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The Origin of the Malpighiaceae—The Evidence from Morphology

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Abstract

Anderson, W. R. (University of Michigan Herbarium, North University Building, Ann Arbor, MI 48109-1057, U.S.A.). The origin of the Malpighiaceae—The evidence from morphology. Mem. New York Bot. Gard. **64:** 210–224. 1990. The Malpighiaceae are a family of some 1200 flowering plants, of which 85% are neotropical and the rest paleotropical. Their habits and fruits are very diverse, especially in the New World, while the flowers are relatively uniform. Calyx glands in most neotropical species secrete oils gathered by pollinating bees, but the glands present on the sepals of four genera in the Old World, where the oil-bees that visit malpighs do not occur, produce sugary nectar similar to that produced by the anatomically similar extrafloral nectaries found on foliar organs in both hemispheres. The inflorescence in most Malpighiaceae is based on single-flowered units, but in ten neotropical genera those units may be cymules. Among diverse pollen types the ancestral condition seems to be colporate. A hypothetical ancestor based on characters that hardly vary supports Engler's view that the Trigoniaceae and Vochysiaceae are the families closest to the Malpighiaceae. An analysis utilizing them as outgroups leads to the conclusion that the likeliest ancestral character-states (inflorescence of cymules, colporate pollen, and dry dehiscent fruits) are heavily concentrated in the New World subfamily Byrsonimoideae, hence my "American" hypothesis that the family originated in the New World in effective isolation from the Old World. I contrast that with Vogel's "Gondwanian" hypothesis, based on the structural and functional similarity of Old World calyx glands to extrafloral nectaries; he proposed that the family originated before the breakup of Gondwanaland and the New World species acquired their oil-producing calyx glands after separation from their Old World relatives. I discuss some of the problems inherent in these hypotheses, and conclude with the hope that new molecular data will enable us to break the impasse imposed by the limitations of the morphological evidence.

Dedication

Almost twenty years ago, in 1971, I completed my Ph.D. and accepted a research position at the New York Botanical Garden. Although my doctoral thesis treated a genus of the Rubiaceae, my real interest since undergraduate days had been the Malpighiaceae, and I was hired at New York to pursue that interest. During my three years at New York, and subsequently at The University of Michigan, I have had the opportunity to study and describe the wonderful series of collections from northern South America amassed by Bassett Maguire and his collaborators. That treasure continues to provide material and inspiration for my research, and I am often moved to consider how impoverished my career would have been if Bassett had not had the vision, determination, and force of personality to do what he did in the Guayana Highland. It is thus with admiration and appreciation for his extraordinary achievements that I dedicate this paper to Bassett Maguire.

Background Information

The Malpighiaceae are a medium-sized family of tropical and subtropical flowering plants, comprising some 1200 species assigned to 66 genera. About 85% of the species occur in the New World, and the balance in the Old World. With two exceptions, no genus or species occurs in both hemispheres. *Stigmaphyllon ovatum* (Cav.) Nied., a Caribbean and Atlantic coast species of a large American genus, has been collected several times in western Africa. *Heteropterys leona* (Cav.) Exell is a well-established species of western Africa, but only with difficulty can it be distinguished from its closest relatives in the Caribbean and on the Atlantic coast of Central and South America, *H. platyptera* DC. and *H. multiflora* (DC.) Hochr. The rest of *Heteropterys,* a genus of some 100 species, is entirely American. All writers who have considered these two disjunctions agree that they have probably resulted from dispersal from Atlantic America to western Africa in geologically recent times. I would be willing to go further and suggest that at least the *Stigmaphyllon* may have been introduced into Africa accidentally by humans in the last several centuries. The *Heteropterys* was described from Africa rather early (Cavanilles, 1790), but even that was long after regular transatlantic travel began, and I cannot help wondering whether *Heteropterys leona* might also be a recent transplant from America. In any case, those two paleotropical plants can be excluded from further discussion here, and when I refer below to the Old World Malpighiaceae my comments will not apply to *Stigmaphyllon ovatum* or *Heteropterys leona.*

While the flowers of the Malpighiaceae are rather uniform, the fruits are extremely diverse (Anderson, 1979b). For that reason, since the time of Linnaeus fruit characters have furnished the most important bases for recognizing genera and for grouping those genera in tribes and subfamilies. In the New World the full range of fruit types occurs, including indehiscent fruits, both fleshy and dry, and dry dehiscent fruits that may be unwinged, bristly, or variously winged. The winged mericarps are mostly of two types, that in which each mericarp has its principal wing dorsal (hereafter referred to as banisterioid) and that in which the principal wings are lateral (hiraeoid). In the Old World genera the fruits are always dry and winged, and with one exception they dehisce into samaras resembling the two principal samara types found in the New World. On that basis Niedenzu (1928) assigned all the Old World genera to two tribes, Banisterieae (those with banisterioid samaras) and Hiraeeae (those with hiraeoid samaras); each tribe was dominated by a large number of New World genera having similar fruits. I have long felt that Niedenzu applied his fruit characters too mechanically, thereby creating several very artificial groupings of genera. My recognition of the wholly American subfamily Byrsonimoideae (1977) was a first step in correcting those excesses. The Byrsonimoideae have fruits that are indehiscent or dehiscent and fleshy or dry, but none are bristly or winged. That paper did not address the problem of the relationships of the Old World Malpighiaceae, which has been complicated somewhat since the time of Niedenzu by the description of *Rhynchophora* (Arènes, 1946), a plant of Madagascar with a most peculiar winged but indehiscent fruit.

All Malpighiaceae are perennials. In habit they include herbaceous stems from a thickened base, shrubs of all sizes, small to large trees, and twining vines varying from slender and subherbaceous to woody lianas that reach the tops of the tallest rainforest trees. No member of the subfamily Byrsonimoideae is a vine; all are trees or shrubs. Both twining and erect habits are found among the non-byrsonimoids of both New and Old Worlds, but the great majority of those many species are vines.

In the New World most species of Malpighiaceae bear large paired multicellular abaxial glands on four or all five of the sepals (Fig. 5C, D). Although they are outside the flower, those glands are accessible to bees visiting the flower because the clawed petals leave a space through which the bee can reach. In a landmark monograph, Vogel (1974) showed that those calyx glands, which he called elaiophores, produce oils that are gathered by female anthophorine bees of the tribe Centridini. Lobreau-Callen (1989) has recently confirmed his findings by analyzing the secretions from the calyx glands of several genera, although she did find traces of sugars in addition to a preponderance of lipids. I have suggested (1979b) that the reason the flowers of neotropical Malpighiaceae are so uniform, in genera that are very diverse in habit and fruit, is that their evolution has been constrained by their dependence on oil-bees for pollination. Most members of the Byrsonimoideae have ten calyx glands, two on each of the five sepals. Most non-byrsonimoids in the New World have only eight calyx glands, on the four lateral sepals; the anterior sepal, which is inaccessible to the bee when she is oriented toward the posterior "flag" petal, is eglandular in those species. A moderate number of New World Malpighiaceae lack calyx glands completely, and are presumably pollinated by bees for which the only reward is pollen.

Most genera and species of Malpighiaceae, in both the New and Old Worlds, bear multicellular glands on various foliar organs—vegetative leaves, reduced inflorescence leaves, bracts, and bracteoles. These glands are usually borne on the petiole or the abaxial surface of the lamina; in one species (*Spachea correae* Cuatr. & Croat) they occur on the adaxial leaf surface, and in several byrsonimoids (*Lophanthera* spp., *Spachea* spp.) one or both of the bracteoles may terminate in a large stalked gland (Fig. 5A, C). It is common for field botanists to observe ants removing the nectar from the glands on young leaves and bracts of Malpighiaceae, so it comes as no surprise that when those secretions have been analyzed (Vogel, 1974: 64; Lobreau-Callen, 1989: 82) they have proved to be rich in sugars and lacking the oils present in the secretions from neotropical elaiophores. Although these extrafloral nectaries are very diverse in size (less than 0.5 mm to 4 mm or more in diameter) they are quite similar in their basic anatomy to each other and to the elaiophores found on the sepals of most neotropical Malpighiaceae (Vogel, 1974: 64). The extrafloral nectaries often occur as paired structures borne abaxially and near the base of leaves and bracts, in a position analogous to the position of neotropical elaiophores on sepals. On the basis of those structural and positional similarities, Vogel (1974: 64–69; 1990) has asserted that the two kinds of glands must surely be developmentally and evolutionarily homologous, in spite of their different secretions.

The oil-bees that pollinate most New World Malpighiaceae do not occur in the Old World (Vogel, 1974). Almost no one seems to have published good field observations on the pollination of Old World Malpighiaceae, but the large size of their anthers suggests that they reward their pollinators with pollen. Since the oil-bees are not available, it is not surprising that most Old World Malpighiaceae lack calyx glands. According to the descriptions of Niedenzu (1928) and Arènes (1950, 1954) only four genera bear calyx glands. In *Hiptage,* which has hiraeoid samaras, most species have one very large elongated gland, borne on the commissure between the two posterior sepals and decurrent onto the pedicel. Four of the 27 species of *Hiptage* have one to several small glands, and two have an eglandular calyx. *Tristellateia* is a genus of some 25 species, most of them endemic to Madagascar. According to Arènes (1950) some of them have the calyx always eglandular but most bear 1–10 small calycine glands in at least some populations. The 29 species of *Acridocarpus* and its closely related segregate *Rhinopterys* have banisterioid samaras and small calyx glands varying in number from none to ten and in position from commissural to (apparently) abaxial and paired (*A. ferrugineus* Engler, fide Niedenzu, 1928: 264). Vogel (1974: 66–67) has investigated the anatomy of the calyx glands in *Hiptage benghalensis* (L.) Kurz and *Acridocarpus smeathmannii* (DC.) Guill. & Perr. and reports that it is similar to that of neotropical elaiophores and extrafloral nectaries in both hemispheres; in details he finds the paleotropical calyx glands to be more like extrafloral nectaries than neotropical elaiophores. On the basis of those structural similarities he considers the Old World calyx glands to be homologous with elaiophores and extrafloral nectaries, in spite of the fact that they are usually not paired. On the same pages Vogel cites previous work indicating that the gland of *Hiptage benghalensis* produces a sugary nectar and is therefore not an elaiophore as defined by Vogel. He himself investigated the calycine secretions in *Acridocarpus smeathmannii* and found abundant production of a nectar rich in sugars and lacking lipids. These results have been confirmed recently for the same two species by Lobreau-Callen (1989).

In most Malpighiaceae each flower is borne on a pedicel, subtended by two bracteoles borne at the apex of a peduncle, which is in turn sub-

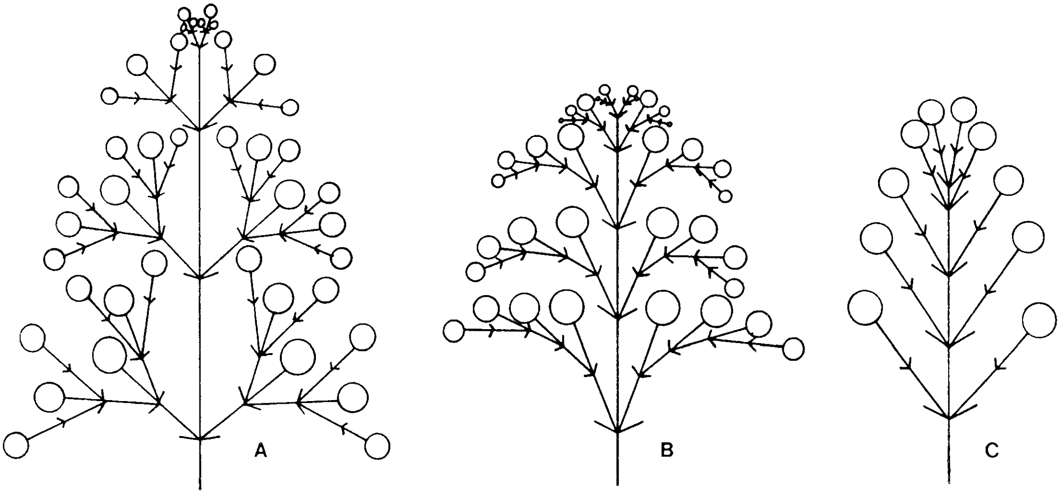

FIG. 1. Inflorescence types in the Malpighiaceae. **A.** Raceme of dichasia; known in the Trigoniaceae and postulated for the Malpighiaceae; the inflorescence diagrammed here is more elaborate than that of *Lophanthera lactescens,* the only malpigh in which dichasia occur. **B.** Raceme of cincinni; known in 10 genera of neotropical Malpighiaceae. **C.** Pseudoraceme (raceme of 1-flowered cincinni); this and condensed derivatives of it are present in all other Malpighiaceae, comprising 56 genera, and in some species in 4 of the genera that show condition B. I interpret evolution of these inflorescences as a reduction series proceeding from A to C.

tended by a single bract (Fig. 1C). In all or some speices of ten neotropical genera one finds cymules instead of the one-flowered units described above. The difference consists in the fact that one of the two bracteoles subtends a shoot comprising a peduncle, two bracteoles, and a pedicellate flower; one of those two bracteoles is in turn fertile, and so on, resulting in a cincinnus of 2–10 flowers (Figs. 1B, 5A, C). Those genera are *Barnebya, Blepharandra, Burdachia, Byrsonima, Diacidia, Glandonia, Lophanthera, Mcvaughia, Spachea,* and *Verrucularia.* All of those except *Barnebya* belong to the subfamily Byrsonimoideae (Anderson, 1977, 1979a). In one byrsonimoid species (*Lophanthera lactescens* Ducke) the cymules are often dichasia instead of cincinni, i.e., both bracteoles subtend flowers instead of only one (Fig. 1A). *Barnebya* is an anomalous genus of uncertain affinities (Anderson & Gates, 1981; Lowrie, 1982). All other neotropical Malpighiaceae, and all paleotropical species, have as the ultimate units of the inflorescence single flowers instead of cincinni.

The pollen of the Malpighiaceae is extremely diverse, and I cannot begin to do justice to that diversity here. For descriptive treatments see Lowrie (1982) and Lobreau-Callen (1983 and earlier papers cited therein, especially 1967). The simplest way to summarize the diversity in the family's pollen is to say that it is either colporate with equatorial pores and colpi at right angles to the equator (or some obvious variant on that theme), or porate with the pores mostly nonequatorial and the ectoapertures variously oriented and modified, or lost completely. Figure 2 shows examples of tricolporate (A & B) and tetracolporate (C) pollens, as well as two very different porate pollens, one with ectoapertures (D) and one without them (E). Lowrie's figure 3.2 is reproduced here (Fig. 3) as a nice summary of the bewildering diversity in the family's pollen. As that shows, Lowrie considered tricolporate pollen to be ancestral in the family and all other types to have been derived from it, ultimately. Lobreau-Callen (1983) also summarized the pollen of Malpighiaceae as either "colporées" or "porés" and assumed that colporate pollen was ancestral in the family. The reason for their agreement on this point is obvious when one considers the distribution of pollen types in the fossil record and in extant families of the Rosidae (Walker & Doyle, 1975; Cronquist, 1981: 521). Tricolporate pollen is common in both, while the bizarre "porate" types of pollen shown in Figure 2 are scattered; indeed, at least some of the grains found in the Malpighiaceae are probably peculiar to this family. Tricolporate pollen or types clearly derived from it (syntricolporate, parasyntricolporate, and tetracolporate) are found in all genera of the wholly New World subfamily Byrsonimoideae, and polycolporate pollens (pores and colpi 5–8) occur in the New World genera *Dinemagonum, Dinemandra, Lasiocarpus,* and *Ptilochaeta.* In the Old World syntricolporate pollen is found only in *Acridocarpus* and its segregate *Rhinopterys* (Lowrie, 1982; Lobreau-Callen, 1967, 1983). According to Lobreau-Callen (1983), *Brachylophon* has "colporate" pollen; she did not say how many pores and colpi are present, and Lowrie did not see material of that genus. Lowrie (1982) and Lobreau-Callen (1967, 1968) both reported *Rhyncophora* to have tricolporate pollen, but in her 1983 paper Lobreau-Callen described it as "inaperturé" (p. 874) without explaining her change in opinion. I am assuming that the earlier reports, including her 1968 drawing, of tricolporate pollen in *Rhynchophora* were correct. All other Old World Malpighiaceae, as well as the majority of New World Malpighiaceae, have various kinds of "porate" pollens considered derived by both Lobreau-Callen and Lowrie. Lobreau-Callen (1983: 876, 879) thought that, for the most part, the porate pollens of the Old World are more similar to each other and to the colporate pollens of both hemispheres than they are to the porate pollens of the New World. She derived the Old and New World porate pollens independently from tricolporate ancestors. Lowrie (pp. 321–323) agreed that most porate Old World pollens are coherent in morphological groups that reflect their geography, but he related two of those groups loosely to two New World groups with porate pollen, and he placed one anomalous Old World genus (*Flabellaria*) within one otherwise neotropical subgroup.

Hypotheses of the Origin of the Malpighiaceae

THE "AMERICAN" HYPOTHESIS

I have suggested (1979b) that the Malpighiaceae originated and diversified in the neotropics, in a close coevolutionary relationship with New World oil-bees, presumably after the separation between South America and Africa was sufficiently great to prevent the ready migration of the plants and their bees across the widening Atlantic. I speculated that the Old World Malpighiaceae, all with wind-dispersed samaras, descended from two or more New World Malpighiaceae that were dispersed from west to east, and further that in the Old World, where oil-bees were not present, the elaiophores degenerated into the calyx glands still present in some species or were eventually lost. Implicit in my speculation was the assumption that the ancestral Malpighiaceae had unwinged fruits ill-adapted to long-distance dispersal, and it was not until more dispersible samaras evolved that the family succeeded in crossing the gap from New World to Old. These ideas had been summarized earlier by Raven and Axelrod (1974) on the basis of my personal communications to Peter Raven.

Arènes (1957) also suggested that the center of origin of the Malpighiaceae was the area in Brazil, the Guianas, and Venezuela where the Malpighiaceae are most numerous and diverse. While it is intuitively tempting to equate center of diversity with place of origin, the idea has been generally discredited and will receive no further consideration here.

My conviction that the Malpighiaceae originated in the neotropics has always depended on the distribution of the character-states that I consider to be ancestral in the family. I have made passing reference to this relationship (e.g., 1981: 22–23; 1983), and Cronquist cited personal communications from me (1981: 771), but I have not elaborated my reasoning in print, which led Vogel (1990) to assume, erroneously, that my hypothesis rested upon the distribution of calyx glands. I shall correct that misimpression here.

The neo-orthodoxy of cladism would dictate that I polarize characters by comparing the character-states in the Malpighiaceae with those found in appropriate outgroups. While I find it impossible to achieve that ideal fully, I agree that in making this kind of argument one should at least be explicit about one's reasons for asserting that any character-state is relatively plesiomorphic or apomorphic, and that much I shall do.

The Malpighiaceae are morphologically rather isolated—there are no transitional forms or obviously closest sister taxa. Every plant I have studied was either clearly assignable to the family or readily excludable from it. (The only group about which I have ever had the slightest doubt is the Brazilian genus *Thryallis.*) It seems to me

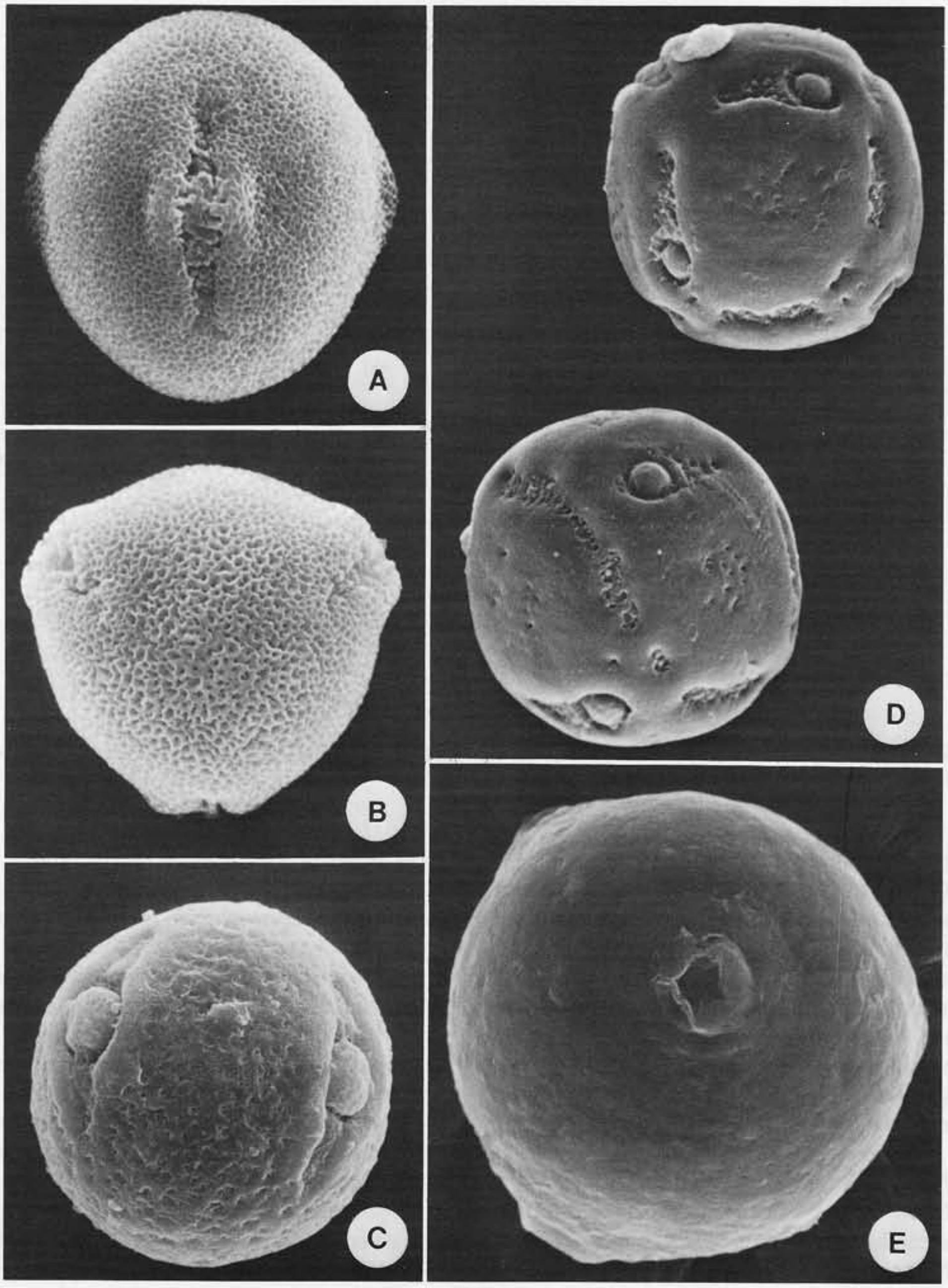

FIG. 2. Pollens of neotropical Malpighiaceae. **A & B.** *Lophanthera longifolia* (H.B.K.) Grisebach, ×3500 (*Prance 26646*). **C.** *Mcvaughia bahiana* W. R. Anderson, ×2500 (*Anderson 11740*). **D.** *Janusia occhionii* W. R. Anderson, ×1700 (*Anderson 11151*). **E.** *Bunchosia decussiflora* W. R. Anderson, ×1500 (*Silva & Brazão 60612*).

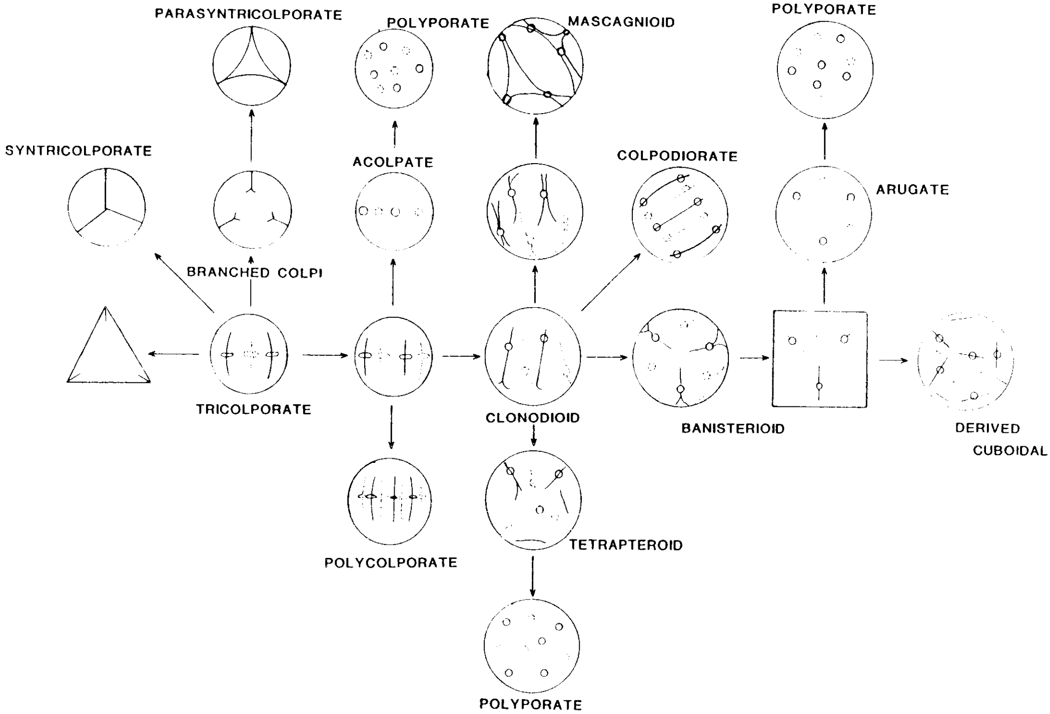

FIG. 3. Lowrie's summary of pollen types in the Malpighiaceae, with all types derived from the tricolporate condition. From figure 3.2 in Lowrie (1982: 38).

that the appropriate method for selecting one or more closest outgroups is to describe the "ur-malpigh" and then compare that description to families that have been suggested as putative relatives. Below I list the character-states that I would expect to find in such an ancestor, on the basis of their ubiquity or near-ubiquity in extant Malpighiaceae. For each character I have added qualifying comments as to that character-state's occurrence.

1. *Habit perennial*—always.
2. *Habit woody*—mostly; a few have minimal secondary growth.
3. *Hairs unicellular*—always.
4. *Hairs 2-armed*—mostly; a few have basifixed hairs, but most are clearly secondarily so with some hairs showing a rudimentary second branch as a basal spur; three otherwise dissimilar clades (*Bunchosia* spp., *Byrsonima* spp., and *Thryallis*) have hairs with more than 2 arms.
5. *Leaves opposite*—mostly; a few taxa have whorled or subopposite leaves, and a very few have them alternate.
6. *Leaves unlobed*—mostly; some *Stigmaphyllon* spp. have lobed leaves.
7. *Leaf margins entire*—always; some are pseudodentate at insertion of glands, cilia, or bristlelike hairs.
8. *Stipules present*—mostly; much reduced in some, to occasionally lacking.
9. *Multicellular extrafloral nectaries present*—mostly; absent from a few species or genera.
10. *Flowers hermaphroditic*—mostly.
11. *Sepals 5*—always.
12. *Petals 5*—always.
13. *Petals clawed*—mostly.
14. *Stamens 10*—mostly; fewer in a few species or genera; very rarely more.
15. *Extra- and intrastaminal nectaries lacking*—always.
16. *Carpels 3*—mostly; 2 in a few clades; very rarely 4.
17. *Styles as many as carpels*—mostly; rarely fewer.

18. *Styles distinct*—mostly; coherent or connate in a few clades.
19. *Ovules 1 per carpel*—always, except where aborted; never 2 or more.
20. *Endosperm lacking in mature seeds*—always, as far as I know.

Bentham and Hooker (1862) placed the Malpighiaceae near the families that have often been grouped as Geraniales and Linales. The plant described above as our "urmalpigh" is most unlike the former (Oxalidaceae, Geraniaceae, Balsaminaceae, Tropaeolaceae, and Limnanthaceae), so they are easy to eliminate from consideration as candidate outgroups. Most of the Linalean families also differ significantly from my urmalpigh; for example, the Humiriaceae have an intrastaminal disk, endospermous seeds, usually five carpels, one style, mostly more than ten stamens, and often toothed leaves. The closest fit among the Linalean families is the Erythroxylaceae, although its alternate leaves and endospermous seeds weigh heavily against choosing it as closest sister group.

The competing view, since the time of Engler (1897), has been that the families closest to the Malpighiaceae are the Trigoniaceae and Vochysiaceae. Takhtajan (1980), Cronquist (1981), Dahlgren (1983), and Thorne (1983) all agreed that the families closest to the Malpighiaceae are the Trigoniaceae, Vochysiaceae, Polygalaceae, and Krameriaceae, with the first two generally favored. Comparing my urmalpigh with the data I can gather about these families, I have to agree that the Trigoniaceae and Vochysiaceae do seem to be the two families most like the Malpighiaceae, although both differ significantly from the plesiomorphic malpigh characters. Thus in Trigoniaceae there are intrafloral nectaries, there is only one style, and the seeds are endospermous. In Vochysiaceae there is only one style, the ovules are mostly two or more per carpel, and the stamens are never as many as ten. Nevertheless, at this time those two families, and especially the Vochysiaceae, seem to be the best candidates for closest sister taxa to the Malpighiaceae.

Now that we have reinvented Engler's wheel, can we polarize characters that vary within the Malpighiaceae? Only a few, as it turns out, but I shall do what I can, using a combination of outgroup and ingroup arguments and identifying them as such so that cladistic purists will know which to reject immediately. The source of most of my morphological data was Cronquist (1981). I also consulted the monograph of Trigoniaceae by Lleras (1978) and studied specimens of Trigoniaceae and Vochysiaceae in the University of Michigan Herbarium.

Geographical Distribution

Both Trigoniaceae and Vochysiaceae occur principally in the neotropics, but there are two species of the former and one of the latter in the Old World. If numbers count, outgroup comparison would favor a New World origin for the Malpighiaceae, but caution is in order. The two paleotropical Trigoniaceae (*Humbertiodendron* and *Trigoniastrum*) have uniovulate locules more like those of Malpighiaceae than most New World Trigoniaceae, and the fruit is a schizocarp with three samaras that are impressively reminiscent of the fruit in the neotropical malpigh genus *Barnebya.*

Habit

Both outgroups include trees, shrubs, and woody vines, although the latter are rare in the Vochysiaceae. Therefore, one cannot on the basis of strict outgroup comparison specify the plesiomorphic habit in Malpighiaceae. I confess to an intuitive bias in favor of viewing vines as derived from shrubs, but it is clear that woody vines can give rise to shrubs and even small trees, as in *Banisteriopsis* spp. in central Brazil, so it is not impossible that a woody vine was ultimately ancestral to all the Malpighiaceae, even the large trees of the Byrsonimoideae.

Inflorescence

I believe that the single-flowered units found in most Malpighiaceae have been derived from several-flowered cymules. That sequence is diagrammed in Figure 1. It is based on Besseyan reductionism—the belief that reduction is evolutionarily easier to achieve than elaboration, especially once a certain point of no return has been passed, in this case the ability to make cymules of more than one flower. Secondarily elaborated inflorescences are common in the Malpighiaceae, but they consist of branched inflorescences composed of many single-flowered units. In the

Vochysiaceae the inflorescence is usually a raceme of cincinni, just like the inflorescence found in many neotropical Byrsonimoideae. In the Trigoniaceae one can find the same racemes of cincinni (e.g., *Trigonia virens* Macbride) as well as various degrees of reduction in the cincinni, terminating in single-flowered units. One also encounters racemes of dichasia, e.g., in *Trigonia rugosa* Bentham. Recall that dichasia occur in one byrsonimoid species, *Lophanthera lactescens.* That is the condition I postulate to have been ancestral in the Malpighiaceae. I would therefore claim that outgroup comparison supports my ingroup argument, but I admit that the presence in the Trigoniaceae of inflorescences with single-flowered units weakens that claim. Unlikely as it seems to me, it is possible that an ancestor with inflorescences constructed from single-flowered units gave rise to descendants with cincinni and dichasia in both Trigoniaceae and Malpighiaceae.

Calyx Glands

Neither the Trigoniaceae nor the Vochysiaceae have abaxial glands on the sepals, so the glands for which the Malpighiaceae are famous are clearly an apomorphy of that family. Does that mean that every malpigh with an eglandular calyx has the plesiomorphic condition? Surely not. Among the neotropical Malpighiaceae one finds eglandular calyces at every taxonomic level—individuals within populations and populations within species (e.g., *Byrsonima* spp., *Heteropterys* spp.), species within genera (e.g., *Banisteriopsis, Byrsonima, Galphimia, Pterandra*), eglandular genera with sister genera that have glandular calyces (e.g., *Echinopterys*), and isolated genera or clusters of genera with eglandular sepals (e.g., *Coleostachys*; *Lasiocarpus* and *Ptilochaeta*; *Thryallis*). While it may well be that among all these taxonomically scattered cases there lurks a species or genus that retains the plesiomorphic eglandular condition, it would be patently absurd to suggest that they *all* show the eglandular condition through unbroken inheritance from an eglandular ancestor. Moreover, I know of no way to examine an eglandular calyx and state objectively on the basis of its morphology alone whether it is primitively or secondarily eglandular. I would be willing to guess in cases where the eglandular plant were embedded within a glanduliferous species or genus, but I really would not be ready to say that *Coleostachys,* for example, could not have retained the eglandular calyx of an urmalpigh. Among the neotropical Malpighiaceae with elaiophores (the vast majority), ten glands on five sepals seem likely to have preceded eight glands on four sepals. This is another Besseyan argument. I assume that it was originally developmentally simplest to make five similar sepals, and that selection eventually (and perhaps repeatedly) favored the loss of glands from the front sepal where they were least accessible to the bee and therefore least likely to justify the expense of making them. In this context it may be worth mentioning that it is common for populations or species in very diverse genera to lose additional glands (e.g., *Lophanthera* spp., *Heteropterys* spp., *Malpighia* spp.), and when that happens it almost always involves loss of the glands that were adjacent to the anterior sepal, which I interpret as a continuation of the same reduction trend in response to the same kind of selection.

Pollen

In the preceding section I presented the opinions of Lowrie and Lobreau-Callen that tricolporate pollen is plesiomorphic in the Malpighiaceae. I agree. Inasmuch as that consensus is based on the condition that is typical of the Rosidae it can be considered an outgroup argument. Closer to home, one finds that in the Vochysiaceae the pollen is tricolporate, while in the Trigoniaceae it is 3–5-porate.

Fruit

Outgroup comparison tells us little about the fruit of the urmalpigh, but since the fruits in both Trigoniaceae and Vochysiaceae are always dry and dehiscent (capsules or schizocarps) it seems probable that the ancestral condition in the Malpighiaceae was a dry fruit that was schizocarpic or whose carpels were free from the beginning.

From these considerations I conclude that the earliest Malpighiaceae had inflorescences composed of cymules. The first ones to have paired calyx glands probably had them on all five sepals. The pollen was surely tricolporate, and the fruit was almost certainly dry and either schizocarpic or derived from free carpels. The distribution of

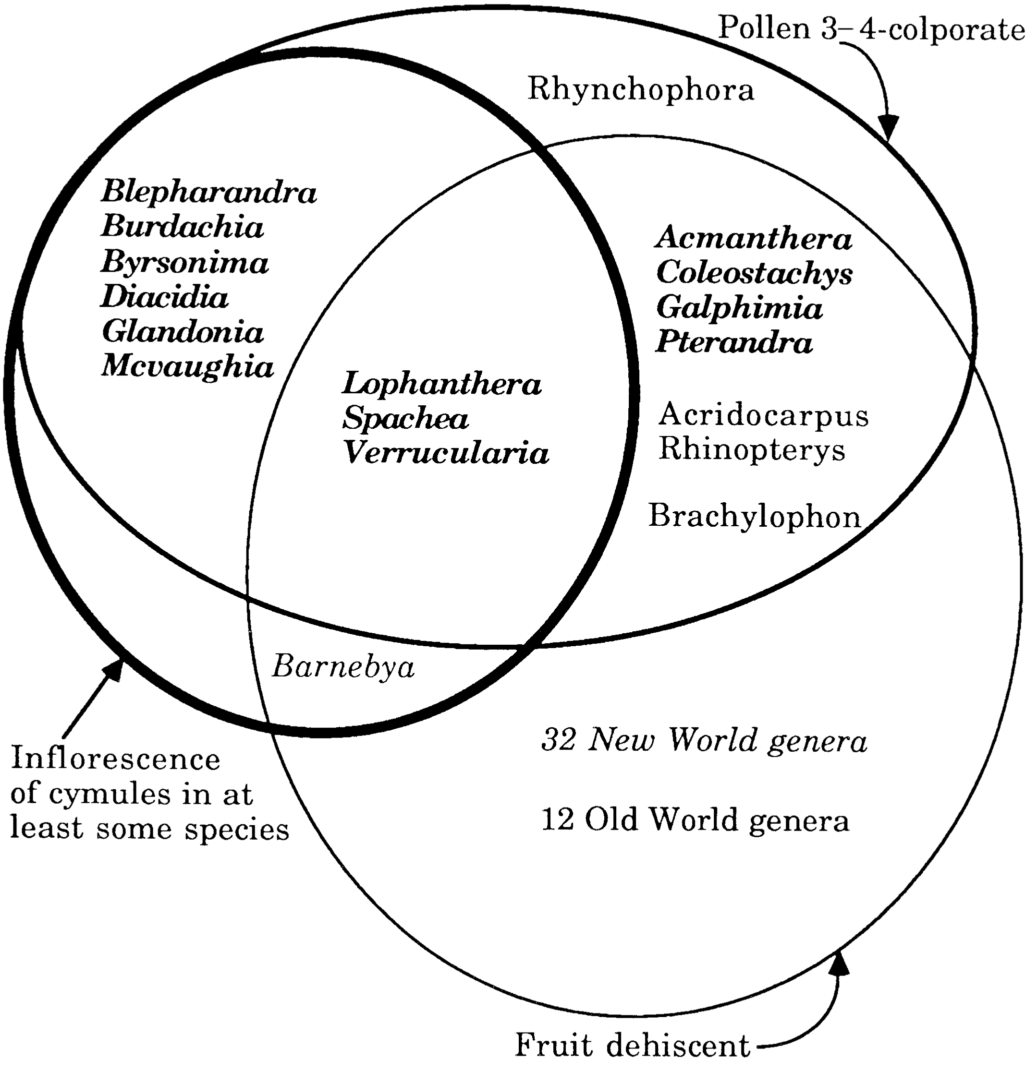

FIG. 4. Distribution of three plesiomorphic character-states among the genera of Malpighiaceae. New World genera are in *italic*, with the byrsonimoid genera **bold**. Old World genera are in Roman. Not shown are the four genera (all neotropical) that lack all three character-states: *Bunchosia, Dicella, Malpighia,* and *Thryallis.*

these inflorescence, pollen, and fruit character-states among extant genera is shown in Figure 4. No Old World genera have thyrsiform inflorescences, and only four have colporate pollen. *Rhynchophora* has an indehiscent fruit, and *Acridocarpus* and *Rhinopterys* have alternate leaves and syncolporate pollen. In the New World, *Barnebya* is the only non-byrsonimoid genus with an inflorescence composed of cymules; its pollen lacks ectoapertures, resembling that of *Bunchosia* shown in Figure 2E. That leaves the neotropical subfamily Byrsonimoideae, all of which are trees or shrubs with colporate pollen; most have ten calyx glands. Four genera have the inflorescence composed of single-flowered units in all species and six have the fruit indehiscent. The only three genera that show all three of the plesiomorphic character-states used to prepare Figure 4 are *Lophanthera, Spachea,* and *Verrucularia. Spachea* is derived in its breeding system—all three species investigated are functionally dioecious (Anderson, 1981: 42–43; Steiner, 1985).

Verrucularia hardly differs from *Lophanthera,* but it is advanced in its complete lack of extrafloral nectaries. *Lophanthera* spp. seem to come closest to fitting the picture constructed here of an ancestral malpigh, but even they are probably derived in their winged anthers and in having the colpi short-bifurcate at the tips in some species, including *L. lactescens,* the species cited above as the only member of the family known to bear dichasia as well as cincinni. *Lophanthera* is a genus of five species, four of them Amazonian and the fifth endemic to lowland forests near rivers on both coasts of Costa Rica (Anderson, 1983). The latter, *L. hammelii* W. R. Anderson, is illustrated in Figure 5. In the 1983 paper I suggested that the basic chromosome number of the family is probably $n = 6$, the lowest number known. I cited previous counts of $n = 6$ in *Lophanthera lactescens* and *Galphimia glauca* Cav., a fairly closely related byrsonimoid. Since then I have counted the chromosomes in *Lophanthera hammelii* (voucher is *Hammel 13339* = *Schatz 1034,* MICH) and *Verrucularia glaucophylla* Adr. Juss. (voucher is *Anderson 13704,* MICH). In both species $n = 6$.

My purpose in this exercise has not been to suggest that the urmalpigh is alive and well and living in the Amazon. I am not so naive as to believe that any taxon could be expected to possess solely plesiomorphic character-states. But Figure 4 and my discussion of it show that the admittedly few such states that I can identify with confidence are heavily concentrated in the Byrsonimoideae, which are wholly American. The simplest hypothesis consistent with these data is that the family originated in northern South America in effective isolation from the Old World.

The great problem with my "American" hypothesis is that it does not readily account for the presence of tricolporate pollen in three quite separate lineages in the Old World. My earlier speculation (1979b) that all the Old World malpighs descended from samara-bearing plants like those now in the neotropics is too simple, because all such extant neotropical species have "porate" pollen, and it is unlikely that such pollen reverted to the ancestral rosid condition three times in the Old World. There must have existed at one time New World Malpighiaceae intermediate between byrsonimoids with colporate pollen and thyrsiform inflorescences and the present-day samara-bearing plants with derived pollen and inflorescences. *Barnebya* probably represents such an intermediate, in which the plesiomorphic inflorescence was retained associated with derived pollen and winged fruits. Such a plant, but with tricolporate pollen, would be a fine ancestor for *Acridocarpus* and *Rhinopterys,* one of the three Old World clades with colporate pollen (Anderson & Gates, 1981). This kind of *ad hoc* reasoning could account for all the Old World malpighs with colporate pollen, but it suffers from two weaknesses. One is that it postulates more independent introductions from the New World, and while such are not impossible the more of them one has to postulate the less likely they become. The other weakness is that this kind of explanation relies on hypothetical intermediates no longer in existence, except for *Barnebya.* While some such intermediates between the neotropical clades must have existed, I prefer explanations that do not require one to construct hypothetical organisms, since that practice lends itself so readily to special pleading for pet hypotheses.

The other explanation that I can suggest for colporate pollen in the Old World is that my hypothesis that the family originated in isolation in the New World is wrong. The alternative would be that the Malpighiaceae evolved before the breakup of Gondwanaland, and that the three Old World clades with colporate pollen have always inhabited what are now Old World regions. Like the byrsonimoids they simply retained a plesiomorphic pollen type inherited from their

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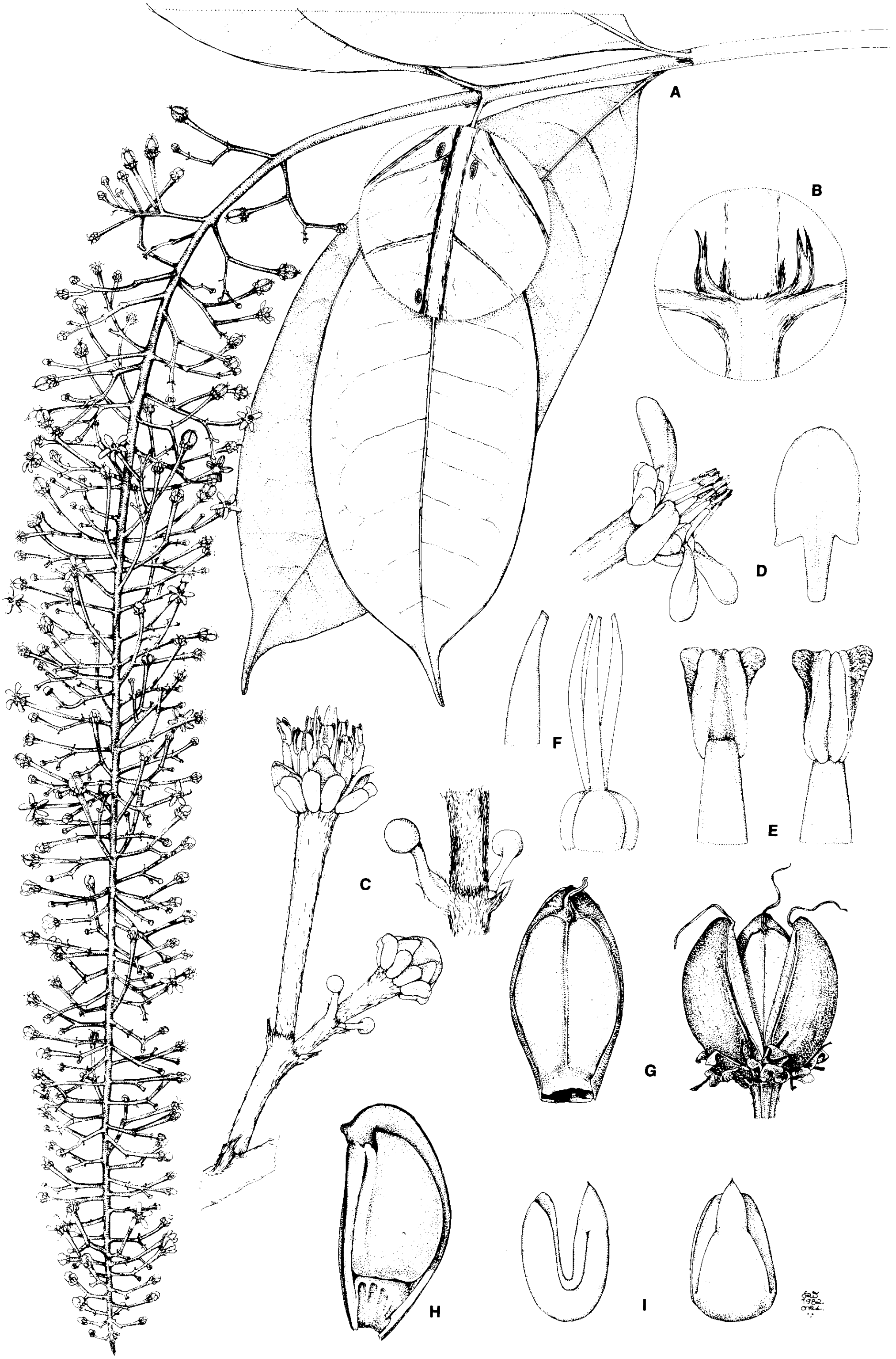
FIG. 5. *Lophanthera hammelii.* **A.** Flowering branch, ×0.5, with circle ×2.5. **B.** Stipules, ×2.5. **C.** Cincinnus of two flowers, ×2.5, with bracteole glands (right) ×5. **D.** Flower, side view with posterior petal erect, ×2.5, with single petal ×3.5. **E.** Stamens, ×10, abaxial view left, adaxial view right. **F.** Gynoecium, ×7.5, with tip of style (left) ×15. **G.** Fruit, ×3, with adaxial view of single mericarp (left) ×4.5. **H.** Mericarp in longitudinal section, with intact seed in position, ×4.5. **I.** Embryos, ×4.5, side view left, abaxial view right. Drawn by Karin Douthit, A–B from *Grayum 2231A,* C–I from *Hammel 9397.* Originally published in Brittonia **35:** 39. 1983.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common ancestors. This is the "Gondwanian" hypothesis, which Vogel has proposed on different grounds. Let us, therefore, turn our attention to that hypothesis now.

THE "GONDWANIAN" HYPOTHESIS

In his 1990 paper Vogel developed an argument based on observations presented in his 1974 book. There he showed that all calyx glands in the Malpighiaceae are anatomically similar to extrafloral nectaries, from which he concluded that all calyx glands are homologous with extrafloral nectaries and that extrafloral nectaries gave rise to calyx glands rather than the reverse. He also showed that the calyx glands in the few Old World genera that possess them are anatomically and functionally more like extrafloral nectaries than like the calyx glands of the New World Malpighiaceae. On that basis he concluded that the Old World malpighs lacking calyx glands are primitively eglandular, and that in those bearing calyx nectaries they evolved directly from extrafloral nectaries, not through degeneration from elaiophores inherited from New World ancestors. In 1974 (pp. 242–243) he seemed equally ready to accept either of two explanations for this situation: "Either the New World Malpighiaceae stemmed from the predecessors of [present-day] paleotropical [Malpighiaceae], and after isolation a general transmutation of their calyx glands to elaiophores and thus nuptial organs occurred, or . . . the Old World groups must have already separated, as did also the American genera of today, [which] although otherwise already possessing their characteristic features, still had no oil glands, i.e., found themselves in a condition which is still conserved in the afroasiatic representatives" [my translation]. The first of these two suggestions is orthogenetic and would be most unlikely to command serious consideration from most evolutionary biologists, so not surprisingly it was deemphasized in the 1990 paper, where instead Vogel developed the second idea, concluding (p. 141): "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 paleotropic descendants whereas the neotropical ones acquired elaiophores as an apomorphy after the separation of the continent."

I accept as a reasonable working hypothesis Vogel's conclusions that all malpigh glands are homologous and that calyx glands were derived from extrafloral nectaries. However, it does not necessarily follow that the calyx nectaries in Old World malpighs could only have come directly from extrafloral nectaries. Vogel cannot have it both ways—if all those glands are anatomically so similar that their homology is unquestionable, then there is no reason why elaiophores that lost their ability to produce oil after migration to the Old World should not revert in structure to a condition similar to that of their homologs. Indeed, that is just what Vogel's conclusions would lead me to expect. Similarly, the fact that those glands produce sugar rather than oil does not mean they are not degenerate elaiophores. As Vogel said (1990: 140): "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." I agree, and if it was feasible once in one direction, the reverse would have been even more feasible, because the genetic ability to make sugary nectar was not lost when the plants evolved the ability to produce oil in elaiophores. Therefore, I cannot accept Vogel's assertion that the calyx nectaries in Old World malpighs could not be degenerate elaiophores. His own evidence as to their homology makes that a reasonable possibility. This point is critical to the Gondwanian hypothesis of the origin of the Malpighiaceae. In fact, it is Vogel's only real basis for that hypothesis.

Vogel emphasized the structure and function of the Old World calyx glands while glossing over the anomalous fact that they exist at all. After going to some trouble (1990: 138) to demonstrate (on the basis of position, not field observations) that they cannot function to reward pollinators, he could advance no plausible explanation for why they should have evolved in what seem likely to be three quite different clades (*Acridocarpus/Rhinopterys, Hiptage,* and *Tristellateia*). He offered only another orthogenetic speculation: "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." When that line of reasoning is weighed against the possibility that some Old World malpighs bear degenerate glands because their ancestors were American and bore elaiophores, the presence of those glands in the Old World can be seen as supporting the American hypothesis. Those Old World calyx glands are as much of a problem for the Gondwanian hypothesis as the presence of colporate pollen in the Old World is for the American hypothesis.

Another, analogous difficulty with the Gondwanian hypothesis was not recognized by Vogel. Almost all Malpighiaceae have clawed petals. The functional significance of those claws in neotropical malpighs with elaiophores was made obvious by Vogel in his 1974 monograph—they leave a space through which the bee can gain access to the elaiophores. The fact that the petals are clawed in malpighs without elaiophores, including those of the Old World, presents no problem for my hypothesis of an American origin of the family; I see it as simply a retained plesiomorphy. But if the Old World malpighs did not have an American origin, what is the functional significance or the selective basis for their clawed petals?

Finally, it seems inescapable that the Gondwanian hypothesis requires a great deal of parallel evolution of apomorphies, as Vogel admitted (1990: 138–139): "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 acquired elaiophores in independent parallel lines, as repeated apomorphies that commenced to develop soon after the isolation from the Old World stock. . . . 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." The first suggestion recalls Vogel's 1974 orthogenetic speculation, quoted above in translation, and seems just as incredible now as it did then. Anything is possible, I suppose, but I really cannot believe that the bizarre and elegant suite of identical character-states found in the oil-flowers of the New World Malpighiaceae evolved independently four or more times. I am much more receptive to the second suggestion, because my own monographic studies of neotropical Malpighiaceae indicate that there has been parallel evolution among those genera of at least superficially similar fruits. I suspect that banisterioid and hiraeoid samaras represent aerodynamically optimal designs, which have been achieved independently several times in the New World, and the same may have happened in the Old World. On the other hand, I must admit that some Old World samaras are very similar indeed to some New World samaras. Niedenzu was not without some grounds for allying Old World and New World genera. Not having studied any of the Old World Malpighiaceae in detail I am not prepared to speak further to this problem, but for the moment the multiple convergences required by the Gondwanian hypothesis would seem to constitute something of a problem.

Where Do We Go from Here?

I have emphasized the inflorescence and pollen and concluded that an American origin for the Malpighiaceae is most likely. Vogel emphasized characteristics of the calyx glands and concluded that the family had a Gondwanian origin. Some data are inconsistent with or at least inconvenient for each hypothesis, and it is possible that the truth lies in some other explanation, perhaps one that combines elements of both hypotheses. At this point it seems best to seek additional data that might shed new light on the problem. Since we have exploited morphology rather thoroughly and remain at a stalemate, I have decided to explore non-morphological data. Therefore, I have recently embarked on a study using molecular data, in collaboration with Mark W. Chase. We hope that the sequence of nucleotides in one chloroplast DNA gene will give us an improved basis for specifying a closest outgroup to use in polarizing characters within the Malpighiaceae. We shall also try to use restriction site analysis to group the genera within the family, independently of the morphology that seems so subject to homoplasy. Therefore, we hope to follow this paper in the fairly near future with a new contribution to the discussion, and I cannot at this time predict the contents of that report. If molecular techniques enable us to find a way out of the thicket of conflicting morphological data, they will demonstrate their power and their value for traditional systematists.

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Literature Cited

Anderson, W. R. 1977[1978]. Byrsonimoideae, a new subfamily of the Malpighiaceae. Leandra **7**: 5–18.

———. 1979a. *Mcvaughia,* a new genus of Malpighiaceae from Brazil. Taxon **28**: 157–161.

———. 1979b. Floral conservatism in neotropical Malpighiaceae. Biotropica **11**: 219–223.

———. 1981. Malpighiaceae. *In* B. Maguire & collaborators, The botany of the Guayana Highland—Part XI. Mem. New York Bot. Gard. **32**: 21–305.

———. 1983. *Lophanthera,* a genus of Malpighiaceae new to Central America. Brittonia **35**: 37–41.

——— **& B. Gates.** 1981. *Barnebya,* a new genus of Malpighiaceae from Brazil. Brittonia **33**: 275–284.

Arènes, J. 1946. Trois genres de Malpighiacées nouveaux pour la flore malgache et pour la science. Notul. Syst. (Paris) **12**: 126–136.

———. 1950. Malpighiacées. *In* H. Humbert, Flore de Madagascar et des Comores, Fam. 108. 183 pp. Muséum National d'Histoire Naturelle, Paris.

———. 1954. Malpighiaceae malesianae novae. Reinwardtia **3**: 67–74.

———. 1957. Répartition géographique des Malpighiacées vivantes et fossiles (1). Compt. Rend. Sommaire Séances Soc. Biogéogr. **290**: 81–108.

Bentham, G. & J. D. Hooker. 1862. Genera Plantarum. Vol. 1, part 1. Reeve & Co., London.

Cavanilles, J. 1790. Nona Dissertatio Botanica. Madrid.

Cronquist, A. 1981. An integrated system of classification of flowering plants. Columbia University Press, New York. xviii + 1262 pp.

Dahlgren, R. 1983. General aspects of angiosperm evolution and macrosystematics. Nord. J. Bot. **3**: 119–149.

Engler, A. 1897. Übersicht über die Unterabteilungen, Klassen, Reihen, Unterreihen und Familien der Embryophyta siphonogama. *In* A. Engler & K. Prantl, Die natürlichen Pflanzenfamilien II–IV (Nachträge): 341–357. W. Engelmann, Leipzig.

Lleras, E. 1978. Trigoniaceae. Fl. Neotropica Monogr. **19**: 1–73.

Lobreau-Callen, D. 1967. Contribution a l'étude du pollen des Malpighiaceae d'Afrique. Pollen & Spores **9**: 241–277.

———. 1968. Le pollen des Malpighiacées d'Afrique et de Madagascar. Bull. Inst. Fondam. Afrique Noire 30, Sér. A, Sci. Nat. **1**: 59–83.

———. 1983. Analyse de la répartition géographique des Malpighiaceae d'après les caractères du pollen et de la pollinisation. Bothalia **14**: 871–881.

———. 1989. Les *Malpighiaceae* et leurs pollinisateurs. Coadaptation ou coévolution. Bull. Mus. Hist. Nat. (Paris), Sect. B, IV, **11**: 79–94.

Lowrie, S. R. 1982. The palynology of the Malpighiaceae and its contribution to family systematics. Ph.D. Dissertation. University of Michigan, Ann Arbor. 354 pp. University Microfilms #82-24999.

Niedenzu, F. 1928. Malpighiaceae. *In* A. Engler, Das Pflanzenreich IV, **141**: 1–870.

Raven, P. H. & D. I. Axelrod. 1974. Angiosperm biogeography and past continental movements. Ann. Missouri Bot. Gard. **61**: 539–673.

Steiner, K. E. 1985. Functional dioecism in the Malpighiaceae: The breeding system of *Spachea membranacea* Cuatr. Amer. J. Bot. **72**: 1537–1543.

Takhtajan, A. L. 1980. Outline of the classification of flowering plants (Magnoliophyta). Bot. Rev. **46**: 225–359.

Thorne, R. F. 1983. Proposed new realignments in the angiosperms. Nord. J. Bot. **3**: 85–117.

Vogel, S. 1974. Ölblumen und ölsammelnde Bienen. Tropische und subtropische Pflanzenwelt **7**: 283–547 (also paginated independently [1–5] 6–267; citations here use the independent pagination).

———. 1990. History of the Malpighiaceae in the light of pollination ecology. *In* G. Gottsberger & G. T. Prance (eds.), Reproductive biology and evolution of tropical woody angiosperms. Mem. New York Bot. Gard. **55**: 130–142.

Walker, J. & J. A. Doyle. 1975. The bases of angiosperm phylogeny: Palynology. Ann. Missouri Bot. Gard. **62**: 664–723.