpighiaceae have adapted to diverse habitats in the neotropics, including wet, mesic, and seasonally dry forests, shrubby savannas, and grasslands. Few grow high in the Andes because few can tolerate the temperatures at higher elevations, and few have succeeded in extreme deserts. Although they are not rare in wet forests like those of Amazonia, Malpighiaceae are more numerous in well-drained savannas like those of the Brazilian Planalto, and in the shrubby associations found in upland habitats of the Venezuelan Guayana.

Family classification. Cronquist followed earlier workers and put the Malpighiaceae in his order Polygalales, on the basis of morphological similarities. That placement is not supported by molecular data, and recent authors have recognized the morphologically diverse order Malpighiales, comprising Malpighiaceae, Euphorbiaceae, Passifloraceae, Violaceae, and other families. Both morphological and molecular data agree that the family is monophyletic, but so isolated that one still cannot say which families are closest to it.

The infrafamilial classification of the Malpighiaceae is in a state of flux. Earlier authors divided the family on the basis of fruits: two subfamilies with the fruits unwinged versus winged or bristly, with each subfamily then divided into tribes defined principally by details of the fruits. Some of these groupings have been supported by later studies that incorporated other aspects of the morphology and molecular data, but in many cases the family is proving to be much more complicated. William R. Anderson asserted many years ago that the three genera with similar fleshy fruits (*Bunchosia, Byrsonima*, and *Malpighia*) were quite unrelated to each other, and chloroplast DNA supports that conclusion. Bristly fruits like those found in *Echinopterys, Henleophytum, Lasiocarpus, Ptilochaeta*, and *Tricomaria*, rather than marking a natural and convenient tribe, clearly evolved independently at least three times in the family. While it does seem likely that the relative development of the lateral and dorsal wings on the samaras will continue to be useful in grouping many genera of wing-fruited vines, those "rules" have been violated a number of times. For example, *Heteropterys*, with a large dorsal wing, belongs in a clade of lateral-winged genera (a molecular result supported by the nonfruit morphology); on the other hand, *Diplopterys* and *Cordobia*, both with the lateral wing dominant, are sisters to genera with a dominant dorsal wing, and this result is supported by nonfruit morphology. A number of genera that are morphologically isolated are still not satisfactorily placed by molecules or morphology, and the large wing-fruited clade that comprises the vast majority of the family's genera and species is still poorly resolved. Nevertheless, certain things can now be stated with some confidence: 1) The Malpighiaceae probably originated in the Western Hemisphere and the Malpighiaceae of the Eastern Hemisphere are probably derived from at least eight independent dispersal events. 2) The original Malpighiaceae were very likely shrubs or trees, with the habit of woody vines evolving between one and four times. 3) The earliest Malpighiaceae probably produced fruits that lacked flesh, wings, or bristles; dispersal by water may have been ancestral. 4) The base chromosome number in the family was probably $x = 6$; however, all but the lowest branches of the family tree seem to have numbers based on $x = 10$, and that shift (perhaps by aneuploidy from an ancestor with $n = 12$) probably occurred at about the time of the origin of winged fruits. 5) The pollen was originally radially symmetrical, probably tricolporate, and the shift to globally symmetrical pollen happened once, at the base of the clade containing most of the wing-fruited genera. 6) Winged fruits may have evolved several times or once; but if only once, the wings were ± completely lost in several descendant clades. 7) There is a strong correlation between the vining habit and winged fruits versus the shrubby or arborescent habit and unwinged fruits, but the phylogenetic path to that correlation is probably not simple, suggesting repeated evolutionary convergence on an adaptive association of habit and method of dispersal.

As morphological data are combined with more and better molecular data, the resolution of the phylogeny of the Malpighiaceae should improve enough to allow the proposal of a new infrafamilial classification that will be both useful and phylogenetically accurate.

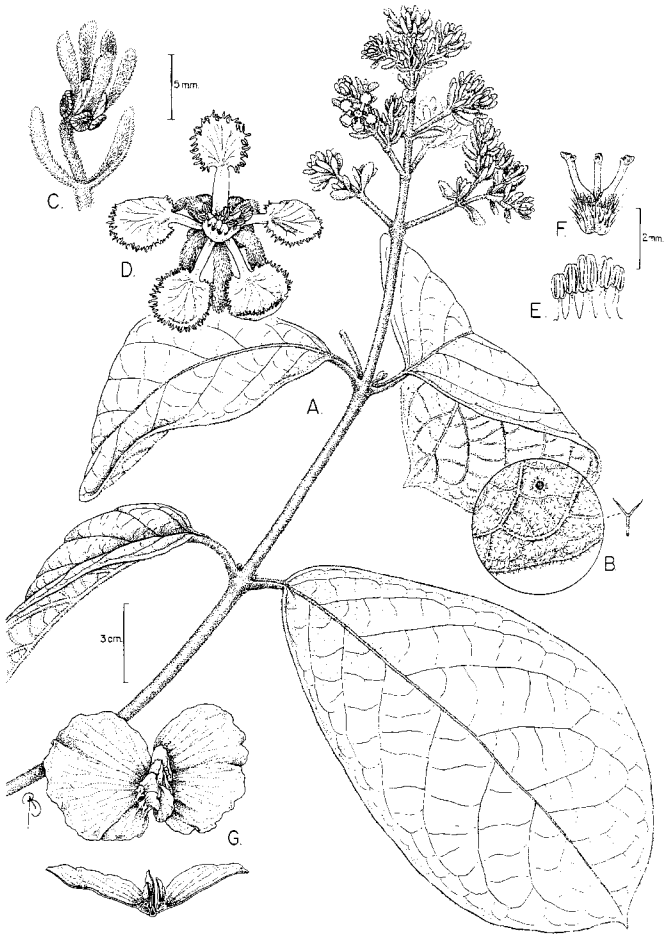

Figure 116. MALPIGHIACEAE. *Jubelina rosea*. **A.** Stem with leaves and inflorescence. **B.** Detail of abaxial leaf surface showing gland and stalked, bifurcate hair. **C.** Oblique-apical view of flower bud showing spatulate bracteoles and sepals, each lateral sepal bearing one large abaxial gland. **D.** Oblique-apical view of flower, the posterior petal uppermost. **E.** Adaxial view of part of the androecium; the central stamen would be opposite one of the posterior-lateral petals. **F.** Lateral view of gynoecium with anterior style in center. **G.** Abaxial view (above) and medial section of fruit (below). Reprinted with permission from Mori et al. (2002). Artist: Bobbi Angell.

Features of the family. Habit: Trees, shrubs, erect or trailing subshrubs or herbs with perennial underground stems, and woody to herbaceous, perennial vines that climb by twining stems. **Latex** rarely present (*Galphimia, Lophanthera, Spachea*, and *Verrucularia*). **Indument**: hairs always unicellular, usually 2-branched and medifixed or submedifixed, basifixed or stellate in a few genera. **Stipules** usually present beside or on the petiole or axillary to it, distinct or variously connate, minute to more than 14 cm long, absent in some genera or species. **Leaves** usually opposite and decussate, sometimes whorled, subopposite or alternate in a few genera or species, often bearing large multicellular glands on the petiole or blade (usually the abaxial surface or margin) or both; blade simple, mostly entire, rarely lobed, the margins never truly toothed but sometimes pseudodentate or ciliate at the location of marginal glands or stout bristlelike hairs. **Inflorescences** terminal or axillary, very diverse, most often racemose or paniculate but with the flowers often ultimately borne in umbels or corymbs of 4 or more. **Flowers** subtly to strongly bilaterally symmetrical in most Neotropical species with the plane of symmetry passing through the anterior (often eglandular) sepal and the posterior (often erect and differentiated) "flag" petal, a few radially symmetrical or nearly so, mostly bisexual, a few genera dioecious or functionally dioecious, hypogynous except perigynous in *Barnebya*, small (about 6 mm in diameter) to fairly large (about 4 cm diam.); sepals 5, mostly imbricate in bud, the great majority of Neotropical species bearing 2 (rarely only 1) large, multicellular, abaxial glands on all 5 sepals or on lateral 4 (most Paleotropical species with calyx glands much reduced in number and size or absent); petals 5, distinct, mostly clawed, alternating with sepals, imbricate, the posterior innermost and 1 of anterior-lateral pair outermost, most often yellow, pink, or white, sometimes other colors but very rarely blue; androecium usually of 10 stamens in a single whorl, the stamens sometimes fewer, up to 15 in *Lasiocarpus*, borne on receptacle between perianth and gynoecium, the filaments always present, short to long, alike or heteromorphic, distinct or partially connate, the anthers alike or heteromorphic, 4-locular, mostly longitudinally dehiscent along inner edge of each locule, with apical or subapical pores or very short slits in a few genera; gynoecium superior, usually comprising 3 distinct to connate carpels, mostly 1 anterior on plane of symmetry and 2 posterior on each side of plane of symmetry, the carpels only 2 in several genera and very rarely 4, mostly all fertile, each fertile locule containing 1 pendent anatropous ovule, the styles mostly as many as carpels and distinct, but connate or reduced in number in a few genera. **Fruits** fleshy or dry; fleshy fruits mostly an indehiscent drupe or berry, yellow, red, blue, or black; dry fruits indehiscent in a few genera, but schizocarpic in most, splitting apart into mericarps (typically up to 3); dry fruits or mericarps of some genera nutlets with smooth walls, those of some genera or species containing aerenchyma, but most bearing wings or bristles. **Seeds** 1 per locule or mericarp, never released (i.e., dehiscence never loculicidal, or at least not sufficiently so to allow the seed to escape); endosperm absent.

The family is easier to recognize in flower than in fruit because the flowers are so uniform, but once one has placed a plant in the Malpighiaceae, it is much easier to identify it to genus with fruits than with flowers because the genera are defined primarily by characters of the fruits.

Natural history. As noted above, most Neotropical Malpighiaceae are recognized easily by the large paired glands on the abaxial surface of the sepals and by the clawed petals. Stefan Vogel has shown that these structures are adaptations for pollination by oil-collecting bees, which land on the flower, reach between the petals (hence the importance of the space left by the claws), and collect the oil produced by the glands. They mix this oil with pollen and pack it into brood cells with one egg each, and the mixture eventually is consumed by the growing larvae. The flower produces no sugary nectar so, except for the oil, pollen is the only reward for pollinators. Malpighiaceae that have lost the calyx glands must rely on pollen to attract pollinators, and in some such groups (e.g., *Galphimia*) the anthers are enlarged. Almost nothing has been published on the pollination of these eglandular species. William R. Anderson has postulated that the Malpighiaceae now in the Eastern Hemisphere descended from several species that emigrated from South America to Africa after the separation of the continents. The oil-bees that pollinate Neotropical Malpighiaceae did not reach the Eastern Hemisphere, so it is not surprising that the calyx glands of Eastern Hemisphere species are mostly reduced or absent.

The majority of Malpighiaceae in the Western Hemisphere have winged or bristly fruits adapted for dispersal by wind. Three Neotropical genera (*Bunchosia, Byrsonima*, and *Malpighia*) produce edible, fleshy fruits that presumably are bird-dispersed. Several genera, mostly trees that grow along Amazonian rivers, have smooth aerenchymatous fruits that surely are dispersed by water, and scattered species in genera with winged fruits have more or less completely lost their wings and become adapted secondarily for water dispersal. Finally, a number of genera, most relatively near the base of the phylogenetic tree, produce small, smooth, dry fruits without any obvious adaptation for dispersal. These fruits, generally 1 to several millimeters in diameter, presumably are dispersed by wind or rainwater. It is difficult to understand how some of those groups (e.g., *Pterandra*) have achieved their extensive present-day distributions.

Economic uses. The Malpighiaceae are of modest economic importance. One of the species with fleshy fruits, *Malpighia emarginata* (often erroneously called *M. punicifolia*), has long been cultivated for the red cherrylike fruits, which are rich in vitamin C. It bears many common names, of which the ones most frequently encountered are *acerola* and Barbados cherry. In recent years, manufacturers of vitamins have

taken to adding vitamin C from *M. emarginata* to their concoctions in order to make them more "natural" (and correspondingly more expensive), and commercial plantations for the cultivation of the species exist in Mexico and probably elsewhere. The fruits of *Byrsonima crassifolia*, which look like yellow cherries, are consumed commonly in Mexico, Central America, and northern South America. In Spanish-speaking areas, the common name is usually *nance* or *nanche*, whereas in Brazil it is *muricí* or *murucí*. *Bunchosia glandulifera* has a pleasant-tasting fruit the size of a small plum and surely has been cultivated by indigenous peoples in South America for a very long time; it is not known from unequivocally wild populations. Fruits of various other species of *Bunchosia, Byrsonima*, and *Malpighia* are consumed from Mexico to Brazil, and the plants (all shrubs or small trees) often are grown in dooryards, both as ornamentals and for the fruits.

A number of other Malpighiaceae are planted as ornamentals, and some are available in warm regions from nurseries. The commonest of these is *Galphimia gracilis* (often misidentified as *G. glauca*), a shrub with bright yellow flowers that give it common names like *lluvia de oro, ramito de oro*, and spray of gold. Other Neotropical species popular in warm gardens and greenhouses are *Malpighia coccigera* (Singapore holly), *Stigmaphyllon ciliatum* (Brazilian gold vine), and *S. floribundum* (orchid vine). *Lophanthera lactescens*, a handsome tree with long inflorescences of yellow flowers, is known in the wild from only one small area in eastern Amazonia, but it thrives when planted along busy, polluted streets and is now popular in towns and cities throughout Brazil. Two species native to the Eastern Hemisphere are cultivated occasionally in the neotropics, *Hiptage benghalensis* and *Tristellateia australasiae* (*bagnit*). Many other members of the family are very showy and, hence, are also candidates for cultivation.

At least one member of the family, *Banisteriopsis caapi*, is a potent hallucinogen and has become famous among those interested in drug plants under its scientific name and such vernacular names as *ayahuasca, caapi*, and *yagé*. It is cultivated widely in Amazonian South America, where it is used by native populations as one ingredient in the preparation of a beverage that is said to produce spectacular multicolored visions after some hours of preliminary vomiting.

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