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THE FLORAL MORPHOLOGY AND POLLINATION BIOLOGY OF THREE SPECIES OF BAHAMIAN MALPIGHIACEAE

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ABSTRACT

Observations of floral morphology in three species of Bahamian Malpighiaceae, *Byrsonima lucida*, *Stigmaphyllon sagraeanum* and *Malpighia polytricha* ssp. *confusa*, were made using flowers collected on North Andros Island. Field observations of pollination in *Brysonima* and *Stigmaphyllon* were made, and the pollinators were collected and identified. These studies had not been previously conducted on any Bahamian Malpighiaceae.

Although the flowers differ morphologically, they retain a uniformity of function in those parts which attact, orient and reward pollinators. The pollinator of *Byrsonima* and *Stigmaphyllon* is the female of the anthophorid bee *Centris inermis*, a member of the group of oil collecting bees that are known to be the primary pollinators of the New World species of Malpighiaceae.

INTRODUCTION

The Malpighiaceae is a large and widespread family of tropical and subtropical plants. Most recent authors agree that there are 60 genera in the family, but reports of species numbers vary from at least 850 (Correll, 1982) to more than 1200 (Cronquist, 1981). This is primarily a New World group of plants, with most species and genera growing only in the neo-tropics. The remainder of the family grows in the tropical and subtropical areas of Africa, Asia and Australia (Heywood, 1978).

The Malpighiaceae show considerable diversity in habit and habitat requirements (Anderson, 1979). The plants range in habit from herbaceous perennial vines and small shrubs to large woody lianas and trees. As to habitat, they grown in situations including forests, wet areas and grasslands.

Despite the great diversity found in the family, the flowers of the plants show a general similarity in structure, especially in those aspects that are "concerned with attracting, orienting and rewarding pollinators" (Anderson, 1979). While color, ornamentation and size are variable, the flowers preserve a basic structure of five sepals with two basally located oil-producing glands, five free clawed petals and a centrally located cluster of ten stamens and three carpels. The flowers are generally slightly to markedly zygomorphic, and can exhibit this bilateral symmetry in any or all of the floral whorls. The claw of the ventral petal, the flag petal, is often thickened. The number of sepal glands varies among species and genera.

The oil producing elaiophores are particularly interesting in the Malpighiaceae, as they appear to provide the primary reward for the pollinator in the New World (Vogel, 1971, 1974; Anderson, 1979; Raw, 1979). Vogel (1974) notes the presence of elaiophores in 89% of the genera of the Malpighiaceae, with most occurring in the New World.

Pollination in the family, at least in the New World, involves a unique interaction between the pollinator and the calyx glands. Although there are few recorded observations of pollination, the primary pollinators for the family in the New World are female bees in the anthophorid tribes Centridini (genera *Centris* and *Epicharis*) and Exomalopsini (genus *Paratetrapedia*). The behavior of the insects on the flowers involves the bee grasping the claw of the flag petal in its mandibles and extending its legs between the claws to gather oil from the calyx glands.

The Malpighiaceae is represented in the Bahamas by five native species and one species of adventive origin (Correll, 1982). The native Bahamian species are: *Bunchosia glandulosa* (Cav.) DC, *Byrsonima lucida* (Mill.) DC, *Malpighia polytricha* A. Juss. (with subspecies *polytricha* and *confusa*

Vivaldi), *Stigmaphyllon sagraeanum* A. Juss., *Triopteris jamaicensis* L. and the adventive species is *Galphimia gracilis* Bartl. Two cultivated species of *Malpighia* are also found in the Bahamas, *M. glabra* L. and *M. punicifolia* L., but neither species is known to be adventive.

There are no existing studies of floral morphology or pollination biology for the Bahamian Malpighiaceae. With this in mind, we began our research on North Andros Island in 1983 and 1984, hoping to collect floral specimens and observe pollination for as many species as we could find. All of the wild growing Bahamian Malpighiaceae except for *Galphimia* are said to occur in the region of the Bahamas Archipelago which includes North and South Andros Islands, the Berry Islands and the Biminis (Correll, 1982). However, only three of the species were found in the study area for this research: *Byrsonima lucida, Malpighia polytricha* spp. *confusa*, and *Stigmaphyllon sagraeanum.*

MATERIALS AND METHODS

Field observations of the three plants were made on North Andros Island in the general vicinity of Forfar Field Station at Blanket Sound and at numerous other locations around the northern half of the Island. Specimens of the flowers were collected for study in the laboratory and voucher specimens were deposited in the herbarium of Miami University. Preserved flowers were sectioned for anatomical studies which are not included in this paper. Observations of pollination for *Stigmaphyllon* and *Byrsonima* were made on North Andros, although none could be made for *Malpighia.* One pollinator, a bee, was photographed and captured on a specimen of *Stigmaphyllon*; another bee was collected visiting a plant of *Byrsonima.* For comparison, a different bee was collected visiting *Bidens alba.* The collected insects were sent to Dr. Wallace LaBerge at the Illinois Natural History Survey for identification, and have been deposited in their collection. A number of flowers of each species were bagged to test for self-fertilization.

OBSERVATIONS

General Comments -- The three species studied exhibit differences in habiat, size and morphology, but still show the considerable uniformity of floral structure characteristic of the Malpighiaceae. The plants are all commonly encountered on North Andros, growing in a variety of different habitats. They are often found in the same general vicinity, growing quite close to one another. All three produce zygomorphic flowers and, during flowering periods, normally bear abundant flowers.

Morphologically, the flowers of *Byrsonima, Stigmaphyllon* and *Malpighia* show uniformity in the numbers of floral parts, differing primarily only in the shapes and sizes of those parts. Each flower has a calyx composed of five sepals. In *Byrsonima* and *Malpighia*, each sepal bears two oil producing elaiophores on its basal, adaxial surface; *Stigmaphyllon* has one eglandular sepal. The flowers each bear five free clawed petals. The dorsal petal, the flag petal, has a prominently thickened claw and generally protrudes distinctly from the flower. The androecia are composed of ten fertile stamens and the gynoecia of three synovarious carpels.

Byrsonima lucida is a small shrub to a large shrubby tree, 6 to 8 meters tall. The plant is very common on North Andros especially on the drier parts of tidal flats, along roadsides and in coppices. The flowers of *Byrsonima* are the least zygomorphic in the three plants studied. The white to pink flowers are approximately 1.5 cm across and are borne in terminal racemes containing a variable number of flowers (Fig. 1). The five clawed petals are slightly zygomorphic and are persistent, usually changing to a dark pink or red before wilting on the flower. Occasional plants bear flowers that do not change color, remaining white until they wilt. The pedicels of the flowers vary considerably in length and are densely covered with tiny malpighian hairs. The calyx consists of five uniform sepals, each bearing two glands on its basal, adaxial portion. The androecium contains ten uniform stamens. The gynoecium consists of three carpels with fused ovaries (synovarious) and free styles.

Stigmaphyllon sagraeanum is a woody vine. It can grow as a short, free-standing plant or as a long clambering vine, often twisted around neighboring shrubs or trees. The plants do not appear to be as common as *Byrsonima*, but are still abundant, growing

Fig. 1. Photograph of the inflorescence of *Byrsonima lucida*, taken on North Andros Island.

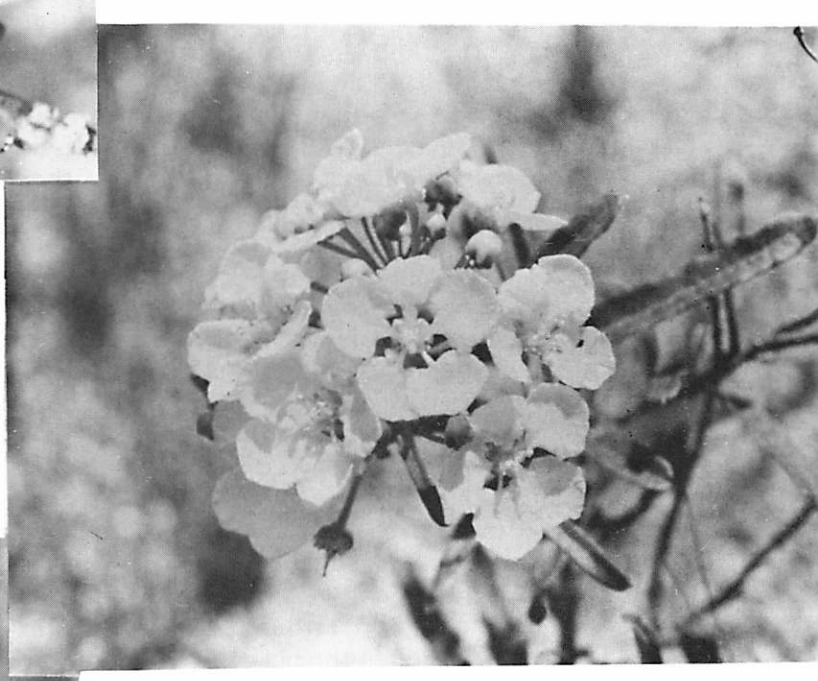

Fig. 2. Photograph of the inflorescence of *Stigmaphyllon sagraeanum.*

Fig. 3. Photograph of the inflorescence of *Malpighia polytricha* ssp. *confusa.*

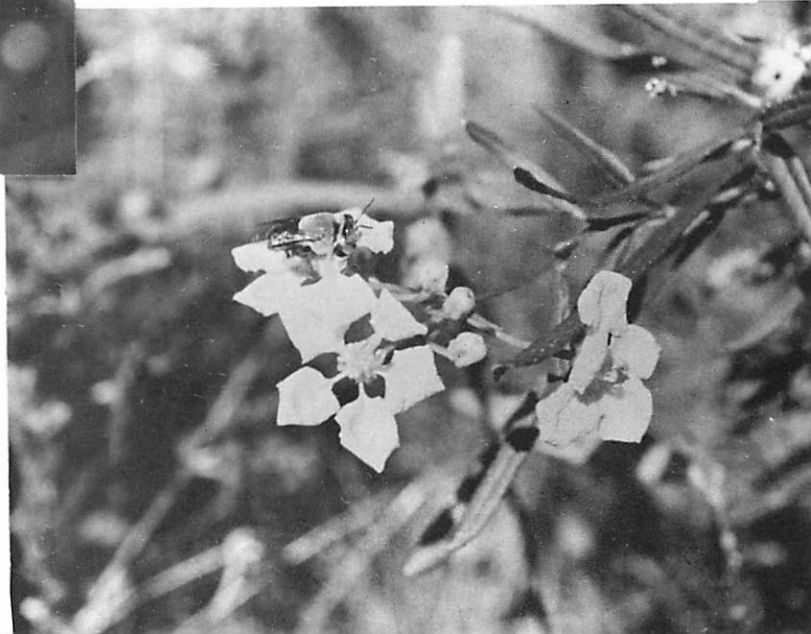

Fig. 4. Photograph of an inflorescence of *Stigmaphyllon sagraeanum* being visited by *Centris inermis.* The head of the insect is directed toward the flag petal.

in the pinelands, along roadsides and on sunny limestone pavements. They seem to occur in a drier habitat than either *Byrsonima* and *Malpighia*. The flowers are 2 to 2.5 cm in diameter and are considerably more zygomorphic than the flowers of the other two plants. All of the floral whorls show considerable bilateral symmetry. The inflorescence is a terminal umbel-like corymb, containing a variable number of flowers (Fig. 2). The pedicels are glabrous and vary in length. The five yellow, clawed petals drop from the flower one to two days after anthesis. The claw of the flag petal is more heavily thickened than in either *Byrsonima* or *Malpighia*. Only four of the five sepals bear elaiophores, the dorsal sepal opposite the flag petal being eglandular. As in *Byrsonima*, there are ten stamens and three synovarious carpels, but they are in a zygomorphic arrangement.

Malpighia polytricha ssp. *confusa* is a small to medium sized shrub, generally no more than 3 meters tall. The opposite leaves have sinuate margins armed with sharp, stinging malpighian hairs, a distinctive characteristic of this subspecies. The plants are much less common than *Byrsonima* or *Stigmaphyllon*, growing either singly or in large colonies which appear to spread by underground runners. The plants grow in well shaded, moist forest situations such as those found in the high coppices or in moist pine groves. The flowers, similar to those of the other two plants, are borne either singly or in pairs, in the leaf axils or terminally (Fig. 3). The pedicels are sparsely covered with malpighian hairs. The five sepals are uniform, each having two elaiophores. The five clawed petals are white and persistent. The ten stamens and three synovarious carpels are in a zygomorphic arrangement.

Distinctive Morphological Features--Morphologically, the most important differences among the three flowers, other than those of color and basic shapes, are found in the organization of the androecia and gynoecia. The plants can be segregated into two groups based upon the symmetry found in the fertile parts. *Byrsonima* exhibits radial symmetry in these parts; *Malpighia* and *Stigmaphyllon* show considerable zygomorphism.

Byrsonima has uniform, elongate styles which protrude up above a ring of ten uniform stamens. The stigmas are tiny cavities at the tips of the styles.

In the flowers of *Stigmaphyllon* and *Malpighia*, two of the styles project laterally in the ventral region of the center of the flower. The third style projects dorsally, away from the two lateral styles. Prominent extensions are present at the top of each style. In *Stigmaphyllon*, the two ventral styles have flattened, foliaceous extensions; the dorsal style bears a narrow, finger-like projection on its abaxial side. In *Malpighia*, all of the extensions are finger-like, projecting abaxially from the styles. The stigmas in both plants are sunken in fleshy protuberances found on the adaxial side of the top of each style.

The stamens in both plants cluster in groups of three around the styles; the tenth stamen stands solitary in the ventral portion of the flower, directly adjacent to the flag petal. The central stamen in each group of three is upright, thickened and enlarged and generally appressed to the style. The stylar extensions cover the tops of the anthers of the large stamens. The other, smaller stamens are often irregularly twisted and bent.

The elaiophores in the Malpighiaceae are of significant interest as they play such an important role in the pollination mechanism. The elaiophores in the three species studied differ in shape, but are anatomically and, apparently, functionally quite uniform. In *Byrsonima* the glands are vertically elongate, with the appearance of an inverted triangle in face view. They are somewhat flattened and creased, with a prominent bulging ridge along the upper portion and they form a tightly packed ring around the base of the flower. The elaiophores of *Stigmaphyllon* are round to oval in shape and bear prominent creases. Each gland is closely appressed to the neighboring gland on the same sepal. The elaiophores of *Malpighia* are narrow and elongate, with the upper portion bulging out from the sepal and often abaxially recurved.

The glands are made up of a basal mass of cells covered with a single layer of elongate, rod-shaped cells, which are densely cytoplasmic and have large nuclei. These cells form a palisade-like layer oriented perpendicularly to the surface on the gland. The entire elaiophore surfaces in *Byrsonima* and *Malpighia* are covered with these cells; in *Stigmaphyllon* they are found only on the external face. This palisade-like layer of

cells is covered with a thick cuticle which becomes loosened in mature flowers to form a collection area for glandular products.

The palisdade-like cells appear to have a secretory function and the elaiophores clearly produce an oily product which can be extracted with a fingernail. The flowers leave distinct greasy marks on the paper used in pressing herbarium specimens. Preliminary chemical analysis indicates the presence of triacylglycerols, but a more exacting quantitative study is needed to determine this with certainty.

Pollination Observations -- Observations of the pollination of *Byrsonima* and *Stigmaphyllon* were made during May, 1984. Unfortunately, no direct observations of the pollination in *Malpighia* could be made. Pollination in the two species appears to occur in a similar manner as documented for other species, and the pollinator also appears to be characteristic for the family.

The pollinator for both plants on North Andros Island is the female of *Centris inermis* Friese. This is a large bee belonging to the anthophorid tribe Centridini. The bees are slightly larger then the common honey bee and appear to be solitary. The insects are quite noisy, their sounds being audible from a considerable distance, which easily enables the researcher to locate the insect in a large plant or cluster of plants. *Centris* is a strong and rapid flyer.

The bees seem to favor the cooler parts of the day for foraging and are most commonly seen in the morning, although a number of sightings were made in the afternoon. Their behavior on flowers of both species is quite similar. *Centris* appears to usually alight on a flower with its head oriented toward the flag petal (Fig. 4). Should a bee alight on the flower in a different orientation, it immediately moves in the flower so that its head is once again oriented towards the ventral flag petal. No bee was ever observed proceeding with pollination while in any other orientation within the flower.

Once properly positioned within the flower, the bee clasps the claw of the flag petal with its mandibles and extends its legs through the gaps between the claws of the petals. The insect then rubs its legs over the surface of the glands, collecting the oil produced there. As the insect is collecting the oil, it appears to vigorously press its body into the center of the flower. The visits to each flower are only a few seconds in duration, making it difficult to observe the exact leg motions employed by the bees in collecting oil from the glands. After remaining in a flower for four or five seconds, the bee flies on to other flowers. The pollen of *Byrsonima* is occasionally found in the stigmatic cavities of *Stigmaphyllon*, indicating that the bees are not specific in their foraging.

We have observed the bees attempting to collect oil on unopened buds of *Stigmaphyllon* and *Malpighia*. This behavior has not been observed involving *Byrsonima*.

Honey bees are quite common on Andros, and they are often encountered foraging among other plants in the vicinity of Malpighiaceous plants. The honey bees occasionally came close to the flowers of *Byrsonima* and *Stigmaphyllon*, but none were observed alighting upon them.

Pollination appears to be quite successful, with abundant fruit set apparent on all three species. Bagging studies indicate that the plants are not self-pollinating. Bagged flowers set no fruit and they wither and fall from the plants.

DISCUSSION

The floral morphology and pollination biology of the three species of Bahamian Malpighiaceae studied appear quite similar to those of previously described species. Although differing in habit and habitat requirements, the flowers retain the characteristic similarities found in the family, as well as exhibiting some notable morphological differences. The pollination observations add reinforcement to previous authors' conclusions about pollination in the Malpighiaceae.

Considerable differences in the organization and structure of the androecia and gynoecia exist among the three plants in the study group. Variation in these structures appears to be quite widespread in the family and would seem to indicate either specialization for a particular pollinator in some plants or adaptation to a more generalist pollination mechanism in others. The irregular styles and prominent stylar extensions in *Stigmaphyllon* and, to a lesser extent, those of *Malpighia polytricha* would appear to be adaptations to a specific

pollinator while the straight, uniform styles of *Byrsonima* seem to indicate an adaptation toward a generalist pollination strategy. This, however, is not the case in the New World, where the family is pollinated by two or three groups of similar insects (Anderson, 1979; Vogel, 1974). On North Andros, *Byrsonima* and *Stigmaphyllon* share the same pollinator, which also contradicts an interpretation of these differences as adaptations to a specific pollinator.

The stylar extensions in *Stigmaphyllon* and *Malpighia polytricha* clearly play a role in the plants' pollination mechanisms and are open to a number of interpretations. One possibility is that the extensions interfere with self-pollination. The styles of *Malpighia* are located to the inside of the upright stamens and the stylar extensions cover the tops of the anthers. This configuration provides a barrier between the pollinator's body and the stamens, which may allow pollen from different flowers to be deposited in the stigmas before the flower's own pollen can be picked up and deposited there. Only the dorsally oriented style and stylar extension have this configuration in *Stigmaphyllon*, but the two broad stylar extensions form a similar if not more impenetrable barrier for the ventral styles. A similar interpretation of this structural configuration as a barrier to self-pollination is given for *Stigmaphyllon litorale* by Vogel (1974), who calls it a form of "herkogamy" (the spatial separation of anther and stigma, thereby preventing self-pollination). *Byrsonima*, while not having these physical barriers to self-pollination, does extend its styles above the tops of the stamens, allowing the pollinator to deposit previously collected pollen in the stigmas before transfer within the same flower can occur. This organization can be seen as a spatial barrier to self-pollination.

The calyx glands in all three studied plants, although they differ in shape, are anatomically and functionally quite similar. The elongate, rod-shaped cells which comprise the surface of each elaiophore clearly have a secretory function, exhibiting a dense, dark-staining cytoplasm and large nuclei. Vogel (1974) illustrates similar structures for a number of other species of Malpighiaceae and there appears to be considerable uniformity among the elaiophores in the family.

The pollination of *Byrsonima lucida* and *Stigmaphyllon sagraeanum* on North Andros Island appears to be consistent with observations by other researchers of pollination in New World Malpighiaceae (Anderson, 1979; Raw, 1979; Vogel, 1974). The plants are both visited by the female of *Centris inermis*, an oil collecting bee in the tribe of anthophorid bees known to include many of the primary pollinators for the Malpighiaceae in the New World. The behavior of the bees also appears to follow the pattern described by Vogel (1974) and Anderson (1979). Our observations indicate that honey bees play no role in the pollination of these plants, and that individual *Centris* bees do not restrict their foraging to only one of the malpighiaceous flowers on the island, as the pollen of *Byrsonima* is found in the stigmatic cavities of *Stigmaphyllon*. It is quite probable that the flowers of Malpighia polytricha on North Andros are also visited by *Centris inermis*.

The behavior of the bees in landing on the flowers indicates that there is some mechanism at work directing the insects to position themselves in the flower with their heads pointing towards the ventrally oriented flag petal. This behavior is exhibited each time an insect lands on any of the flowers and is repeated as the bee moves from flower to flower in an inflorescence. In flowers such as *Byrsonima* that exhibit uniform stamens and styles and have elaiophores on each sepal, there is no need to have the insect oriented in any one particular direction to insure pollination. For *Malpighia* and *Stigmaphyllon*, however, which exhibit irregular configurations of stamens and styles, correct positioning of the insect is necessary for consistent pollination to occur. The exact cause of this behavior has not been investigated, but it is probable that ultra-violet patterns or a visual response to the flag petal are involved.

The flowers of the three species of Bahamian Malpighiaceae exhibit the specific relationship of structure to function characteristic in the flowers of New World members of the family. The flowers retain a uniformity of function in those parts which attract, orient and reward pollinators despite differences in shape, size and color. The calyx elaiophores, while differing in shape and size, have similar anatomical structure and a similar function in attracting and rewarding the pollinator. Each flower has a

flag petal to orient the pollinator and the structure and arrangement of the fertile parts, while differing considerably among the plants, maintain a form which facilitates pollination and inhibits potential self-pollination.

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