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A REVISION OF THE GENUS GUAZUMA[1]

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THE GENUS GUAZUMA, because of its omnipresence in the American tropics, is well represented in the larger herbaria. In spite of this, little systematic attention has been paid to this genus, with the result that the collections in these herbaria seem to consist of a confusing array of species. Several of the earlier systematists had worked out parts of the genus and because of the many variations and lack of material had been led astray on others. Many of their conclusions were inadequately stated. The results of their work have been scattered among the numerous publications of taxonomic literature and modern systematists have not had the time, nor the incentive, for the genus is of little economic importance, to uncover and recombine this literature. It has been attempted in this treatment to rectify some of the above conditions. It should be noted however that the species *Guazuma tomentosa* is still a complex entity offering material for further study. A key has been provided by which it should be possible to classify fruiting, flowering, and vegetative material. Indices to types and exsiccatae have been provided for convenience.

More than 400 specimens of the four species have been examined during the course of this study. The specimens were loaned from the herbaria at the Chicago Natural History Mu-

[1] Part of a thesis submitted to Henry Shaw School of Botany in partial fulfillment for the degree of Master of Arts. The author is deeply grateful to the curators of the herbaria at the Missouri Botanical Garden and Chicago Natural History Museum for the loan of study material used in the preparation of this revision.

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seum and the Missouri Botanical Garden. The work was carried out in the laboratories of the Missouri Botanical Garden under the direction of Dr. R. E. Woodson, Jr.

TAXONOMIC HISTORY

Guazuma was described first from the West Indies by Gonzalo Fernández de Oviedo y Valdés (Hist. Nat. 8: 7). In the first edition (Seville 1535) he observed that the tree is common in the West Indies and on 'tierra firme', by which he probably meant Mexico and Central America. In the second edition (Madrid 1851), published with additions and by José Amador de los Ríos, the original text was followed and some experiments described on the quality of powder made from the wood of *Guazuma* in the town of Santo Domingo. In neither of these books was the word Guazuma used in the generic sense. One would be led to believe that this name was taken from 'Guácimo' which is still in use by the natives of the West Indies.

Father Plumier (Nov. Pl. Am. Gen. 36. 1703) indicated that he had taken the name Guazuma from Oviedo. He recognized three entities, "The elm-leaved Guazuma with purple-black fruit", and two "Tree Guazuma with spreading foliage and woolly fruit", the first with large, the second with small fruit. The latter two are probably the same. A diagnosis and several drawings were given; though the drawings show the stamens free and petals without appendages, still one would not mistake them for other than those of *Guazuma*. Linnaeus (Sp. Pl. 782. 1753) placed *Guazuma* under *Theobroma* as a second species of that genus and it was to remain there until Adanson (Fam. Pl. 2: 383. 1763) observed the differences between them. He credited Plumier as the pre-linnaean author and presented in tabular form the characteristics of *Guazuma* and the other related genera. No species were given. Lamarck (Encycl. 3: 52-53. 1789) gave a very lucid description of a plant which he called *Guazuma ulmifolia*. Sufficient characteristics were given so that there is little doubt as to the species observed. His type specimen as well as his description clearly shows that his species had dehiscent fruit. For some reason most plants now labelled *Guazuma ulmifolia* Lam. bear the name regardless of whether the fruit is dehiscent or not. Humboldt, Bonpland, and Kunth (Nov. Gen. et Sp. Pl. 5: 320.

1823) described a species with indehiscent fruit which they named *Guazuma tomentosa*. Under this name they published two very good descriptions of plants in their herbarium, suggesting the possibility that they might in reality represent two distinct species.

Martius (Flora 20, Belbi. 2: 95. 1837) published a very short diagnosis of *Guazuma crinita*, a species collected near Sebastianopolis, Brazil, which he indicated as having fruit with long plumose hairs. It is interesting that his type (photograph seen) seems to contain two distinct elements. It consists of a single fruit and a flowering branch. The former has long plumose hairs, coinciding with his diagnosis, and therefore belongs to his species. The flowering branch obviously belongs to *Guazuma ulmifolia* Lam. Thus there are two species under the single Martius herbarium N° 89. It is suggested that the fruit become the type of *Guazuma crinita* Mart., and that the flowering branch be labelled *G. ulmifolia* Lam. One can only conjecture as to how the obviously different species came to be mounted on the same sheet.

Schreber (Gen. 513. 1791) seems not to have known of Adanson's earlier work when he published the name *Bubroma* though he cites Plumier and Linnaeus in his synonomy. This event initiated a series of name changing from *Guazuma* to *Bubroma*. Willdenow (Sp. Pl. 3^2: 1423. 1803) transferred the specific name *Guazuma* from *Theobroma* to a like status under *Bubroma*, and later (Enum. Pl. Berol. 806. 1809) described two new species from Brazil. Sprengel (Sys. Veg. 3: 332. 1826) upheld the names proposed by Willdenow and described a new species which he indicated might be conspecific with *Guazuma tomentosa* HBK.

Turczaninov (Bull. Soc. Nat. Mosc. 25^2: 156. 1852) described a monotypic genus *Diuroglossum* which, according to his description, is indistinguishable from *Guazuma*. He mentions its proximity to *Herrania* and *Buettneria* but does not mention *Guazuma*. K. Schumann (Fl. Bras. 12^3: 81. 1886) recognized *Guazuma crinita*, *G. rosea*, and several varieties of *G. ulmifolia*. Since that time, regardlees of their morphological makeup, most northern plants of this genus have been named as *Guazuma tomentosa* HBK. while those more southern in distribution usually bear the name *G. ulmifolia* Lam.

RELATIONSHIPS

The most inclusive treatment of the *Malvales* is that by K. Schumann published in Engler and Prantl's Natürlichen Pflanzenfamilien 3^6: 1-99. 1890. There seems to be no doubt that *Guazuma* belongs in this order, nor is it difficult to place in the *Sterculiaceae*. *Guazuma* is closely allied to several other genera with which it forms the subtribe *Theobromineae* of the *Sterculiaceae*, which is characterized by stamens united into groups of two or three. This character separates it from the subtribe *Buettnerineae* which has the stamens borne singly. It is doubtful whether a division on this basis is natural since it separates from *Guazuma* the genera *Buettneria*, *Ayenia* and *Commersonia* all of which closely resemble *Guazuma*, particularly *Commersonia* which perhaps is as closely related to *Guazuma* as is *Theobroma*. The two subtribes form the tribe *Buettnerieae*, which is separated from the other tribes of the *Sterculiaceae* by the following major characters; bisexual flowers, absence of androgynophore (except in *Ayenia*), short staminal tube, and large separate cap-shaped petals. The last character though used as a key character in K. Schumann's treatment does not hold for the genera *Leptonychia* and *Glossostemon* of the subtribe *Theobromineae*. The differences of the *Theobromineae* are best summarized in table form. See figure 1.

Though the genera are quite distinct and sharply differentiated from each other, they are also clearly related one to another. It should be immediately apparent that *Guazuma* resembles the other genera in single characters more than in groups of characters. For instance the staminal arrangement of *Guazuma* is very similar to that of *Abroma;* in both genera there are 15 stamens grouped into threes. *Guazuma* has simple staminodia which are small, acute, triangular, and flat. On the other hand the staminodia of *Abroma* are large and petal-like, while representing a somewhat median position is *Theobroma* with rather long triangular staminodia. In *Scaphopetalum* the staminodes seem to be reduced to miniature teeth, two between each fertile staminal group. *Leptonychia* shows a condition of multiplication of stamens, some of which become sterile forming filamentous staminodes, and a resulting variable arrangement and number of alternating stamens and staminodes. When the staminal column is split between the sta-

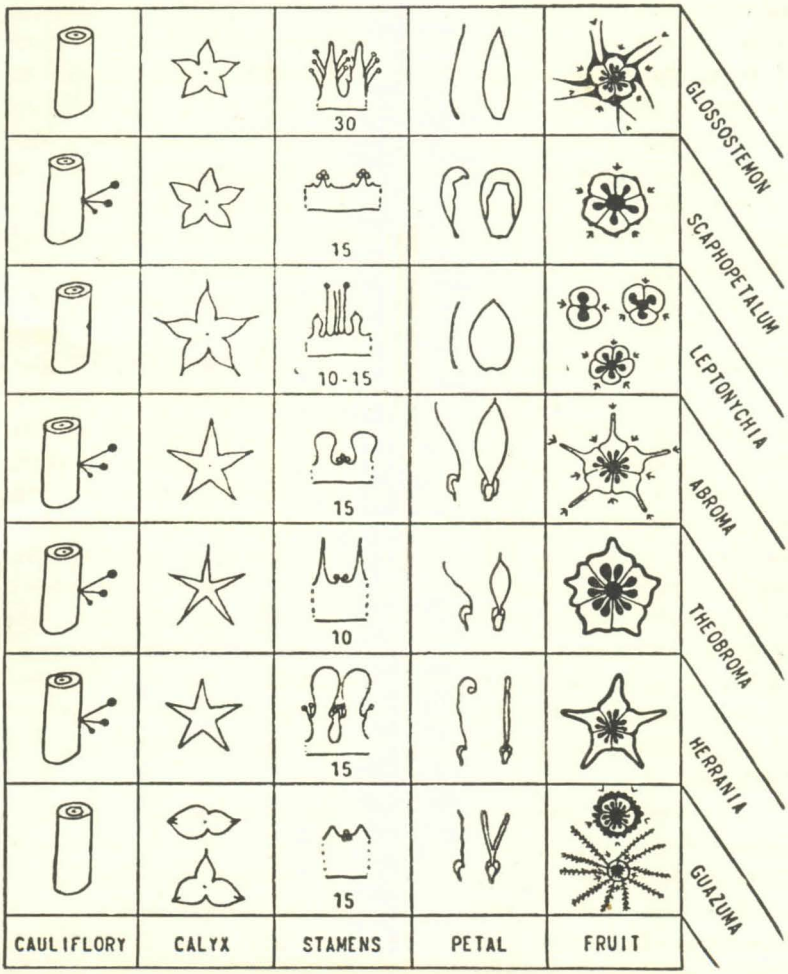

Figure 1.—Morphological differences in the **Theobromineae.** Drawings are not to scale. Complete arrows indicate locations on fruit where dehiscence always occurs; partial arrows indicate locations where deshiscence may or may not occur.

mens nearly to the base, we find that, in *Herrania*, the 15 stamens become grouped in ones and twos on each side of the staminodes, or in *Glossostemon* the stamens become more numerous with a group of three on either side of a staminode.

All the genera of the *Theobromineae* have cap-shaped or hooded petals, except *Leptonychia* and *Glossostemon* in which

the petals are definitely flat. In *Leptonychia* the petals are scale-like while in *Glossostemon* they are quite showy. Neither of these two genera nor *Scaphopetalum* has appendages on the tips of the petals.

In those genera having apical appendages on the petals one finds a good series. Starting with *Abroma*, in which the appendage is scarcely differentiated but is very large and petal-like, the series passes through *Theobroma* with a well differentiated but small and petal-like appendage, to *Herrania* where it is extremely differentiated and extraordinarily long-linear. At the climax of this series might be found *Guazuma* in which the appendage is bifid and almost filiform.

On the basis of flower and fruit resemblances there are several other genera worth mentioning. *Buettneria*, which consists of vines or scandent shrubs and has only five stamens, resembles *Guazuma* to a remarkable degree in flower structure. The petals are hooded and with an apical appendage, the staminal tube closely resembles that of *Guazuma* although the petals are much more firmly attached, and the calyx is five-parted instead of somewhat united as in *Guazuma*. The fruits of *Buettneria* resemble those of *Guazuma* but have long spines and a more complicated dehiscence. The fruit of *Buettneria* first splits septicidally and later loculicidally nearly to the base, while that of *Guazuma* splits loculicidally only or is indehiscent.

The fruit of *Guazuma crinita* Mart. so closely resembles that of *Commersonia* that it is practically impossible to distinguish them offhand. In both genera the fruiting inflorescence bears many globose fruits covered with long plumose hairs. The mature leaves and fruits are nearly identical in size, shape, and coloration. *Commersonia* differs from *Guazuma* in that its mature fruit dehisces like that of *Buettneria*. There are usually one to two erect seeds in each carpel of the fruit of *Commersonia* while *Guazuma crinita* has two to five seeds in each carpel. The staminal arrangement in *Commersonia* is the same as that of *Guazuma* except that the two lateral anthers of each group have become minute filamentous staminodes. Perhaps the petals of *Commersonia* are an intermediate step from petals like *Guazuma* to those like *Buettneria* since they resemble the latter except that they are not so firmly attached to the staminal tube nor are the petals and appendages so large. A

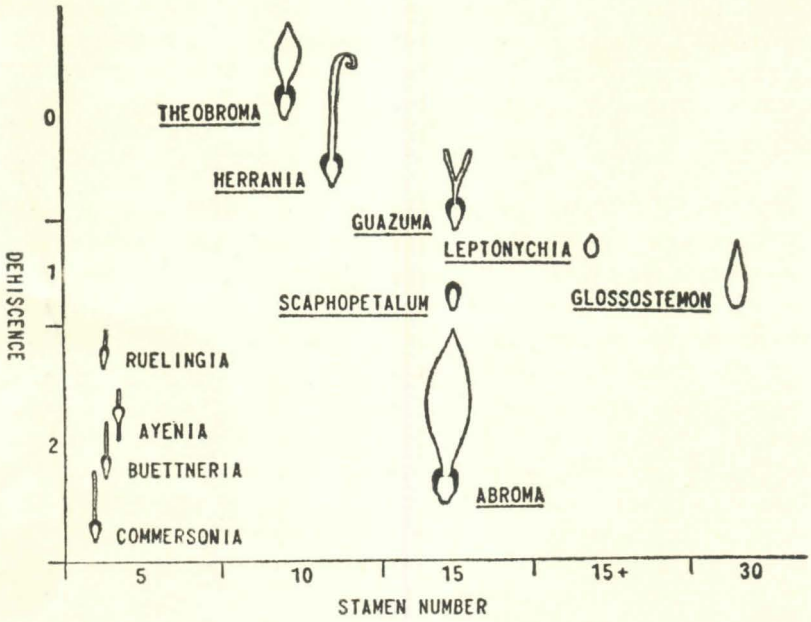

Figure 2.—Theoretical phylogeny for the **Buettnerieae.** The positions of the genera are indicated by drawings of petals representative of each. Th drawings are not to scale. Genera of **Theobromineae** are underlined. Dehiscence numbers indicate: 0, indehiscent; 1, loculicidally or septicidally dehiscent; 2, loculicidally and septicidally dehiscent.

chart depicting the theoretical phylogenetic relationships of the genera of the *Buettnerieae* is given in figure 2.

Guazuma was divided by K. Schumann into two sections: *Commersoniopsis* containing the single species *Guazuma crinita*, and *Euguazuma* containing *G. ulmifolia* and *G. tomentosa*. Fruit and seed characters were used as a basis for this division. *Guazuma crinita* has long plumose hairs on the fruits while the other two species have short murications. There are only two to five seeds in the carpels of *Guazuma crinita* in contrast to the large number of seeds in *G. ulmifolia* and *G. tomentosa*. To support this division it may be noted that in the two species of *Euguazuma* the petals are quite large, while those of *Guazuma crinita* are very small. The fact that *Guazuma ulmifolia* and *G. crinita* dehisce alike while *G. tomentosa* is indehiscent weakens the basis for this division.

With the addition of the species *Guazuma longipedicellata*, unknown in Schumann's time, a new section *(§ Gynophoriola)* must be formed if one is to follow Schumann's scheme for subdivision of the genus. The presence of a gynophore accompanied by apiculate buds and exceptionally long pedicels seem sufficient basis for this division even though fruit characters upon which the other two sections are based, are lacking for this species.

EVOLUTION

The evolution within the genus is, of course, speculative since one does not have the historic populations on which to base one's judgment but instead works only with the results of that population, the living representatives. To make it even more difficult one is dependent on specimens (only part of an individual plant) collected sporadically rather than systematically, with the result that there is but a fraction of the present population with which to work. Nevertheless it is quite easy to obtain some notion of the phylogeny of the four species of *Guazuma*. If one should attempt to explain the phylogeny of the genus by use of its present distribution, *Guazuma tomentosa* would be the most modern species while *G. crinita* becomes a relict population. *Guazuma ulmifolia* is placed as an intermediate, but very close to *G. tomentosa* because of their similarity of distribution. Not only has *Guazuma tomentosa* become adapted to a xerophytic habitat, while *G. crinita* prefers the rain forests, but it is seen that because of its variability and non-specificity of habitat it has occupied a larger geographic area than has the latter. Based on these criteria *Guazuma tomentosa* would seem to be the most recent species and *G. crinita* the oldest. In addition the fruit, the best taxonomic character of the species, is indehiscent in *Guazuma tomentosa*. This is presumed to be a specialization more advanced than dehiscent fruit.

Here too the flowers are the largest and the plants are by far the smallest of the genus, sometimes becoming shrubs. All of which tends to substantiate the derived condition of *Guazuma tomentosa*. Primitive characters are also found in this species. Among these are: numerous seeds, many flowers, and large anthers. *Guazuma ulmifolia* so resembles *G. tomen-*

tosa morphologically that there is no doubt but that it should be placed very near the latter. However it is less advanced by reason of its dehiscent fruits, and the species consists mostly of medium sized trees. The distribution is very similar to that of *Guazuma ulmifolia* though somewhat more restricted. *Guazuma crinita* seems to be the most primitive of the genus in that it is arborescent, the most restricted geographically, and has dehiscent fruits. However, we find many morphological dissimilarities from the other two species, the most striking of which is the long plumose hairs of the mature fruit. This character would tend to separate it rather sharply from the former species. Occupying a somewhat similar position to that of *Guazuma crinita*, *G. longipedicellata* is sharply separated from the rest of the genus by its morphology as well as by its restricted distribution. See figure 3.

MORPHOLOGY

In a discussion of the morphology it seems worth while to give a more complete description of the characters of the species with some idea of their variability, as well as the terms employed in the descriptions. *Guazuma tomentosa* Lam., the most variable of the species, differs not only geographically but also within single specimens and the amount of variation within this species is greater than that within the others. The variations of all species occur in the same organs and to a proportionate degree.

HABIT: The general habit, at least in the upper portions, is similar to that of an elm formed by a multiply branched trunk resulting in a broad spreading, open crown. The branches are horizontal or slightly drooping, and wide spreading. The plants vary from shrubs as in *Guazuma longipedicellata* to semi-shrubs or broad low trees as in *G. tomentosa*. *Guazuma ulmifolia* is somewhat taller with a larger trunk, while *G. crinita* is the largest although a more slender tree.

LEAVES: These are the most variable organs. The stipules are minute, flat, acuminate scales sometimes almost filamentous or linear, about 3 mm. long, one on each side of the petiole. These are early deciduous. The petioles are short, pubescent and distichous with a peculiar thickened portion just below the leaf blade. This thickened portion is striate and

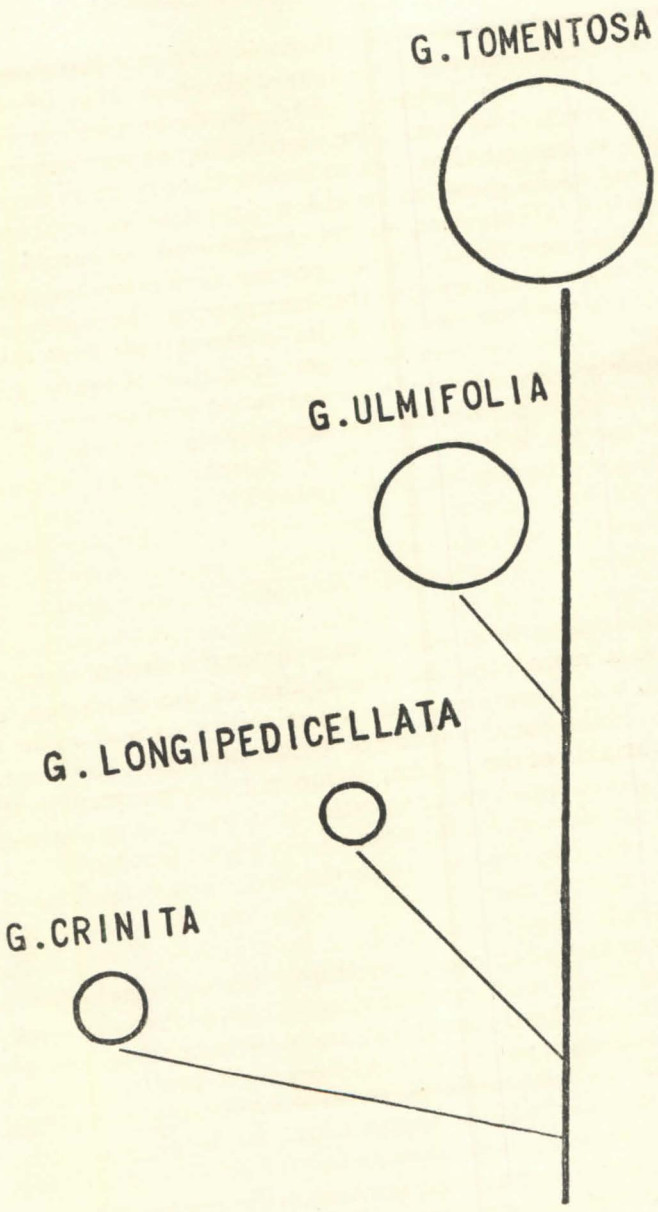

Figure 3.—Theoretical phylogeny for the genus Guazuma. Circles indicate posi'ion of species with the most advanced at top. Area of circle is proportional to distribution.

enlarged and is possibly connected with the sleep movements of the leaves noticed by George Don (Gen. Hist. Dich. Pl. 1: 522. 1831). The petiole at the base of the leaf blade divides into three to five veins, the middle of which extends up the blade to the tip. The lateral veins diverge from the base of the leaf equally with the smallest at the leaf margin. This gives an aspect of palmateness to short leaves. When the leaves are inequilateral the smaller portion of the blade bisected by the vein is always towards the branch axis. The leaves are predominantly stellate-pubescent with a few simple hairs intermingled. In *Guazuma tomentosa* both surfaces of the leaves may be densely pubescent or they may be densely pubescent on the lower but nearly glabrous on the upper surface. The leaf blade in all species is very thin, in dried specimens a fraction of a millimeter, and in the more pubescent leaves the pubescence may account for the greater part of the apparent leaf thickness.

There are all stages of intermediate pubescence. The leaves of *Guazuma longipedicellata* resemble those of *G. tomentosa* though generally thinner, while not even in the most glabrous specimens of *G. tomentosa* are there leaves that are lustrous as are those of *G. ulmifolia*. The lustrous quality seems to be due to the smoothness of the surface of the leaves. The leaf surface of *Guazuma tomentosa* is very minutely wrinkled. In the leaves of *Guazuma crinita* the surface is somewhat lustrous but the lustrous quality is slightly modified by the presence of many sessile and short stellate hairs which give a rough feel to the leaves. The degree and type of serration is variable, but in most cases is twice crenate-serrate with the largest teeth about 2 mm. long.

INFLORESCENCES: The cyme is the basic structure of the inflorescence in *Guazuma*. The main axis of an inflorescence appears to be thyrsiform but at each secondary branch it is jointed. Thus the main axis ends abruptly usually in a flower that may or may not develop. At the base of this 'flower' and subtended by two bracts are two lateral peduncles, one of which may become a scorpioid cyme, the other continuing the main inflorescence axis. This thyrsiform branching may occur but once at the base of each inflorescence as is usually the case in *Guazuma tomentosa*, several times as in *G. ulmifolia* and *G. longipedicellata*, or five to eight times as in *G. crinita*. This branching in conjunction with longer internodes results in *Guazuma crinita* having the largest inflorescences. The sec-

ondary peduncles of all four species may also branch in this manner but only a few times. The terminal scorpioid cymes have very much fore-shortened internodes which results in the flowers being tightly clustered at the tips of the secondary peduncles, a character remarkably well shown in *Guazuma ulmifolia*. The genus characteristically has very short pedicels, usually no longer than the length of the petals; however, *Guazuma longipedicellata* has pedicels 3 5 times longer than the petals. The inflorescences of *Guazuma tomentosa* are, on the whole, few-flowered and rather small when compared to those of *G. ulmifolia*, though there are many more inflorescences. In spite of the large number of flowers in *Guazuma ulmifolia* it sets no more fruit per inflorescence than does *G. tomentosa*. In both these species there are few fruits on each inflorescence while in *Guazuma crinita* there are usually many. See figure 4.

FLOWER, GENERAL: The flowers are relatively stable. The buds just before anthesis are spherical except in *Guazuma longipedicellata* in which they are nearly conical with an apiculate tip. As the bud opens a slit develops in the calyx, spreading from the apex down two or three sides to the receptacle. It may also split somewhat between the other sepals but here it never seems to progress to the base. The sepals therefore are valvate. The petals are also valvate but with the edges inrolled. The apical appendage is crumpled on the top of the petal in bud. The flowering in all cases occurs with the flush of leaves but tends to be earliest in *Guazuma ulmifolia* and latest in *G. crinita*. The perianth is absent in fruit.

CALYX: As mentioned above the calyx is slightly split between all sepals but only split to the base in two or three places. At maturity it is densely stellate on the dorsal surface and is cup-shaped, probably because of its form in the bud. The cup may be turned inside-out or not, and may be nearly perpendicular to the flower axis to definitely reflexed.

COROLLA: The bases of the petals may be elongated, forming claws which attach the petals to the receptacle. There are usually five large and several smaller veins extending up the petal to its apex. The petals are usually appressed-stellate on the dorsal surface. They are hooded over the stamens and weakly attached to the inside edge of the staminal column by two tiny teeth, one on each side of the petal apex. The appendage, though well differentiated from the basal hood of the

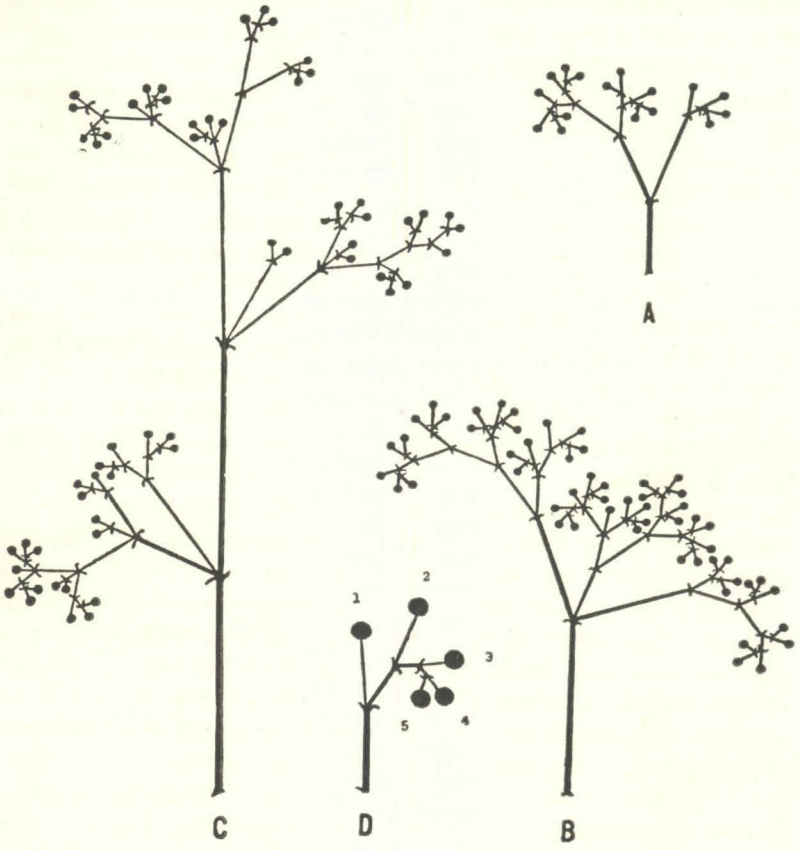

Figure 4.—Inflorescence diagrams for the genus Guazuma. A. Inflorescence diagrams for **Guazuma tomentosa.** X 1 1/2 B. Diagrams of inflorescence found in **Guazuma ulmifolia** (X 1 1/2) and in **Guazuma longipe icellata** (X 1/2). C. Inflorescence diagram for **Guazuma crinita.** X 1 D. Diagram of ultimate inflorescence showing order of flowering.

All diagrams have been simplified as to number of buds and flowers present, which are indicated by black dots. All peduncles are to scale.

petal, is no more than the elongated, reflexed apex. Three of the median veins of the petal extend up the appendage to the bifurcation where the middle vein splits into two smaller veins. In *Guazuma crinita* the resulting veins and, or, the two lateral veins, may then branch in the portions of the appendage above the bifurcation. This secondary vein branching does not seem

to occur to such an extent in the other three species; however there may be extremely small veinlets in all four.

ANDROECIUM: There are five staminodes, alternate with the petals, which are united into a hollow cylinder narrower at base than at the top. The tips of the staminodes are slightly shorter than the petals and usually do not project above them. The staminodes are somewhat bladdery, short, triangular structures. Between these staminodes are five subsessile groups of fertile anthers. In each group, if one looks at the flower centripetally, there are two anthers on the right attached by their very short filaments to each other and then to the staminal tube, while on a somewhat longer filament, and to the left of the first two, is attached the third anther. The filaments, all of which are extremely short, are reflexed towards the receptacle so that the anthers are pendent and on the outside of the staminal tube. There are no clearly defined veins in the staminal tube leading to these structures, although there is a trace of one to each staminode and perhaps the remnants of two to each stamen group. The anther at dehiscence is extremely small, consisting of two divergent and nearly separate loculi which are united at the base and attached to a short filament. The basal body of each loculus is ellipsoidal and dark colored, usually a deep red. The valves, about the length and width of a loculus, are on the opposite end from the stalk; they are membranaceous and white or cream-colored. At maturity the valves diverge from the filament axis at an angle of approximately 80 degrees. The valves of one loculus of an anther are almost contiguous with the valves of the other loculus, and nearly form a straight whitish disk over the top of the anther.

GYNOECIUM: The pistil is minute and hidden within the staminal column, only the stigma protruding slightly above the top. However, in *Guazuma longipedicellata*, because of the presence of a distinct gynophore of about the same length as the style, the entire style may protrude above the staminal column. The stigma is as long as the style and, though usually cleft into five parts, these seldom diverge. Nevertheless the lobes can be separated by mechanical means quite easily. The stigma and the style are covered with minute bristles. The base of the style has a whorl of five geniculate lobes which extend directly onto the top of the carpels of the ovary. In § *Euguazuma* and § *Gynophoriola* the ovary is covered with erect, simple and branched hairs. In § *Commersoniopsis* the

ovary is covered with longitudinal rows of minute knobs which later develop into the long plumose structures of the mature fruit.

FRUIT: The fruit of *Guazuma longipedicellata* is unknown so will not be mentioned in the following discussion. In the other species the fruit is a capsule consisting of five more or less heavily vascularized carpels. It may dehisce loculicidally by splitting from the apex or may release the seeds through pores which are formed by the disintegration of nonvascular tissue of the carpel wall, or may remain indehiscent if the fruit does not fall to the ground and partially decompose. The capsules of *Guazuma tomentosa*, which are more or less dehiscent by pores, may vary considerably in shape and structure. They may be quite oblongoid in the more xerophytic forms which have small, very pubescent leaves, and more spherical in mesophytic plants. The fruits of *Guazuma ulmifolia* are loculicidally dehiscent from the apex and are spherical or somewhat depressed at the ends with little variation in size and shape. *Guazuma crinita* fruits vary but little and are very small, spherical, and dehisce loculicidally. They are borne on a very short but distinct stipe formed from the base of the carpels as the fruit matures. Perhaps this may be a repressed gynophore.

The gross structure of the carpel wall is quite interesting. Here are found three distinct layers which are, centrifugally, the inner vascular or structural network, the more or less fleshy tissue or cortex, and the appendages or murications. The innermost layer in all species is quite distinct and remains hard and durable after the other tissues have rotted away in those fruits which fall to the ground. It is a network of large thick veins variously branching and forming a foundation for the other tissues. Surrounding and especially external to this network of vascular tissue is a more fleshy tissue which in dry fruits separates irregularly. In *Guazuma crinita* this separation is not noticeable while in *G. tomentosa* it is shrunken and contracted, particularly in the rounder capsules. The very outside of the carpel walls develops extremely long filamentous appendages which are plumose as in *Guazuma crinita* or short pyramidal protuberances or murications in the other species. The plumose appendages consist of a many-celled central stalk several times as long as the fruiting body, at maturity covered by numerous multicelled stellate hairs which, at times, are

quite long. The central stalk seems to develop from smalla meristematic region occuring as knobs in rows on the ovary and, as it forms cells basally which become hairs and stalk, it is carried up at the apex of the plumose emergence. The meristem of the murications on the other hand seems to be basal and functions for a relatively short time immediately after fertilization. When the murications have reached their full size, the fruit then begins to enlarge and at maturity may cause the murications to separate basally from one another to a greater or less degree. In *Guazuma ulmifolia* the murications are strictly pyramidal with few lateral stellate hairs, while those of *G. tomentosa* are usually conical and covered with pubescence. The mature capsule of *Guazuma ulmifolia* is extremely mucilaginous while those of the other species exhibit this character to a lesser degree.

The seeds of the three species are very similar and covered with very clear and translucent mucilage. On the seed coat are found various slightly raised groups of colored cells, and in *Guazuma crinita* they form minute, blunt, short horns. In the other two species they form irregular blotches scattered over the seed coat. The testa is extremely cartilaginous and hard but not very thick and forms a good protective layer for the embryo, which occupies the whole of the central cavity. The small amount of endosperm present is pressed into the crevices formed by the folds on the cotyledons. The embryo is straight with a micropylar plumule. The cotyledons are reflexed and rolled around the hypocotyl.

ECONOMICS

Guazuma crinita and *G. longipedicellata* have no uses other than as ornamentals while the other two species have been variously employed. Oviedo (Nat. Hist. 8: 7. 1535) must have believed the trees to be of considerable importance to the Indians of the West Indies. He mentions that a beverage made from the fruit contributed to their well-fed appearance and general healthiness. Many other uses have been noted since. They may be summarized as follows.

FOOD

1. Fruit is eaten by animals, particularly horses and cows in the periods of drouth. The dried and ground fruit is at present used as a molasses substitute for feed concentrates in the tropics. Leaves are also eaten.

2. The succulent fruits are eaten by humans: they are a very mucilaginous affair with the taste of green figs. In the case of *Guazuma tomentosa*, the succulent tasteless fruit is edible but by no means delicious.

3. Used as a beverage by soaking the crushed fruit in water and straining off the liquid.

WOOD

1. A very light and easily worked wood, it has been used for making slack cask staves, furniture, violins, and side pieces for coaches, general carpentering, and interior construction.

2. Used to make charcoal which is supposedly very excellent in the manufacture of gunpowder.

3. Has been used by the natives as a base board for making fire by the crossbow and stick method.

ORNAMENTAL

The tree makes a very good shade tree since it is widespreading. Also interesting as the leaves hang vertically at night. Has been transported to Hawaii, Java, and India where it has escaped.

OTHER

The tree should be mentioned as a weed since it has so many tendencies in common with those plants with widespread distribution and found in disturbed localities. *Guazuma tomentosa* particularly fits this description.

COMMON NAMES

General: American elm, bastard-cedar, caulote, guácima, guácimo, guásima, tapaculo.

West Indies: Bay cedar, West Indian elm.
Cuba: guácimo baba.
Haiti and French Antilles: bois d'orme, bois puant, bois zombre.
St. Thomas: jackocalalu.
Tobago: congo calliloo.
Mexico: aquiche, bulines, cabal-pixoy, cuahulote, cahuilote, cuaulote, majahua de toro, palote negro, pixoi, pixoy tablote, vácima, yaco granadillo.
Guatemala: cablote.
El Salvador: caca de mico, chicharrón.
Costa Rica: diankrá, kudzir, serúru, shumgín, sungí, sungín, surruru, udzir.
Panama: guácimo de ternero.
Colombia: guácimo colorado.
Venezuela: guácimo blanco, guácimo dulce, guácimo macho.
British Guiana: wonan.
French Guiana: anhuiba, cédre, cédre jaune, mahot baba.
Brazil: ibixuma, motamba, mutamba.
Ecuador: guamo.
Peru: bolaina, iluminasi, lluicho-vainilla, papayillo.
Argentina: cambá-acá, cabeza de negro, inga-hú, inga negro, marmelero.

TAXONOMY

GUAZUMA Plum. ex Adans., Fam. 2: 382. 1763.
Bubroma Schreb., Gen. 513. 1791.
Diuroglossum Turcz. in Bull Soc. Nat. Mosc. 25[2]: 157. 1852.

Trees. Leaves simple, alternate, stipulate, 3- to 5-costate, shortly petiolate, crenate-serrate, stellate-pubescent. Inflorescences axillary, more or less asymmetrical, thyrsiform, aggregate, scorpioid cymes; flowers perfect, regular, small. Calyx valvate, 2- to 5-parted at anthesis, reflexed at maturity, deciduous, stellate-pubescent dorsally. Petals 5, valvate, involute in bud, cucullate, the tips somewhat involute and minutely bifid, bearing an erect, elongate, bifid apical appendage. Stamens 15, united into a cyathiform column, the reflexed, dithecous, divergent anthers in 5 groups of 3 alternating with 5 dentiform staminodia; pollen spherical, 12.8-19.0 mu in diameter, light yellow to gray, the exine tricopate, minutely

rugose, transparent, the intine appearing slightly tetragonal or flattened on several sides. Pistil superior, sessile, or on a minute gynophore, the ovary ellipsoidal to spherical, stellate-pubescent, 5-celled, the few to many 2-seriate, anatropous ovules on axile placentae, the style filiform, confluent at the base with 5 minute, geniculate lobes, the stigma 1- to 5- cleft, the lobes divergent or erect and connivent. Fruit a more or less woody, indehiscent or dehiscent capsule, muricate or bearing filiform appendages; seeds small, obovoid, albuminous, mucilaginous, the testa maculate, the embryo typically dicotyledonous, erect, the cotyledons supervolute.

Type species: *Guazuma tomentosa* HBK. *(Theobroma Guazuma* L.)

KEY TO SECTIONS AND SPECIES

A. Flowers white, the buds narrowly ovoid, acuminate, the pedicels 3 times longer than the sepals, the gynophore manifest. Leaves ovate to oblong-ovate, slightly pubescent below and not lustrous above. (Fruit not known.) Shrubs. El. Salvador. (Sect. *Gynophoriola* G. F. Freytag) .... 1. *G. longipedicellata* G. F. Freytag

AA. Flowers yellowish to lilac or pink, the buds spherical, the pedicels less than twice as long as the sepals, gynophore absent. Trees or shrubs.

B. Fruit covered with relatively short, stout murications; seeds many in each cell; petal appendages scarcely longer than the basal hood. (Sect. *Euguazuma* K. Schumann)

C. Fruit indehiscent, the murications separating irregularly at maturity; petals prominently clawed; leaves ovate to oblong-ovate, pubescent and not lustrous above. Mexico, Central America, and Antilles, south to Ecuador ..... 2. *G. tomentosa* HBK.

CC. Fruit dehiscent, the murications not separating at maturity; petals not prominently clawed; leaves oblong

to ovate-oblong, glabrate and lustrous above. British Honduras and Antilles, south to Paraguay ..... 3. *G. ulmifolia* Lam.

BB. Fruit covered with filiform, plumose emergences and stellate hairs; seeds 3-6 in each cell; appendages three to four times longer than the basal hood. (Sect. *Commersoniopsis* K. Schumann). Ecuador, northeastern Peru and adjacent Brazil; Rio de Janeiro bay area ..... 4. *G. crinita* Mart.

§ **Gynophoriola** *G. F. Freytag, n. sect.*

Inflorescentia laxiflora, pedunculis pedicellisque pro genere longissimis. Alabastra florum anguste acuminata. Pistillum breve stipitatum, gynophorio manifesto.

1. **Guazuma longipedicellata** *G. F. Freytag, n. sp.*

Frutex ca. 3 m. altus; ramis foliosis obscure flexuosis juventute albo-stellato-pubescentibus, internodiis 1.0-1.5. cm. longis. Folia opaca ovata vel oblongo-ovata, 5-11 cm. longa, et 2.5-5.0 cm. lata, supra glabra subtus pubescentia, basi leviter cordata nunc inaequilateralia nunc aequilateralia, 5-costata, apice acuta vel acuminata; petiolis 0.5-1.5 cm. longis. Inflorescentiae laxiflorae 5-6 cm. longae; pedunculis et pedicellis 15-20 mm. longis. Sepala ovato-lanceolata acuminata, 5 mm. longa, in anthesi irregulariter separata. Petala alba, lamina cucullata apice profunde inflexa, basi minute unguiculata, basi 3-4 mm. longa 2 mm. lata; appendicibus usque 1/2 bifidis 4-6 mm. longis 0.25-0.5 mm. latis. Tubus stamineus 1 mm. longus; antheris et staminodiis 1 mm. longis. Pistillum breve stipitatum, gynophorio manifesto 2.5 mm. longo; ovariis 1 mm. longis pubescentibus et minute papillatis; stylis 1.5 mm. longis; stigmatibus conniventibus. Fructus desideratur.

EL SALVADOR: Usulután: dry flats of Río Lempa, near the highway, altitude 120 m., Feb. 14, 1946, *Margery C. Carlson 651* (TYPE in Herb. Chicago Natural History Museum).

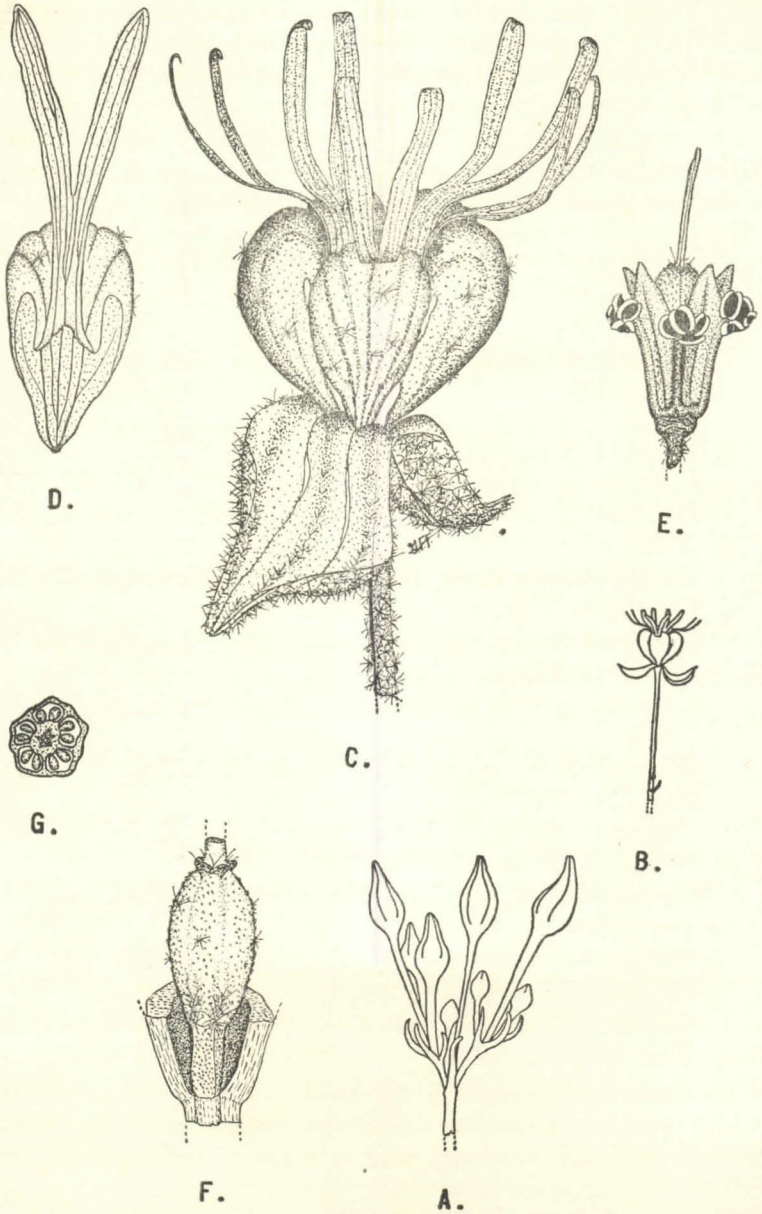

Plate I.—Guazuma longipedicellata G. F. Freytag A. Terminal portion of inflorescence. X 3 B. Flower and pedicel. X 1 C. Flower. X 15 D. Petal and appendage. X 16 E. Flower with petals and sepals removed. X 16 F. Portion of gynoecium showing gynophore. X 20 G. X-section of ovary. X 20.

Though this species resembles *Guazuma tomentosa* vegetatively, its long peduncles and pedicels in addition to the apiculate buds make it quite a distinct species. The presence of a gynophore has been considered of sufficient importance to erect a new section. The fruit no doubt would cast much light on the true position of the species since the other sections are based primarily on fruit characters.

§ EUGUAZUMA K. Schumann in Mart. Fl. Bras. 12^3: 81. 1886.

2. GUAZUMA TOMENTOSA HBK., Nov. Gen. et. Sp. Pl. 5: 320. 1823.

Theobroma Guazuma L., Sp. Pl. 782. 1753.
Bubroma Guazuma (L.) Willd., Sp. Pl. 3^2: 1423. 1803.
Bubroma tomentosum (HBK.) Spreng., Syst. 3: 332. 1826.
Guazuma tomentosa HBK. var. *mompoxensis* G. Don, Gen. Hist. Dich. Pl. 522. 1831.
Guazuma tomentosa HBK. var. *cumanensis* G. Don, 1. c.
Guazuma Blumei G. Don, 1.c.
Guazuma parvifolia A. Rich. in Sagra, Fl. Cuba, 190. 1845.
Diuroglossum rufescens Turcz. in Bull. Soc. Nat. Mosc. 25^2: 156. 1852.
Guazuma ulmifolia Lam. var. *velutina* K. Schumann in Mart., Fl. Bras. 12^3: 81. 1886.
Guazuma ulmifolia Lam. var. *tomentosa* (HBK.) K. Schumann, 1.c.
Theobroma tomentosa (HBK.) Gómez in An. Hist. Nat. 19: 217. 1890.
Guazuma Guazuma (L.) Cockerell in Bull. Torrey Bot. Club 19: 95. 1892.

Trees 2-16 m. tall; leafy twigs obscurely flexuose, with white to orange-brown stellate pubescence when young, the internodes 0.5-4.5 cm. long, with a purple-tinted, minutely reticulate or ridged bark when mature. Leaves ovate to oblong-ovate, 3.0-15.5 cm. long, 1.8-6.5 cm. wide, usually pubescent on both surfaces, prominently 3- to 5-costate at base, cordate, sometimes obtuse, inequilateral or not, the tip acuminate to acute; petioles 0.5-2.0 cm. long. Inflorescences dense, 2-3 cm.

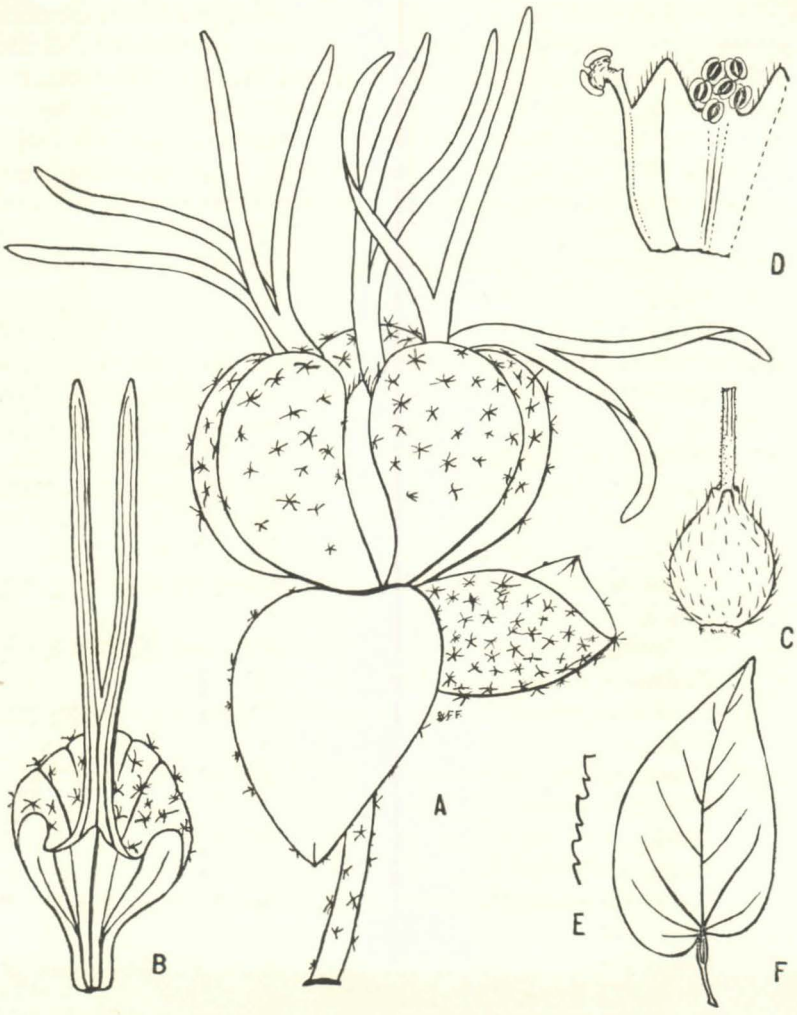

Plate II.—Guazuma tomentosa HBK. A. Flower. X 13 B. Petal and appendage. X 13 C. Pistil. X 13 D. Portion of staminal column viewed centripetally. X 13 E. Leaf margin. X 2 F. Leaf. X 1/2.

long in flower, not enlarging in fruit, the flowers more or less clustered; primary peduncles of inflorescence 0.5-1.0 cm. long; pedicels 3-5 mm. long at anthesis. Sepals 3-4 mm. long, reflexed. Petals green to cream, usually yellowish, 3-4 mm. long, 1.5-3.0 mm. wide, with a claw at times reaching 1 mm. in

length; appendage 4-6 mm. long, 0.2-0.5 mm. wide. Staminal column 1.5-2.0 mm. long, the stamens and staminodes 2-3 mm. long, the anthers 0.5-0.8 mm. in diameter. Ovary 1 mm. long, pubescent, the style 1 mm. long, the stigmas loosely connivent. Fruit spherical to oblongoid, 17-37 mm. long, 14-26 mm. wide, indehiscent, the murications tuberculate to acuminate-pyramidal, separating deeply and irregularly at maturity; seeds numerous in each cell, obovoid, 2.0-3.8 mm. long, covered by reddish-gray papillae visible through the mucilaginous coating, the embryo 1.7-2.5 mm. long.

Growing in dry open forests, 0-3,000 feet above sea level. Mexico and Antilles south through Central America to Ecuador.

By far the most variable species of the genus not only in morphology but also in habitat preference. It is not advisable at present to divide the species complex. Though the fruit is indehiscent it most closely resembles that of *Guazuma ulmifolia.*

3. GUAZUMA ULMIFOLIA Lam., Encycl. 3: 52. 1789.
Guazuma polybotrya Cav., Ic. et Descr. Pl. 3: 51. t. 299. 1794.
Bubroma Invira Willd., Enum. Hort. Berol. 806. 1809.
Bubroma polybotryum (Cav.) Willd., l.c.
Bubroma grandiflorum Willd. ex. Spreng., Syst. 3: 332. 1826.
Guazuma Bubroma Tussac, Fl. Antill. 4: 69. 1827.
Guazuma Invira (Willd.) G. Don, Gen. Syst. Pl. 1: 523. 1831.
Guazuma grandiflora (Willd. ex Spreng.) G. Don, l.c.
Guazuma utilis Poepp. et Endl., Nov. Gen. ac Sp. Pl. 3: 72. 1844.
Guazuma ulmifolia Lam. var. *glabra* K. Schumann in Mart., Fl. Bras. 12^3: 81. 1886.
Guazuma ulmifolia Lam. var. *tomentella* K. Schumann, l.c.
Guazuma Guazuma (L.) Cockerell var. *ulmifolia* (Lam.) O. Ktze., Rev. Gen. Pl. 3^2: 24. 1893.
Guazuma coriacea Rusby in Bull. N. Y. Bot. Gard. 4: 332. 1907.

Trees 1.5-20 m. tall; leafy twigs obscurely flexuose, with orange-brown stellate pubescence when young, the internodes 0.5-2.5 cm. long, with purple-gray, minutely reticulate or ridged bark when mature. Leaves oblong to ovate-oblong, 7-16 cm. long, 2-8 cm. wide, pubescent below, glabrate and lustrous

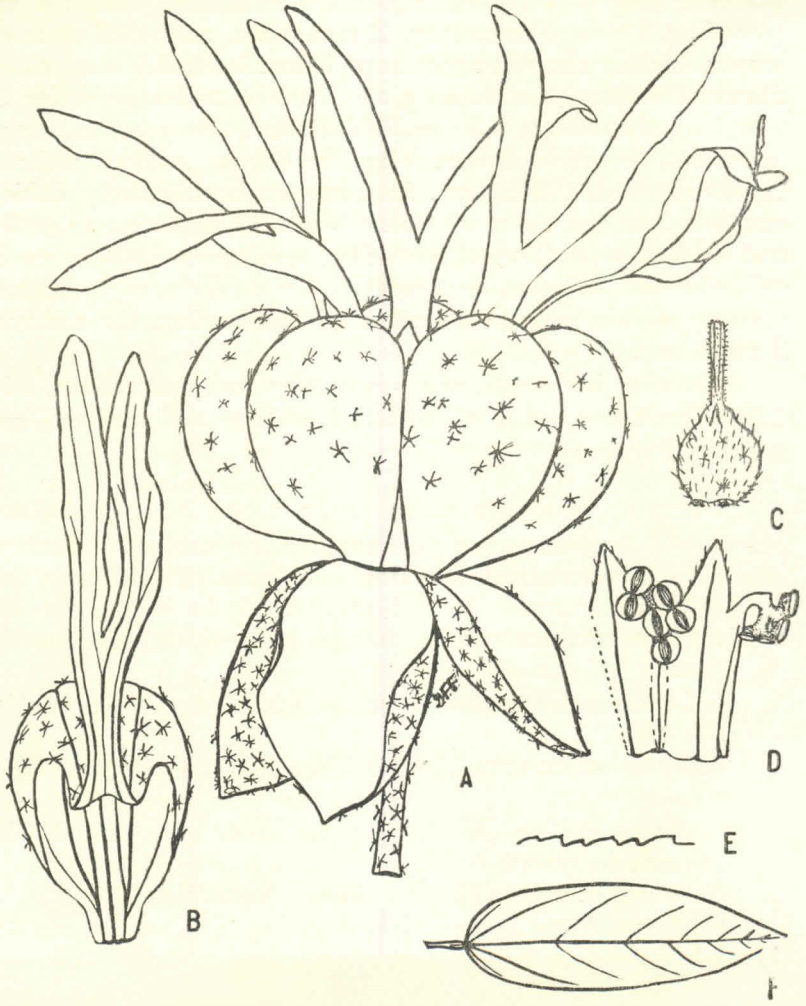

Plate III.—Guazuma ulmifolia Lam. A. Flower. X 13 B. Petal and appendage. X 13 C. Pistil. X 13 D. Portion of staminal column viewed centripetally. X 13 E. Leaf margin. X 2 F. Leaf. X 1/2.

above, distinctly 3-costate at base, obtuse, sometimes cordate, inequilateral or not; petioles 0.8-2.5 cm. long. Inflorescences dense, 3-5 cm. long in flower, not enlarging in fruit, the flowers inequilateral or not; petioles 0.7-2.5 cm. long. Inflorescences 0.5-1.0 cm. long, the others extremely fore-shortened; pedicels

4-5 mm. long at anthesis. Sepals 3-4 mm. long, reflexed or spreading. Petals 4 mm. long, 2 mm. wide, yellow to yellow-brown, slightly clawed; appendage 4 mm. long, 0.5 mm. wide. Staminal column 2 mm. long, the stamens and staminodes 3 mm. long, the anthers 0.5 mm. in diameter. Ovary 1 mm. long, pubescent, the style 1 mm. long, the stigmas loosely united. Fruit spherical, 0.5-2.0 cm. in diameter, loculicidally dehiscent into 5 valves, the murications 4- to 6-sided, obtuse to acute and seldom separating at maturity; seeds numerous in each cell, obovoid, 2.5 mm. long, covered by reddish-gray papillae scarcely visible through the mucilaginous coating, the embryo 2 mm. long.

Growing in forests, swampy to dry rocky situations, 90-1,000 feet above sea level. British Honduras and the Antilles, south to Paraguay.

Guazuma ulmifolia seems to be a species intermediate between *G. tomentosa* and *G. crinita*. It resembles the former in most characteristics, differing most strikingly in that the fruit is dehiscent as is that of *Guazuma crinita*. It seems to be a fairly homogeneous species though quite widely distributed.

§ COMMERSONIOPSIS K. Schumann in Mart., Fl. Bras. 12^3: 81. 1886.

4. GUAZUMA CRINITA Mart. in Flora 20, Beibl. 2: 95. 1837.

Guazuma critina (Mart.) Steud., Nom. Bot. 710. 1841, *sphalm. in synon.*
Bubroma crinitum (Mart.) Steud., Nom. Bot. 233. 1841.
Guazuma rosea Poepp. et Endl., Nov. Gen. ac Sp. Pl. 3: 72. 1844.

Trees 10-20 m. tall; leafy twigs slightly flexuose, with orange-brown stellate pubescence when young, the internodes 2-5 cm. long with nearly black, minutely reticulate or ridged bark when mature. Leaves broadly ovate, 11-13 cm. long, 6.0-8.5 cm. wide, pubescent below, usually glabrate above, prominently 3- to 5-costate at base, obtusely cordate to truncate, the tip acute to slightly acuminate; petioles 1.5-2.5 cm. long. Inflorescences open, 6-7 cm. long in flower, becoming 15 cm. long, 10 cm. wide; pedicels 3-4 mm. long at anthesis. Sepals 3 mm. long, spreading. Petals 2 mm. long, less than

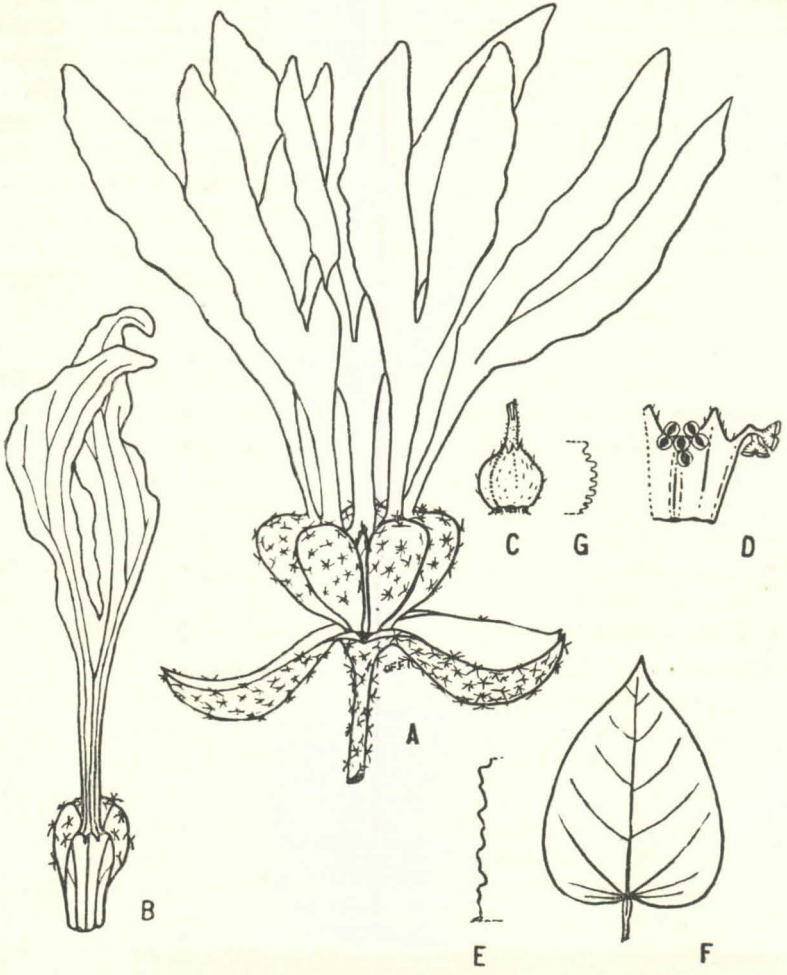

Plate IV.—Guazuma crinita Mart. A. Flower. X 13 B. Petal and appendage. X 13 C. Pistil. X 13 D. Portion of staminal column viewed centripetally. X 13 E. Leaf margin. X 2 F. Leaf. X 1/3 G. Outline of meristematic knobs on ovary. X 50.

1 mm. wide, pink or lilac; the appendage 6-7 mm. long, 1 mm. wide, somewhat crisped above the bifurcation. Staminal column 1 mm. long, the stamens and staminodes 1.5 mm. long, the anthers 0.3 mm. in diameter. Ovary 0.8 mm. in diameter, covered by minute papillae in longitudinal ridges, the style

1 mm. long, the stigmas united. Fruit spherical, the body 5-8 mm. in diameter, loculicidally dehiscent into 5 valves, covered with stellate hairs and numerous, minutely plumose, filiform emergences 30 mm. long, the base produced into a pedestal 1 mm. long; seeds 3-6 in each carpel, broadly obovoid, 2 mm. long, with many short black aculeae which appear through the mucilaginous coating as black speckles, the embryo 1 mm. long.

Growing in forests on frequently flooded river banks, 600-900 feet above sea level. Flowering from November to April. Ecuador, northeastern Peru and adjacent Brazil; Rio de Janeiro bay area.

This species is quite distinct in appearance from the others in that the leaves are considerably larger, the petals very small but with very large appendages, and the fruit quite remarkable because of the long plumose emergences which completely cover it.

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Bubroma grandiflorum Willd. ex Spreng., (Brazil, *Hoffmannsegg s.n.*).
Bubroma Invira Willd., (Brazil, *Willdenow 849.3*).
Diuroglossum rufescens Turcz. *(Jameson 399)*.
Guazuma Blumei G. Don, (Java, collector unknown).
Guazuma coriacea Rusby, (Bolivia, near *Rusby 1859*, Guanai, Bolivia, *Bang 2217*).
Guazuma crinita Mart., (Montis Telegraphici prope Sebastianopolis, Brazil, *Herb. Mart. 89* in part [fruit]).
Guazuma longipedicellata G. F. Freytag, (El Salvador, Usulután, dry flats of Río Lempa, near the highway, alt. 120 m., Feb. 14, 1946, *Margery C. Carlson 651*).
Guazuma polybotrya Cav., (Nova-Hispania, collector unknown).
Guazuma rosea Poepp. et Endl., (Crescit in sylvis provinciae peruvianae Maynas and pagum Yurimaguas, *Poeppig 2366*).
Guazuma tomentosa HBK., (*Theobroma Guazuma* L., Jamaicae campestribus, *Herb. Linn. 934.2*).
Guazuma ulmifolia Lam., (St. Thomas, *Herb. Lam. s.n.*).
Guazuma ulmifolia Lam. var. *glabra* K. Schumann, (Amazonas, Brazil, *Poeppig 2118*).
Guazuma ulmifolia Lam. var. *tomentella* K. Schumann, (Peruvia orientali ad Maynas, *Poeppig s.n.*).
Guazuma ulmifolia Lam. var. *tomentosa* K. Schumann, (In Pro-

vincia Bahia in ripis fluviorum, e.g. Jaguaripe, Aracatay, Brazil, *Martius s.n.*).

Guazuma ulmifolia Lam. var. *velutina* K. Schumann, (In Braziliae provinciis meridionalibus, *St.-Hilaire s.n.*).

Guazuma utilis Poepp. et Endl., (Crescit in ripa fluminis Huallaga ad Yurimaguas, *Poeppig 2118*).

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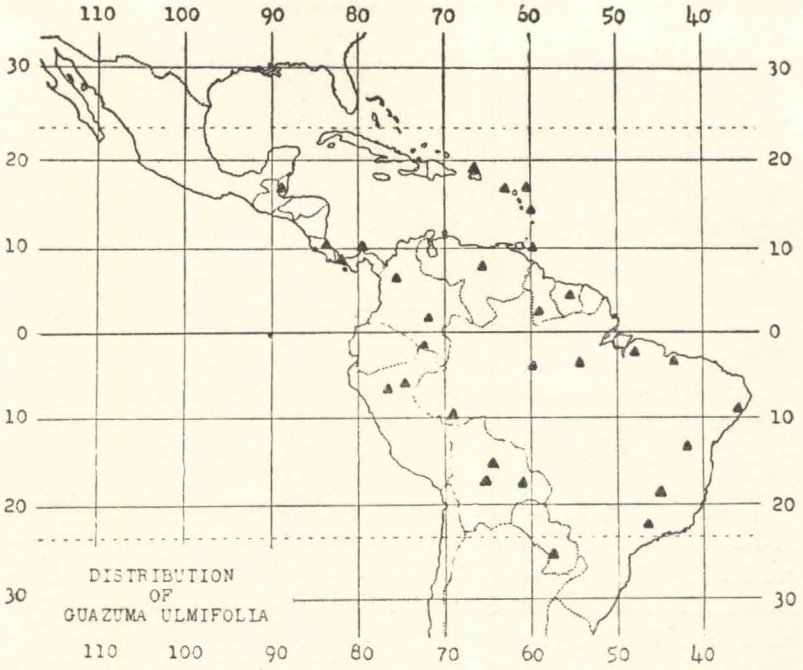
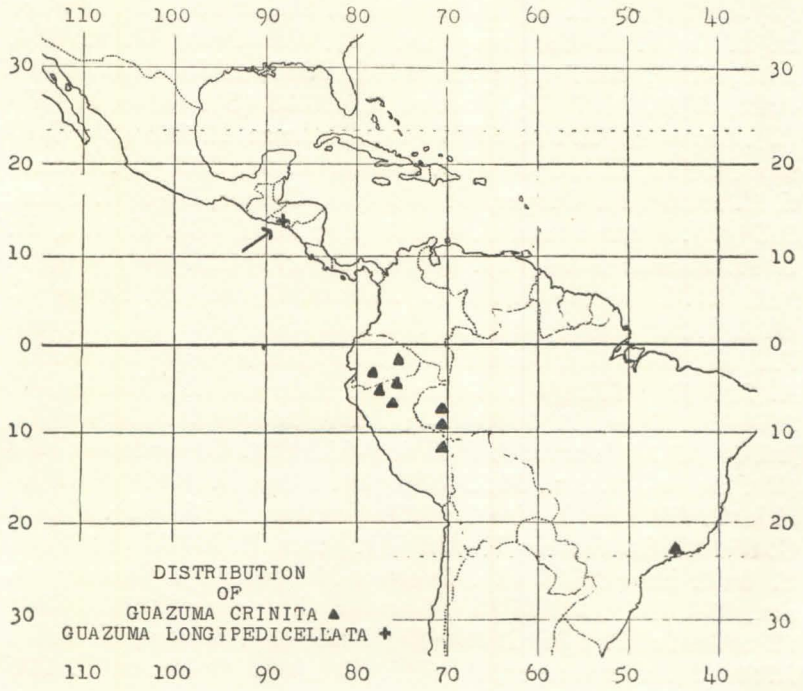


DISTRIBUTION
OF
GUAZUMA ULMIFOLIA



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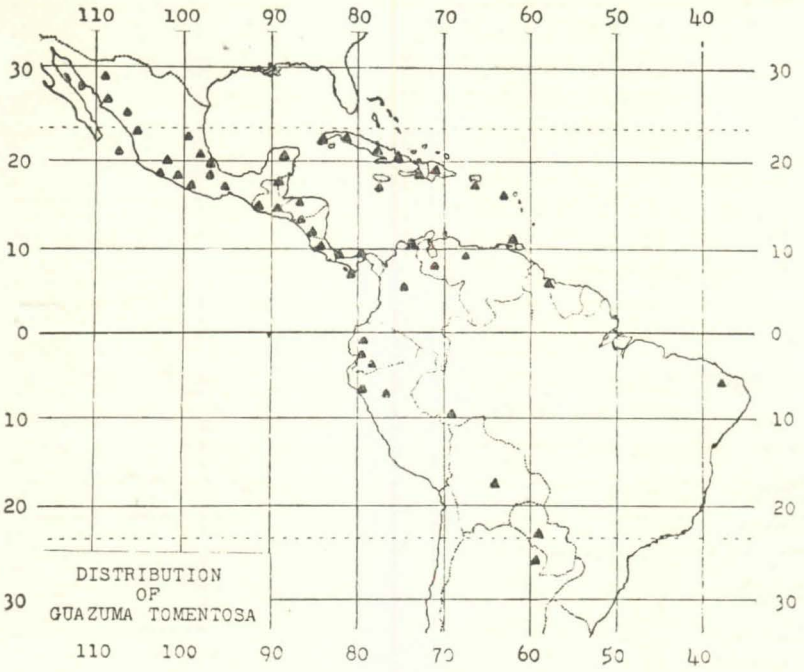
GUAZUMA CRINITA ▲
GUAZUMA LONGIPEDICELLATA +



(2). Grant, V. *926* (2). Greenman, J. *16* (2). Gregg, J. *868* (2). Hagen, C. von & W. von Hagen *1171* (2). Harris, W. *6829, 6994, 11008* (2). Hartman, C. *1015* (2); Harvey, D. *5010, 5181* (2). Hassler, E. *7517* (2); *12133* (3). Hayes S. *171* (2). Heller, A. *6080* (2); *4585* (3). Heller, Mr. & Mrs. Heller *511* (2). Heyde & Lux, *4448* (2). Hinton, G. *692, 745, 6765, 7142, 10891* (2). Hitchcock, A. *s.n.* (2). Holm, R. W. & H. H. Iltis *311* (2). Hodge & Howard & Godfrey *4778* (2). Hooker, J. D. *s.n.* (2). Jack, J. *4561* (2). Johansen, H. *36* (2). Johnston, J. *978* (2). Jones, M. *s.n., 80, 23286* (2). Jorgensen, P. *2084* (2); *2791, 3791* (3). Kellerman, W. *5799* (2). Kenoyer, L. *993* (2). Klug, G. *1995, 2018, 2939, 3952* (3); *2971, 4059* (4). Krukoff, B. *4506, 2550* in part, *5305* (3). *4854* (4). Kuntze, O. *s.n.* (3). Lanjouw, J. *803* (3). Leavenworth, W. *219* (2). Leavenworth, Mr. W. & Mrs. Leavenworth *944* (2). Leavenworth, W. & H. Hoogstraal *1678, 1716* (2). Leonard, E. *3182, 3578, 3845* (2). Leonard, E. & G. Leonard *15196* (2). LeSueur, H. *551, 1410* (2). Little, E. *6434,*

6443 (2). Lloyd *1075* (2). Lundell, C. *818, 1357, 1515* (2). Macbride, J. *2668* (2). MacDaniels, L. *19, 211* (2). Martínez, M. *s.n.* (2). Maxon, W. & E. Killip *1638* (2). Metcalf & J. Cuatrecasas *30090* (3). Mexia, Ynes *1024, 8739, 8862, 9206, 9290, 9318* (2); *5559* (3); *6126* (4). Mille L. *s.n.* (2). Millspaugh, C. *40, 786, 1114, 1470* (2). Moore, C. *33* (3). Morton, C. & E. Makrinius *2519* (2). Muenscher, W. *12377* (2). Nash, G. *28* (2). Nelson, E. *4325* (2). O'Neill, H. *8862* (2). Orozco, J. *78* (2). Ortega, J. *5842, 7076, 7202* (2). Ostenfeld, C. *232* (2). Palmer, E. *24, 149, 273, 353, 437, 677, 960, 1461* (2). Paul, B. *898* (2). Persaud, A. *297* (2). Pickel, D. *4A-20M, 149* (3). Pierre, L. *3759* (2). Piper, C. *5328* (2). Poeppig *2366* (3). Pohl *599* (2). Pollard, C. & E. Palmer, & W. Palmer *201* (2). Pringle, C. *2570, 2571, 11936* (2). Purpus, C. *s.n., 2007, 5876, 8815* (2). Quirós, C. *794* (2). Regnell, A. *280* (3). Rodríguez, J. *366, 1030, 1550, 2090, 2534* (2). Rojas, F. *135* (2). Rose, J. *3261* (2). Rothrock, J. *486* (2). Rovirosa, J. *16* (2). Rusby, H. *1859* (3). Sainz B., V. *66* (2). Saint-Hilaire, A. *231* (4). Salzmann *s.n.* (3). Sargent, C. *38* (2). Scarff, J. *s.n.* (2). Schimpff *363, 1159* (2). Schipp, W. *433* (3). Schott, A. *148, 342* (2). Seibert, R. *1644* (3); *2137* (4). Sessé & Mociño & Castillo & Maldonado *3616, 3617* (2). Shafer, J. *126, 517, 1029, 1198, 1766, 10442, 19562* (2); *527, 579* (3). Shreve, F. *6088, 6777* (2). Sieber *154* (2); *343* (3); Sintenis, P. *2907* (3). Skutch, A. *3976, 4865* (2). Smith, A. *3098* (3). Smith, H. *786, 1984* (2). Smith, J. *2478* (2). Solís, M. *135, 7994, 10628* (2). Standley, P. *1711, 8364, 9309, 55033, 59316, 62075, 64128, 66762, 70658, 17942, 75843* (2). Steere, W. *1024* (2). Steggerda, M. *48* (2). Steinbach, J. *6401a, 6625* (3). Stevenson, J. *2266* (2). Stevenson, N. *114* (3). Steyermark, J. *37887, 47804, 51079, 56570* (2). Stork, H. *4010* (2). Urban, I. *2664* (3). Valeur, E. *238, 335* (2). Von Wedel, H. *1183, 1269a, 1323, 3764, 2875* (3). Walker, F. *10* (2). Weberbauer, A. *7092, 7116* (2). Werdermann, E. *2452, 2609* (2). White, G. *183* (2). White, P. *92* (2). Williams, Llewelyn *5675, 6271, 9379, 10410, 11028, 13251* (2); *4227, 11575* (3); *151, 4221, 5015, 5698* (4). Williams, L. *10234* (2); *4768* (3);