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BYRSONIMOIDEAE, A NEW SUBFAMILY OF THE MALPIGHIACEAE

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The Malpighiaceae can easily be divided into two groups by their fruits, which are usually either winged or unwinged. Species with winged fruits are generally but not always vines, while species with unwinged fruits are usually shrubs or trees. On the basis of these characteristics, plus the shape of the receptacle, the family was divided two subfamilies by Franz Niedenzu, who published his monograph of the family in 1928. Niedenzu used the name Pyramidotorae for the group with winged fruits and Planitorae for the group with unwinged fruits. Morton (1968) pointed out that the Code of Nomenclature requires that the names of subfamilies be based on names of included genera. For Niedenzu's Pyramidotorae he proposed the name Gaudichaudioideae; for the Planitorae the name would have to be Malpighioideae because the subfamily as circumscribed by Niedenzu included the genus Malpighia, the type of the family.

The subfamily Malpighioideae sensu Morton is mostly a natural assemblage of genera linked together by numerous characters. However, certain genera included by Niedenzu do not seem to me to belong with the others, and I would exclude them. Unfortunately, one of the excluded genera is Malpighia, and when it is removed the name of the subfamily goes with it. Therefore it is necessary to describe a new subfamily for the remaining genera. In this paper I shall describe and circumscribe that subfamily and then discuss my reasons for excluding Malpighia and several other genera.

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Byrsonimoideae W. R. Anderson, Malpighiacearum subfam. nov.

Arbores et frutices, raro suffrutices. Stipulae bene evolutae, plerumque intrapetiolares, liberae vel connatae. Inflorescentia thyrsus ex cincinnis 2-10-floris constans, vel pseudoracemus vel spica vel fasciculus (re vera ex cincinnis unifloris constans). Gemma floris saepe circinata. Antherae inter se \pm similares. Pollen plerumque tricolporatum, raro tetracolporatum (in Galphimia Sect. Galphimia parasyncolporatum), 10-30 μ in diametro. Styli plerumque 3, subulati, stigmate minuto (in Spachea 2-3, crassi, stigmate truncato vel subpeltato). Fructus carnosus vel siccus, nunquam alatus nec setifer, ex 3 carpellis liberis vel 2-3 mericarpiis constans vel compositus loculis 1-3.

Chromosomatum numerus: n = 6 vel 12.

Typus. Byrsonima L. C. Richard ex Humboldt, Bonpland & Kunth, Nov. Gen. Sp. (4° ed). 5:147 1821 (1822).

Plants of subfamily Byrsonimoideae are all natives of the tropics and subtropics of the New World. There are no vines among them, and I believe that the vining habit has never evolved in this group. This is in marked contrast to many other genera (e. g. Banisteriopsis, Heteropterys, Tetrapterys), in which the vining habit is probably ancestral and extant shrubs are probably derived. The best single character for recognizing this subfamily is the presence of three subulate styles with minute stigmas; the only exception is Spachea, which cannot be excluded because it seems to be closely related to Lophanthera. Small tricolporate pollen is another important character that unites this subfamily, and another is a chromosome number of n = 6 or n = 12. Almost all chromosome numbers known for other New World Malpighiaceae are n = 10 or a multiple of 10, or aneuploid derivatives of such multiples. However, very few chromosome counts have been published for the Malpighiaceae, and this generalization may or may not be supported when more data are available. It would be especially interesting to have a chromosome count for the troublesome genus Spachea.

No member of this subfamily has the fruit winged or setose, nor is there any evidence of reduction from a winged fruit comparable to the wingless species found in Banisteriopsis, Heteropterys, Stigmaphyllon, Mascagnia, etc. In most genera the fruit is probably dispersed by water or blown about with other detritus-like seeds and fruits. Byrsonima has achieved a major distinction by evolving a fleshy, bird-dispersed fruit, and it is probably no coincidence that Byrsonima is the only genus in the subfamily with more than 15 species. With the advent of small birds there

has probably been strong selection in various lines for fleshy fruits, and it is my opinion that such fruits have evolved separately and repeatedly in the Malpighiaceae. It happened only once in this subfamily, in the ancestor of Byrsonima, which probably had a friut like that of Blepharandra. Somewhat similar fruits also evolved in the ancestors of Malpighia and Bunchosia, but other characteristics of those genera do not support a probable origin in this subfamily, and they are therefore excluded.

KEY TO THE TRIBES OF BYRSONIMOIDEAE

- Carpels connate in flower, bearing apical styles.

 2. Fruit quite indehiscent, neither opening nor breaking apart into mericarps

 1. Byrsonimeae

 2. Fruit breaking apart into dry 1-seeded mericarps, the mericarps often dorsally loculicidal

 2. Galphimieae

 1. Carpels free from each other, borne on a flat or slightly pyramidal torus, bearing ventrifixed sub-apical to almost basal styles

 3. Acmanthereae
- Byrsonimeae W. R. Anderson, trib. nov.

Gemma floris saepe circinata. Glandes calycis 10 vel nullae. Stamina 10 (vel in Diacidia spp. 9-6), antheris glabris vel piliferis, inter se ± similaribus. Carpella 3 omnino (praeter stylos) connata, ovario 3- vel abortu 2- vel 1-loculato, stylis 3 apicalibus subulatisque, stigmate minuto apicali vel parum interno. Fructus indehiscens, drupaceus vel siccus, 1-3-spermus.

Typus. Byrsonima L. C. Richard ex Humboldt, Bonpland, & Kunth, Nov. Gen. Sp. (49 ed.) 5:147 1821 (1822).

KEY TO THE GENERA OF BYRSONIMEAE

- 1. Leaves, bracts, and bracteoles eglandular (except for gland-tipped marginal teeth or cilia on the bracts and bracteoles of some species).

 - 2. Fruit dry; hairs on the anthers basifixed.

- 3. Petals all yellow; anthers bearing 2(-4) stout, apical, awn-like hairs, these strongly differentiated from any other hairs on the stamen; Amazonian Brazil, southern Venezuela, and eastern Colombia

 Diacidia Grisebach

1. Leaves and alternate bracteoles bearing large dorsal glands.

All of these genera are well represented in the Guayana Highland and I shall describe and discuss them further in my forthcoming treatment of the Malpighiaceae from that region. I am also preparing a monograph of the whole genus Byrsonima.

2. Galphimieae Niedenzu, Ber. Deutsch. Bot. Ges. 8:192. 1890.

Floriferous peduncle well developed, even when cincinnus is reduced to 1 flower. Calyx glands 10 or fewer through fusion and loss, to none. Petals subequal or the posterior petal moderately differentiated. Stamens 10, the filaments opposite the sepals usually longer than those opposite the petals, the anthers \pm alike, glabrous. Carpels 2-3, connate in flower for their whole length (except styles), both or all 3 locules uniovulate; styles 2-3, apical. Fruit breaking apart into 2-3 (or fewer by abortion) 1-seeded mericarps, the mericarps often dorsally loculicidal but not opening sufficiently to release the seed; base of the mericarp often with an empty or aerenchyma-filled cavity.

Type. Galphimia Cavanilles, Icon. et descr. pl. 5:61. 1799.

KEY TO THE GENERA OF GALPHIMIEAE

As circumscribed here this tribe is drastically changed from the group recognized by Niedenzu in 1928. Several of his genera have been excluded from the subfamily, and others have been assigned to other tribes. The four genera left form two natural pairs (Galphimia and Verrucularia vs. Lophanthera and Spachea) that have in common similar fruits and a tendency toward reduction of the calycine glands. Most of these genera were recently studied by MacBryde(1970). He gave little consideration to the relationships between genera, but he did describe them thoroughly and his paper is a useful source of descriptive data.

Panamá, and the West Indies Spachea Adr. Juss .

It is not clear to what extent the mericarps of this tribe are naturally loculicidal. In Galphimia and Verrucularia they are probably usually so, although I have seen no evidence that the seed is released. They appear to be at least tardily loculicidal in Lophanthera latifolia and L. pendula, but not in L. spruceana and Spached spp. However, one collection of S. tricarpa (Croat 19971) has fully mature mericarps, and they are loculicidal. This is a problem that can only be resolved by alert collectors who note the condition of the mericarps before they are pressed and dried.

Lophanthera is a difficult genus to place in a tribal taxonomy. It has glands on the leaves and bracteoles like those of Burdachia and Glandonia in the Byrsonimeae and its winged anthers are at least superficially similar to those of Acmanthera and Pterandra in the Acmanthereae. However, I have placed it here in the Galphimieae because its overy and fruit are so like those of Galphimia and Verrucularia.

Spachea is a discordant element in the subfamily Byrsonimoideae, in that its styles are thick and broad at the apex, and its pollen has broad furrows instead of the narrow slit-like colpi found in other genera of the subfamily. On the other hand, it would be difficult to exclude Spachea from the subfamily. The plants are shrubs or trees, some of them large trees. The stipules are intrapetiolar and connate, as in Byrsonima and other genera. The inflorescence is a thyrse of fewflowered cincinni, which is clearly the basic inflorescence for the subfamily. Most important, Spachea resembles Lophanthera in so many ways that their relatedness seems certain, and it is on the strength of this conclusion that Spachea is placed here instead of in a tribe of its own. Some of the similarities between Spachea and Lophanthera are: Stems often with white latex; lamina of the leaf bearing flat glands; inflorescence a thyrse, with the cincinni reflexed; peduncle of the cincinnus twisted so that the bract is adaxial; alternate bracteoles often bearing or terminating in a large gland; calyx often with some loss of glands through fusion of neighboring glands; carpels connate in flower along a relatively narrow vertical axis. Unlike most Malpighiaceae, Spachea appears to be either gynodioecious or functionally dioecious. Plants with enlarging or mature fruit have flat anthers that have never opened and seem not to have formed normal pollen. Plants with open, polleniferous anthers have small but ovuliferous ovaries. I do not know whether these apparently perfect flowers also set fruit or are functionally only staminate. Spachea deserves further study, both for its breeding system and its anomalous phylogenetic position.

Galphimia has its calyx glands strongly reduced or absent. Apparently neighboring glands first fused in pairs. Thus G. hirsuta Cav. (e.g. Rowell 3144, MICH) bears five small glands alternating with the sepals, which suggests a dual origin for each gland. Then these glands were apparently reduced in number, as in G. glandulosa Cav. (Anderson & Anderson 5849, MICH, has four glands; McVaugh 22903, MICH, has two.) Most species are quite eglandular. Section Galphimia has parasyncolporate pollen, while Section Microgalphimia has colporate pollen like most of the subfamily (Lobreau, 1967; MacBryde, 1970). Section Galphimia is also notable for its large stamens and persistent petals; all of its species are Mexican. This situation parallels others in the Malpighiaceae in which Mexican groups are advanced derivatives of South American ancestors. The Mexican character of Galphimia is especially interesting when contrasted with the rest of the subfamily. The only other Byrsonimoideae that occur outside South America are Byrsonima (relatively few species but with wide distribution in Central America, Mexico, the West Indies, and Florida), Spachea (two or three species in Panamá and the West Indies), and Pterandra (one species in Panamá).

3. Acmanthereae W. R. Anderson, trib. nov.

Folia, bracteae, et bracteolae eglandulosae. Flores 1 in quaque bractea (i.e. cincinnus uniflorus). Pedicellus sessilis. Glandes calycis 10 vel nullae. Stamina 10, filamentis ± liberis, antheris glabris, inter se ± similaribus. Carpella libera, in toro plano vel parum pyramidali portata, omnia 3 uniovulata, stylis ventrifixis subapicalibus vel fere basalibus, gracillimis subulatisque, stigmate minuto apicali vel parum interno. Fructus ex 3 (vel abortu 2-1) coccis siccis indehiscentibus constans.

Typus. Acmanthera (Adr. de Jussieu) Grisebach in Martius, Fl. bras. 12(1):29. 1858; Pterandra sect. Acmanthera Adr. de Jussieu, Malp. Synopsis, Ann. Sci. Nat. (2° Sér. Bot.) 13:328. 1840.

KEY TO THE GENERA OF ACMANTHEREAE

- 1. Anthers winged.
 - 2. Inflorescence an elongated pseudoraceme terminating an axillary shoot; stipules 1.5-11 cm long, deciduous; northern Amazonian Brazil

 Acmanthera (Adr. Juss.) Griseb.
 - 2. Inflorescence a tight umbellate fascicle, sessile or subsessile, axillary to leaves or bracts or leaf scars on older stems; stipules up to 0.6 cm long, persistent; Brazil, western Guyana, southern Venezuela, Colombia, and Panamá

 Pterandra Adr. Juss.
- 1. Anthers unwinged; Pará and French Guiana Coleostachys Adr. Juss.

The genera included in this tribe were treated by MacBryde (1970), and I recently published a brief revision of Acmanthera (Anderson, 1975). Pterandra is interesting for the reduction of its inflorescence, and Coleostachys for the rarity of its only species, C. genipifolia Adr. Juss., and for its reportedly poricidal anthers (MacBryde, 1970).

GENERA EXCLUDED FROM THE SUBFAMILY BYRSONIMOIDEAE

It is now appropriate to make some comments about the genera included in the subfamily Planitorae by Niedenzu (Malpighioideae sensu Morton) and excluded from the subfamily Byrsonimoideae. I do not pretend to know where the strongest affinities of all these genera lie. Therefore I shall emphasize my reasons for excluding them from the Byrsonimoideae, whose definition is the purpose of this paper, and leave the proper placement of some problematical genera for future studies.

Malpighia L.

Plants of Malpighia are shrubs, and their fruits are fleshy. Those two characteristics are the only bases for placing the genus in proximity to Byrsonima and its relatives. Against such placement are the following features of Malpighia: Stipules minute and interpetiolar. Flowers strongly zygomorphic, with anthers of different sizes and (in some species) the styles sigmoid, as in Hiraea. Pollen large, polyporate, the 4-8 pores not all equatorial, and with furrows not equivalent to the colpi in the Byrsonimoideae. Styles with large oblique-internal stigmas and dorsally truncate or hooked at the apex. Chromosome number: n = 10 (2n = 56 in M. urens fide Fouët, 1966).

The fruits of Malpighia deserve special attention, since their superficial similarity to the drupes of Byrsonima has been the cause of much confusion. When one removes the flesh from a fruit of Byrsonima one finds a single spheroid stone, smooth or rugose. This stone, which is very hard and bony, is the result of complete fusion of the endocarps of the three carpels that form the ovary. Is is quite indehiscent, but if broken open will be found to contain three one-seeded locules (reduced to two in some species). The entire fruit of Blepharandra is very like the stone of Byrsonima, and I believe that a fruit like that of Blepharandra probably gave rise to the drupe of Byrsonima through gradual increase in the fleshiness of the exocarp in response to selection by small birds. A very different situation is found when the flesh is removed from a fruit of Malpighia. Here one finds three separate stones which, once the exocarp is gone, are joined only along a narrow central axis, where they are borne on a common pyramidal torus. There is no continuity of the endocarps. Each stone, or pyrene, is derived from one carpel, and contains one seed. Its wall is tough and fibrous; it bears two longitudinal lateral ridges or winglets, a dorsal ridge or winglet, and usually smaller parallel or transverse ridges in between. This arrangement is very suggestive of a mascagnioid mericarp in which the wings did not develop.

Please see Plates I and II for a comparison of the flowers and fruits of Byrsonima and Malpighia.

Taking all of the above facts into account, I can only conclude that Malpighia is probably derived from one of the wing-fruited genera, most likely a mascagnioid genus (c. g. Mascagnia, Hiraea, Jubelina, Mezia, Cabi, etc.). There

are extant mascagnioids, e.g. Cabi, in which the fruit is reduced to three wingless mericarps. If such a fruit were modfied by the addition of a fleshy exocarp, it would resemble that of Malpighia. The superficial resemblance of the fruits of Byrsonima and Malpighia is surely a case of parallel evolution. It is interesting that Malpighia has also abandoned the vining habit of its ancestors, but as I have noted elsewhere in this paper, that particular shift in habit has happened so often in this family that its occurrence here would be a slim basis indeed for postulating a relationship between Malpighia and Byrsonima.

Bunchosia Rich. ex H.B.K.

This is a genus of shrubs and trees. Collectors occasionally describe Bunchosia as a climber, but this probably means a lax or leaning shrub rather than a twining vine. The stipules are small and interpetiolar or epipetiolar. The leaves bear large glands embedded in the lamina and alternate bracteoles bear dorsal glands. The glands of the calyx are 8-10, the number apparently reduced through lateral fusion in some species and through loss in others. The pollen is polyporate, with 5-8 non-equatorial pores in the species examined, and without furrows or colpi-There are two or three carpels, quite connate in the ovary. The two or three styles are stout, free to connate, with large terminal stigmas that are capitate, peltate, or reniform. The fruit consists of two or three one-seeded pyrenes in a common fleshy exocarp. When the flesh is removed the pyrenes are found to be clongated, round or elliptical in cross-section, free from each other, with a smooth, brittle, cartilaginous wall. The only published chromosome number is that of Fouët (1966), 2n = 72 for Bunchosia montana. Fouët's higher counts are suspect because they were made from sections rather than squashes, and I consider this report an inadequate basis for any phylogenetic speculation.

The above description should make it abundantly clear that Bunchosia is not at all closely related to Byrsonima. Moreover, there is little basis for postulating a much closer relationship to Malpighia. Its fleshy fruit was surely derived from some other ancestor, and represents another case of parallel evolution in this family. When I come to consider what may be the closest extant relatives of Bunchosia, I find the genus an enigma. The genus that seems closest to Bunchosia is Heladena, which has similar inflorescences, pollen, and stigmas. The cocci of Heladena, if enveloped in a common fleshy exocarp, would constitute a fruit similar to that of Bunchosia. Bunchosia is also somewhat similar to Spachea in their laminar and bracteolar glands and their styles and stigmas.

Dicella Grisebach

Dicella is a genus of woody vines. The stipules are tiny and interpetiolar. The calyx glands are eight on the four lateral sepals, none on the anterior sepal (this is the characteristic condition for vining genera). The pollen is large and polyporate with non-equatorial pores, and has broad fissures that are probably not equivalent to the colpi of the Byrsonimoideae. The ovary comprises three completely connate carpels, two of them well developed and one usually rudimentary. The two fertile locules each bear one ovule, but one often fails to produce a seed. The styles are stout, with truncate, oblique-internal stigmas, and are dorsally angled at the apex; when only two carpels are fertile, the third style is rudimentary or absent. The fruit is a spheroid, indehiscent, nut-like structure with a thick, fibrous wall. At maturity it is dry and hard, not fleshy, and the only apparent adaptation for dispersal is the enlarged, wing-like sepals, which are much larger than the fruit in some species but smaller in others. The one or two large seeds contain a small embryo and abundant perisperm, an interesting anomaly in this family (I have observed perisperm formed during growth of the seed in Gaudichaudia, but by maturity it has been completely resorbed). The chromosome number is unknown.

There is not a single feature of Dicella that suggests derivation from or close relationship to the Byrsonimoideae. The fruit is not even fleshy, although a worker who had never seen it alive could be forgiven for thinking it so. Dicella certainly belongs with other vining genera, but beyond that I cannot speculate at this time. When sufficient data are available about chromosome numbers, pollen morphology, and embryology in many genera, perhaps its correct phyletic position will become apparent.

Thryallis Martius

This is a peculiar genus of shrubby vines, almost unique in the family in their stellate pubescence. The tiny stipules are epipetiolar. The calyx is eglandular. The pollen is polyporate and without colpi or furrows. The three styles bear oblique-internal stigmas. The fruit is small and pyramidal, comprising three dry indehiscent cocci, each with a hard, rugose wall. The cocci can be separated, but they do not seem to fall apart in nature. The calyx is dry and persistent, and probably aids in dispersal by the wind of the whole fruit as a single unit. Each locule contains a tiny, hardly-developed embryo; the rest of the space is filled by an aerenchyma-like tissue, perhaps modified perisperm. The chromosome number is unknown.

I do not know where this genus belongs, but its habit, pollen, and stigmas suggest derivation from one of the wing-fruited vines. There is no basis whatsoever for placing it in the Byrsonimoideae.

Clonodia Grisebach

This is a small genus of woody vines, strongly similar to Heteropterys spp. but with the mericarp dorsally verrucose or cristate instead of winged. The fact that Niedenzu was willing to place this genus so far from the wing-fruited genera demonstrates that he was more interested in maintaining intact his arbitrarily defined hierarchy than in devising the most natural taxonomy possible. For further discussion of Clonodia see Cuatrecasas, 1960.

Heladena Adr. Juss.

Heladena is a genus of shrubs and woody vines with small epipetiolar stipules. The calyx bears eight stalked glands on the four lateral sepals. The pollen is large, without furrows, and polyporate, the pores not all equatorial. The styles have large oblique-internal stigmas. The fruit comprises three unwinged indehiscent cocci that fall from a pyramidal torus. The chromosome number is not known.

The four or five species of Heladena are all rare and poorly known. They are similar to Bunchosia in their inflorescence, pollen, and stigmas, and the two genera may actually be fairly closely related. Niedenzu probably placed Heladena near Spachea because their stigmas and fruits are similar. It is possible that their fruits do indicate a close relationship between these two genera, in which case Heladena might constitue an intriguing link between the Byrsonimoideae and the other Malpighiaceae. However, the similarity could also be coincidental, and Heladena may be derived from some wing-fruited vining genus with a reduced fruit. At present, a possible relationship to Spachea, itself an anomaly in the Byrsonimoideae, is hardly enough to justify including Heladena in the new subfamily.

SUMMARY

The exclusion of Malpighia from Niedenzu's subfamily «Planitorae» forces the recognition of a new subfamily of Malpighiaceae. It is named Byrsonimoideae, described, and divided into the tribes Byrsonimeae, Galphimieae, and Acmanthereae. Each tribe is described and a key to its genera is provided. The reasons for excluding six genera included by Niedenzu in his «Planitorae» are discussed.

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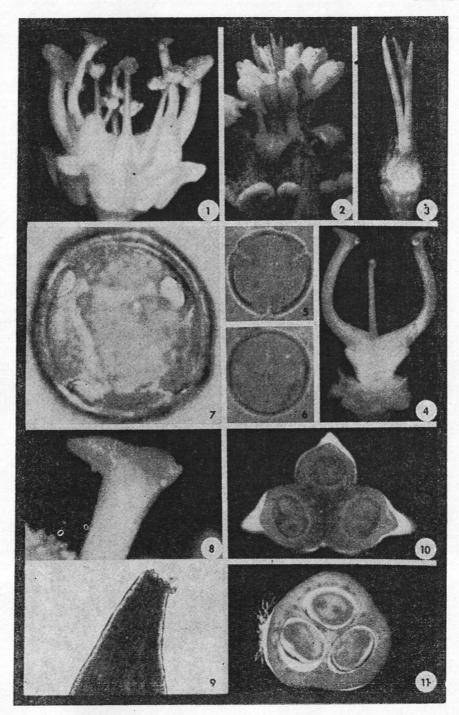
RESUMO

A exclusão de Malpighia da subfamília «Planitorae» de Niedenzu força a necessidade de se instituir uma nova subfamília de Malpighiaceae. É nomeada Byrsonimoideae, descrita, e dividida nas tribos Byrsonimeae, Galphimieae, e Acmanthereae. Cada tribo é descrita e uma chave para os géneros é incluída. As razões para excluir seis gêneros incluidos por Niedenzu na subfamília «Planitorae». são discutidas neste trabalho.

LEGEND FOR THE PLATES

Plate I (Figures 1 - 11): Comparison of flowers of Byrsonima and Malpighia

- Fig. 1 Androecium and gynoecium of Malpighia coccigera, x 7.4
- Fig. 2 Androecium and gynoecium of Byrsonima viminifolia, x 5.3
- Fig. 3 Gynoecium of Byrsonima viminifolia, x 5.3 Fig. 4 — Gynoecium of Malpighia coccigera, x 8.5
- Fig. 5 Pollen of Byrsonima basiloba, polar view, x 1250
- Fig. 6 -- Pollen of Pyrsonima basiloba, side view, x 1250
- Fig. 7 Pollen of Malpighia glabra, x 1250
- Fig. 8 Stigma of Malpighia coccigera, x 31 Fig. 9 — Stigma of Byrsonima viminifolia, x 120
- Fig. 10 Ovary of Malpighia coccigera, cross-section, x 21
- Fig. 11 Ovary of Byrsonima basiloba, cross-section, x 14



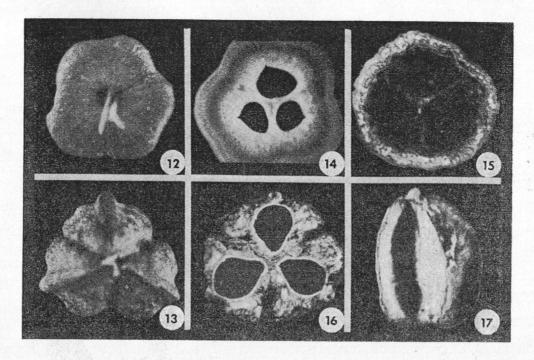


Plate II (Figures 12 - 17): Comparison of fruits of Byrsonima and Malpighia

Fig. 12 — Fruit of Byrsonima basiloba, apical view, x 4. Fig. 13 — Dried fruit of Malpighia giabra, apical view x 4. Fig. 14 — Fruit of Byrsonima basiloba, cross-section, x 4.4 (seeds removed; boundary between stone and flesh marked by dark vascular bundles). Fig. 15 — Dried fruit of Byrsonima umbellata, cross-section, x 6 (seeds removed; boundary between stone and flesh marked by fine white line). Fig. 16 — Dried fruit of Malpighia glabra, cross-section, x 4 (seeds removed; flesh is a thin layer adherent to the fibrous endocarp). Fig. 17 — Dried "mericarp" of Malpighia infestissima, side view, x 2.7 (note strong similarity to a mascagnioid mericarp).