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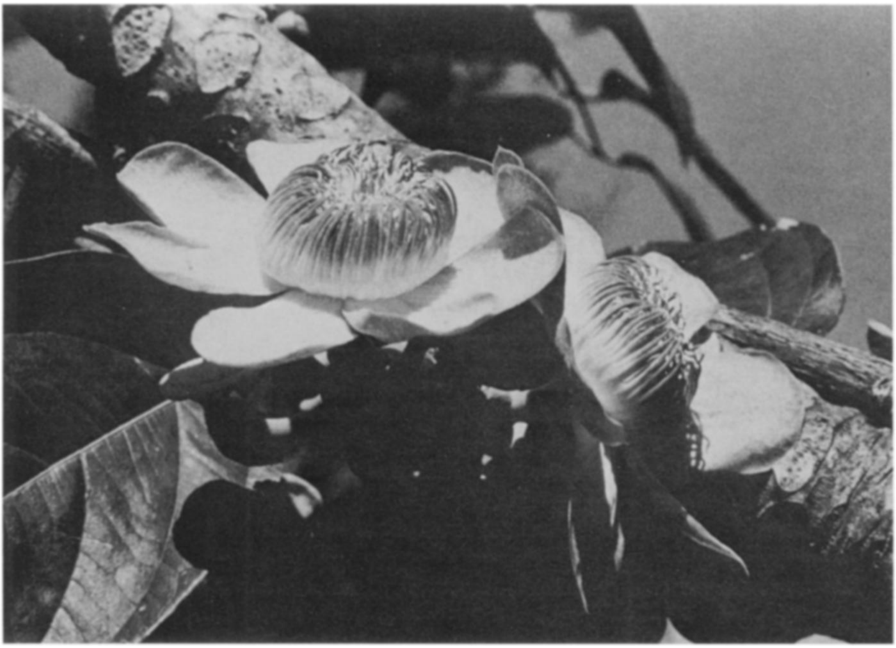

Frontispiece. *Gustavia superba* (unvouchered). Photo by Mori & Kallunki.

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MONOGRAPH NO. 21

LECYTHIDACEAE—PART I

The Actinomorphic-flowered New World Lecythidaceae

(Asteranthos, Gustavia, Grias, Allantoma, & Cariniana)

by

Ghillean T. Prance and Scott A. Mori

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Organization for Flora Neotropica

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LECYTHIDACEAE—PART 1

GHILLEAN T. PRANCE[1] AND SCOTT A. MORI[2]

I. INTRODUCTION

This is the first of a two part monograph of the New World Lecythidaceae. The family has about 200 neotropical species in eleven genera. This first part presents introductory material about their morphology, biology and ecology and treats taxonomically 64 species in the five genera with actinomorphic or slightly zygomorphic androecia. The second part will treat the remaining six genera which have highly zygomorphic androecia.

The Lecythidaceae is an important woody element of the lowland rainforest areas of the neotropics. The section on ecology points out their abundance in this habitat and their relative scarcity in other neotropical habitats.

The authors began work on the family independently at about the same time. After several years of work we decided to join forces, and the present monograph was completed during a two year period in which we worked together at The New York Botanical Garden. The order of authorship of this monograph will be reversed in the second part, thereby reflecting the equal partnership of the authors in their studies of neotropical Lecythidaceae. The introductory material has been compiled jointly and is based on work done together and separately, both in the field and laboratory. The taxonomic treatments of *Gustavia* and *Grias* were prepared by Mori and those of *Asteranthos, Allantoma* and *Cariniana* by Prance.

Although species of Lecythidaceae are ecologically important in lowland neotropical forests, they have never previously been subjected to a detailed field study. Consequently, many taxonomic problems have arisen because of the difficulty in matching flowering and fruiting material of the same species and in interpreting the stage of fruit maturity from herbarium material. In addition, lack of field studies has limited the knowledge of the biology of the family. The present study is based on extensive field work by both authors throughout the range of the family in the neotropics. This has resulted in much new biological and ecological information which is incorporated in this monograph. The authors have seen well over half of the species in the field.

We are also grateful to the additional collaborators and contributors to this monograph who are acknowledged elsewhere. The team approach to the systematic treatment of a family helps to broaden the coverage of the monograph. We are especially grateful to Dr. Jan Muller of Leiden, Holland for contributing the chapter on pollen and to Dr. Carl de Zeeuw of Syracuse, New York, who is studying the wood anatomy of the family which will be published in Part 2. Discussions with both these collaborators has been extremely helpful to us.

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Our studies of the genera of Lecythidaceae with zygomorphic androecia are advanced but not complete. Consequently, names of all species in these genera appearing in the introductory chapters are subject to change. All such changes will be reported in the second part of this monograph. As a matter of convenience we have also chosen to treat the Lecythidaceae as one family subdivided into four subfamilies. However, pending future study, especially of cytology and anatomy, we may decide to realign these groupings. We are especially concerned with the relationship of *Asteranthos* to the remainder of the family.

II. TAXONOMIC HISTORY OF THE LECYTHIDACEAE

The first known description and illustration of a member of the Lecythidaceae were made by Frei Christovão, a Portuguese Franciscan missionary, who lived in Maranhão, Brazil from 1624 to 1635. His *Historia dos animais e árvores do Maranhão,* not published until 1967 and then in manuscript facsimile accompanied by a modern translation, includes a description and illustration of *Sapuqaiha,* which without a doubt refers to *Lecythis pisonis,* as well as of *Sequeriba,* which may be the first reference and illustration of the brazil nut, *Bertholletia excelsa.* Frei Christovão's work is poorly known to systematists outside of Brazil but recently has been discussed in detail by Whitehead (1973).

The Dutch capture of the northeastern coast of Brazil prematurely ended the studies of Christovão and made possible those of the German George Marcgrave and the Dutch Willem Piso. Marcgrave (who lived 1610-1644) figured and described *Japarandiba (=Gustavia), Jacapucaya (=Lecythis),* and *Ibiraba (=Lecythis)* in his *Historiae rerum naturalium brasiliae,* a work edited by Johannes de Laet who had to decipher the secret code in which it was originally written by Marcgrave to prevent it from being pirated by Piso. It was published in 1648, four years after Marcgrave's death (Marcgrave, 1648). Another, somewhat altered edition was prepared by Piso (1658) under the title of *De Indiae utriusque re naturali et medica* (generally referred to today incorrectly as authored by Marcgrave and Piso). Piso and Marcgrave were contemporaries in Brazil but apparently the relationship between America's first naturalists, like so many that followed, was strained (Whitehead, 1973). Gudger (1912) claims that Piso plagarized much of Marcgrave's work. Whitehead (1973) provides a detailed account of the Brazilian sojourn, publications, and drawings of Piso and of Marcgrave.

Another pre-Linnean reference to the family is that of Barrère (1741) who referred to *Couroupita guianensis* under the name *Pekea,* which he took from the earlier works of Marcgrave (1648) and Piso (1658), but it is extremely doubtful that *Pekea* of Marcgrave and Piso is the same as either *Couroupita* or Barrère's *Pekea.*

In 1758, Linnaeus posthumously published Pehr Loefling's description of a new genus and species, *Lecythis ollaria.* Perhaps Linnaeus' most promising student, Loefling had died two years earlier in Venezuela at the age of 27. *Lecythis* was placed in the Linnean order Polyandria Monogynia. A type specimen for *L. ollaria* has never been found. However, Prance and Mori (1977) have matched modern collections with the original description and have selected a neotype. One year later, Linnaeus (1759) described *Grias* in the tenth edition of his *Systema naturae,* also placing it in his order Polyandria Monogynia, and basing it on *Grias cauliflora* from Jamaica.

Adanson (1763), in his *Familles de plantes,* treated *Lecythis* under the name *Bergena* in the Pistaciae and used Marcgrave's name *Japarandiba* for the genus now known as *Gustavia.* Adanson placed *Japarandiba* and *Grias* together in the Cisti. *Gustavia* was described by Linnaeus (1775) in his *Plantae surinamenses* where he proposed *G. augusta,* based on the collections of Allamand and Solander made between 1750 and 1770 in Dutch Guiana (Surinam). *Gustavia* was named in honor of Gustave III, king of Sweden, who presented Linnaeus with the collections of Allamand and Solander (Smith, 1812).

Also in 1775, three new genera, *Couratari, Couroupita* and *Pirigara* were proposed by Aublet in his *Histoire des plantes de la Guiane Française.* The genera *Couratari* and *Couroupita* have been maintained up to the present, but *Pirigara* was later placed in synonymy under *Gustavia* (Sprengel, 1825, Berg, 1856).

The large Asiatic genus *Barringtonia* was described by George Forster (1776). *Foetidia* was described by Commerson from Mauritius in 1788.

Following his custom of changing 'barbarous names,' Scopoli (1777) illegitimately substituted the name *Pontopidana* for *Couroupita* and *Teichmeyeria* for *Gustavia,* but neither was ever adopted by later authors.

It was Antoine Laurent de Jussieu (1789), in his pioneering *Genera plantarum* which forms a basis for all later systems of classification, who first brought most of the above genera together in his all-encompassing order (= the Myrti). This order was quite a heterogeneous assemblage, containing not only genera now referred to as Myrtaceae and Lecythidaceae, but the genus *Philadelphus* (Hydrangeaceae) and other unrelated elements. Nevertheless, Jussieu did bring together most genera that are now considered part of the Lecythidaceae. He placed *Barringtonia* (under the name *Butonica* Rumphius), *Couroupita, Gustavia* (under the name *Pirigara*), and *Lecythis* (including *Couratari* as a synonym) in his second section of the Myrti. *Foetidia* was located in the first section of the same family, but *Grias* was aligned among the Guttiferae. Jussieu, apparently, had taken the generic characters mainly from Linnaeus' descriptions.

Necker (1790) added to the generic synonymy of the family by creating the illegitimate names *Elsholtzia* for *Couroupita,* and *Spallanzia* for *Gustavia.*

Gmelin (1791, 1792), in his edition of Linnaeus' *Systema naturae,* used the Linnaean sexual system of classification. He placed *Lecythis* (with 8 species) and *Grias* (with 1 species) in the Polyandria Monogynia and *Barringtonia, Gustavia, Curupita* (an orthographic variant of *Couroupita*), and *Curatari* (an orthographic variant of *Couratari*) in the Monadelphia Polyandria. Willdenow (1799), in his edition of Linnaeus' *Species Plantarum,* treated under *Lecythis* a mixture of 8 species now divided between *Lecythis* and *Eschweilera.*

In a generally overlooked publication, Palisot de Beauvois (1804) described, in honor of the Emperor of France, the African genus *Napoleonaea.* This genus was again discussed by Palisot de Beauvois (1810) under the orthographic variant *Napoleona,* a spelling adopted in most later works, until Liben (1971a) (see also Heine, 1967) discussed the original publication of *Napoleonaea* in his monograph of the genus.

Humboldt and Bonpland (1807) described the genus *Bertholletia* to accommodate the single species *B. excelsa,* the Brazil nut. As they had seen only leaves and fruit but no flowers, they placed it, with some doubt, in the Linnaean order Monodelphia Polyandria, and did not suggest a position for it in the Jussieuan system as they did in the same work for other genera based on complete material.

Roxburgh (1814) published *Careya* from Malesia, with its single species, *C. arborea.*

Desfontaines (1820) proposed the new genus *Asteranthos* from Brazil which he related to *Napoleonaea* from Africa. He did a remarkable job of reconstructing the morphology of *Asteranthos* since he had only fragmentary material. One year later, Schrank & Schrank (1821) described another new genus from Brazil, *Lecythopsis,* which has since been regarded as synonymous with *Couratari.* Robert Brown (1821) proposed the new family Belvisieae to accommodate the genera *Asteranthos* and *Belvisia* Desv. (= *Napoleonaea*).

In his edition of Linnaeus' *Systema vegetabilium,* Sprengel (1825) was the last major worker to classify the group by the Linnaean sexual system. *Asteranthos, Grias,* and *Lecythis* (including *Couroupita*) were placed in Polyandria Monogynia, *Gustavia* in Monadelphia Polyandria, with *Pirigara* cited in synonymy, and *Couratari* was left unmentioned. Also in 1825, Humboldt, Bonpland and Kunth treated three genera—*Lecythis, Pirigara* (with *Gustavia* cited in synonymy) and *Bertholletia*—as members of the family Myrtaceae, tribe Lecythideae. Poiteau (1825) made an important contribution to knowledge of the neotropical members of the family known up to that date. Referring to the second section of Jussieu's Myrtaceae, he said:

> Ayant eu l'occasion d'examiner la plupart de ces plantes, pendant mon séjour à la Guyane français, j'ai reconnu qu'en effet elles n'ont pas les caractères des Myrtes, et qu'elles en possèdent d'autres qui leur sont particuliers. Je propose donc d'en former une nouvelle famille sous le nom de Lecythidées.

Because of his statement that the Lecythidaceae merit the rank of a family separate from the Myrtaceae the family name Lecythidaceae should be attributed to Poiteau rather than to Lindley. Poiteau included in the family the genera *Lecythis, Couroupita, Bertholletia, Gustavia* and *Couratari,* and made no reference to the extra-American genera.

De Candolle (1828) did not follow Poiteau, keeping the Lecythidaceae within the Myrtaceae and dividing the latter into 5 tribes. His fourth tribe, Barringtonieae, contained *Barringtonia, Stravadium* Juss. (now considered as part of *Barringtonia*) and *Gustavia;* and his fifth tribe, Lecythideae, held *Lecythis, Eschweilera* Mart. ex DC, *Bertholletia, Couroupita* and *Couratari. Eschweilera* was the only new genus proposed by de Candolle, and it contained 2 species. *Lecythis* included 19 species many of which were transferred to *Eschweilera* by later authors. *Grias, Careya* and *Foetidia* were placed at the end of the Myrtaceae in an assortment of genera labelled "Myrtaceae dubiae." De Candolle did not treat *Napoleonaea* and *Asteranthos* until a much later volume of his *Prodromus* (1839), where he placed the two genera together in the Napoleoneae between Collumeliaceae and Vaccinieae, two quite unrelated groups. The classification of de Candolle was followed with slight modifications by Reichenbach (1828), Dumortier (1829), Bartling (1830), Meisner (1839), Endlicher (1839), and Baillon (1877). Reichenbach, Meisner and Endlicher treated *Asteranthos* and *Napoleonaea* as a separate family.

Lindley (1830) kept the Barringtoniae in the Myrtaceae, noting that they probably did not belong to the order, and placed the Lecythidaceae near the Ternstroemiaceae apart from the Myrtaceae. However, in 1836, he again placed the Lecythidaceae near the Myrtaceae. In the 1836 edition of his system, the Barringtoniae contained *Barringtonia, Stravadium, (=Barringtonia) Gustavia, Catinga* Aubl (=*Eugenia* of the Myrtaceae), *Coupoui* Aubl. (=*Duroia* of the Rubiaceae), *Careya* and *Foetidia.* The Lecythidaceae contained *Lecythis, Eschweilera, Bertholletia, Couroupita, Couratari,* and ?*Touroulia* (=Quiinaceae). *Napoleonaea* and *Asteranthos* were retained in Robert Brown's Belvisiaceae, placed between Styracaceae and Sapotaceae in 1830 and in his alliance Campanales in 1836. However, in 1846, Lindley was the first worker to relate the Belvisiaceae to Myrtaceae and Lecythidaceae, placing them between the Rhizophoraceae and Melastomataceae in his alliance Myrtales. Lindley (1846) decided that the Lecythidaceae, in which he included *Couratari, Cariniana, Lecythis, Eschweilera, Bertholletia, Couroupita* and *Crossostylis* Forst. (Rhizophoraceae), were a family separate from Myrtaceae but retained them in the myrtle alliance. He supported the separation of the Lecythidaceae at the family level because of "the great almond-like seeds and alternate, often serrated, non-punctate leaves." Furthermore he removed the Barringtoniaceae *(Barringtonia, Stravadium, Careya, Gustavia* and *Foetidia)* from the myrtle alliance to the Grossales. Although he admitted the similarity of the Barringtoniads to the Lecythids, he concluded that the presence of stipules and the hooded plate of sterile or additional stamens in the latter warranted their separation. Stipules have since been shown to be present in both groups (Pittier, 1927; Weberling, 1957; Payens, 1967).

Don (1832) retained Barringtonieae as a tribe of the Myrtaceae and recognized the Lecythidaceae as a separate family. In Brogniart's 1850 enumeration of the plants in the Museum of Natural History in Paris the Lecythidaceae are also recognized as a separate family.

Casaretto (1842) described the new genus *Cariniana* from Brazil with a single species *C. brasiliensis* (=*C. legalis* (Mart.) Kuntze). One year later (1843) he published a second species *C. excelsa* (=*C. estrellensis* (Raddi) Kuntze). Blume (1852) published *Planchonia* based on *P. sumatrana.*

Otto Carl Berg (1858), after a series of smaller publications (1856, 1857), presented a monograph of the Brazilian members of Lecythidaceae in Martius' *Flora Brasiliensis.* Berg, a specialist in the Myrtaceae, described over 1000 species of myrtles (McVaugh, 1958). He accepted de Candolle's classification without change and likewise did not include *Asteranthos* in the Myrtaceae. By that time a large number of Brazilian species were known: *Gustavia* with 5, *Couroupita* with 2, *Bertholletia* with 1, *Lecythis* (including *Eschweilera*) with 37, *Lecythopsis* with 2 (one a *Couratari,* the other an *Eschweilera*) and *Couratari* with 12 (including some species now placed in *Allantoma* and *Cariniana*).

Bentham (1859) followed Lindley (1846) by suggesting that *Asteranthos* was related to the Myrtaceae (including Lecythidaceae).

Bentham and Hooker (1865) combined the Barringtonieae and Lecythideae into one tribe, the Lecythideae, which in turn they subdivided into three subtribes: the Barringtonieae (*Barringtonia, Petersia* Welwitsch ex Bentham & Hooker, *Careya, Planchonia, Gustavia,* and *Grias*), the Eulecythideae (*Couratari, Couroupita, Lecythopsis (=Couratari), Lecythis* and *Bertholletia*), and the Napoleoneae[3] *(Napoleonaea* and *Asteranthos*). *Foetidia* was treated by them as an anomalous genus. The only new genus proposed by Bentham and Hooker was *Petersia* based on a Welwitsch manuscript name. The genus has generally been accepted but the name is illegitimate because of *Petersia* Klotsch (1861) of the Capparidaceae. *Petersia* Welw. ex Benth. & Hook. was renamed *Petersianthus* by Merrill (1916).

Le Maout and Decaisne (1873) followed essentially the same classification as Bentham and Hooker, but elevated two of the subtribes of the Myrtaceae to full tribes: the Barringtonieae and Lecythideae and raised the rank of the Napoleoneae to a family close to the Myrtaceae.

The first monographer of the Lecythidaceae as a separate family was John Miers (1874, 1875a, 1875b). He recognized three families, the Lecythidaceae, with *Gustavia* (21 species), *Couroupita* (9), *Bertholletia* (2), *Lecythis* (42), *Chytroma* Miers (25), *Eschweilera* (46), *Jugastrum* Miers (6), *Couratari* (8), *Cariniana* (7), *Allantoma* Miers (12), *Grias* (4), and *Cercophora* Miers (1) (=*Strailia* Th. Dur.); the Belvisiaceae, with a single genus *Napoleonaea,* and the Barringtoniaceae, with *Barringtonia, Agasta* Miers, *Butonica* Rumph., *Stravadium, Planchonia, Careya, Doxomma* Miers, *Petersia, Megadendron* Miers and *Chydenanthus* Miers. He also concluded that *Asteranthos,* which he mistakenly thought had a superior ovary, was related to the Rhododendreae (Ericaceae). As can be seen from the summary given above, Miers described eight new genera. He also described many new species, many of which have been placed in synonymy in the present work. The following comment on Miers' work by Stearn (1971), in a paper on the Jamaican Boraginaceae, is useful in understanding Miers' taxonomic philosophy:

> In 1869 John Miers, at the age of 79, published a survey of *Bourreria* which he divided into two genera, i.e. *Bourreria* proper and *Crematomia,* typified by *B. exsucca.* This appeared in Ann. Mag. Nat. Hist. IV. 3: 199-210, 300-313, (Mar.-Apr.) 1869, and was reprinted in his *Contributions to Botany* 2: 230-242. He was an acute and accurate observer, who retained into old age an intense curiosity about morphological details which he investigated with assiduity, and as a retired chemist and engineer, he brought to his botanical studies the precision of his former calling, together with a somewhat mechanical aproach. As William Carruthers remarked in his obituary of Miers (Jour.

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[3] The correct orthography for this subtribe is Napoleonaeae. Throughout this chapter the spelling used in each work cited is given.

> Bot. (London) 18: 36. 1880), 'he had a very quick sense of differences but he sometimes failed to distinguish the real value of the differences he saw.' The editor, M.T. Masters, of the *Gardeners Chronicle* (cf. 1879. 2: 522 (Oct.) 1879) said much the same: 'as a botanist his tendency was to minute elaboration rather than judicial estimate of the relative importance of details. In practice, therefore, he multiplied species, and even genera and orders, to an extent opposed to the prevailing tendencies of his contemporaries. Miers never adopted the doctrine of the mutability of the species'; he was 70 when Darwin published *The Origin of the Species.* Seemingly he took as representing well-marked species any herbarium specimen or little group of herbarium specimens which differed in appearance from other specimens. Thus, on the evidence of sixteen specimens in the British Museum and Kew Herbaria, he recorded nine taxa from Jamaica under the names *Bourreria succulenta, B. ovata, B. rigida,* . . . these being described accurately but defined vaguely. O. E. Schulz in 1911 reduced them all to three. . . .

The Lecythidaceae lent themselves well to the mechanical approach of Miers who placed great emphasis on fruit characters, especially minute differences in pyxidium shape and form. He described 14 species of *Lecythis* from material consisting of pyxidia alone, 7 in *Chytroma,* 2 in *Jugastrum,* one each in *Couratari* and *Cariniana,* and 5 in *Allantoma,* making a total of 28 species! He also recognized an additional six species already described by Berg from pyxidia alone. Along with scientific specimens, Miers used as taxonomic material a large number of pyxidia brought back as curiosities by travellers. The classic example of this is the type of *Lecythis ampullaria* Miers, which is a pyxidium carved and scraped to form a utensil. Field studies have shown that there is much variation in the pyxidia from individual trees (Dugand, 1947; Mori, 1970 and *Allantoma* in the present work), and thus, while Miers gave an accurate description of what he saw, his species are not based on the genetic species concept of modern systematists. Miers' monograph, however, provided a thoroughly accurate, descriptive and well-illustrated account of all the material available at that time. The illustrations are especially helpful for the placing and matching of his species.

Masters (1869) gave a detailed account of the flower of *Napoleonaea* and provided additional evidence of its relationship to *Asteranthos,* but he did not try to suggest relationships within the family.

Sagot (1885) reviewed the Lecythidaceae of French Guiana, using the de Candolle system of tribes, i e Barringtonieae and Lecythideae in the Myrtaceae, and added a few new species.

Asteranthos was not treated in Martius' *Flora Brasiliensis* until thirty years after Berg's account of the Lecythidaceae. In Eichler's (1889) account for *Flora Brasiliensis, Asteranthos* was placed in the Napoleonaeaceae, which he hesitantly related to the Cactaceae or *Mesembryanthemum.*

Costantin and Dufour (1885) recognized anatomical differences between the Myrtaceae and Lecythidaceae, the Myrtaceae having secretory cavities and internal phloem which are absent in the Lecythidaceae. Furthermore, the latter family has cortical bundles which are not found in the former. These authors also concluded that there is no anatomical evidence to warrant the separation of the Napoleonaeaceae and the Barringtoniaceae from the Lecythidaceae and that *Foetidia* belongs in the Lecythidaceae. On the basis of a very detailed anatomical study of *Gustavia, Barringtonia* and *Napoleonaea,* Lignier (1890) divided the family into the following three tribes: Barringtoniées, Lecythidées, and Napoleonées. He was able to separate those tribes in terms of stem and petiole anatomy, and reinforced the separation of the Lecythidaceae from the Myrtaceae on anatomical grounds.

Niedenzu (1892), in Engler's *Natürlichen Pflanzenfamilien,* divided the family into four subfamilies. In the Foetidioideae he placed *Foetidia;* in the Planchonioideae, *Planchonia, Petersia, Careya, Barringtonia,* and *Chydenanthus;* in the Napoleonaeoideae, *Asteranthos* and *Napoleonaea* and in the Lecythidoideae, *Japarandiba (=Gustavia), Grias, Couroupita, Lecythis, Eschweilera* (including *Chytroma* and *Jugastrum*), *Bertholletia, Cariniana, Cercophora, Couratari,* and *Allantoma.*

During the first part of the present century several new genera were added to the family. Huber (1902) proposed *Goeldinia* from Brazil, which later proved to be a synonym of *Allantoma,* and Chevalier (1909) proposed *Combretodendron* from Africa. However, Liben (1968) has pointed out that Chevalier (1909) later concluded that *Combretodendron* was a synonym of *Petersia* and added this to his publication of the protologue (appended as a note on page 301). According to the Code of Nomenclature (Article 34) a name is not validly published if it is not accepted by its author in the original publication. This invalidated *Combretodendron,* making Merrill's (1916) *Petersianthus* the correct name for the genus. As noted earlier *Petersia* was already pre-empted for a genus of Capparidaceae. E. G. Baker (1913) described *Crateranthus* from Africa, and Ducke (1925) described *Holopyxidium* from Brazil. Five years later Ducke (1930), after further field observations on the dehiscence of the fruit, decided that *Holopyxidium* was not a good genus and accordingly placed it in synonymy under *Eschweilera.*

The present century has also seen several regional accounts of the Lecythidaceae in various Floras. The most notable in the New World are those of Pittier (1927) for Central America, Eyma (1932, 1934) for Surinam, Benoist (1933) and Lemée (1953) for French Guiana, Macbride (1941) for Peru, and Woodson (1958) for Panama. Perhaps the most significant of these is the work of Eyma who made a critical study of the Surinam species and cleared up many taxonomic and nomenclatural problems pertaining to extra-Surinam species, especially in the circumscription and differential characters of *Allantoma* and *Couratari* which had previously been confused. The other regional works cited above were mainly compilations from the literature and did not present much new critical taxonomic work, although most included descriptions of a few new species.

Thompson's (1927) classical study of the floral morphology of the Lecythidaceae entitled "A study in advancing gigantism" led him to divide what he called the Lecythideae, a tribe of Myrtaceous affinity, into four series; the Barringtonieae (*Barringtonia, Careya, Planchonia, Gustavia,* and *Grias*); the Napoleoneae (*Asteranthos, Crateranthus,* and *Napoleonaea*); the Couratarieae (*Couratari* and *Lecythopsis*); and the Bertholletieae (*Couroupita, Lecythis,* and *Bertholletia*). He gives a detailed analysis of the flowers of each tribe and genus. The author also concluded here, and in his earlier work on *Couroupita* (Thompson, 1921), that progressive staminal sterilization within the family is accompanied by cell gigantism, which in turn produces floral zygmorphy.

An anatomical study of the wood of Old and New World Lecythidaceae by Diehl (1935) supports the separation of the Lecythidaceae from the Myrtaceae, stressing the homogeneity of the former, with banded metatracheal parenchyma as its only distinctive feature. He also noted that the New World genera possess crystal strands, which are lacking in all but *Foetidia* of the Old World, and supported the inclusion of *Asteranthos* and *Napoleonaea* in the Lecythidaceae.

Despite his prestigious publications in Engler's *Das Pflanzenreich* Rheinhard Knuth (1939a, b, c), a botanist with the Berlin Botanic Garden who compiled an "Initia Florae Venezuelensis" in 1928, added little to the comprehension of the family. Knuth recognized the Barringtoniaceae, the Lecythidaceae *(Gustavia, Grias, Cariniana, Allantoma, Couroupita, Corythophora* Knuth, *Lecythis, Holopyxidium, Sapucaya* Knuth, *Chytroma, Eschweilera, Jugastrum, Bertholletia, Cercophora* and *Couratari),* and the Asteranthaceae *(Asteranthos)* as separate families. He made no further subdivisions of the Lecythidaceae and Asteranthaceae but divided the Barringtoniaceae into five tribes: the Barringtonieae *(Barringtonia, Careya, Planchonia,* and *Chydenanthus);* the Combretodendreae *(Combretodendron),* the Foetidieae *(Foetidia);* the Craterantheae *(Crateranthus);* and the Napoleoneae *(Napoleonaea).* As in other families monographed by Knuth, his species separation is not based on the biology of the group. Like Miers, he was concerned with morphological minutiae rather than a biological and evolutionary comprehension of the taxa. The keys do not work, and species are described from inadequate material. More species known only from pyxidia were added by Knuth, and most of Miers' similarly described species were uncritically accepted. With so many species recognized from inadequate material, the monograph is not very useful for the identification of specimens but does provide a good replication of the species descriptions of Lecythidaceae known to that time. All subsequent monographic work in Lecythidaceae points to the need for drastic reduction in the number of species recognized by Knuth, e g Payens (1967), Liben (1971a) and the present work. For example, Payens' (1967) monograph of *Barringtonia* reduced Knuth's 109 species to 39, and Liben's (1971a) monograph of *Napoleonaea* included 8 species as compared to the 18 recognized by Knuth (1939a). It is rather unfortunate that both major monographers of the Lecythidaceae, Miers and Knuth, had the same descriptive approach characteristic of "splitters," thus producing a classification independent of the group's biology.

Recently two further neotropical genera which cannot be maintained were added to the family by Ledoux. *Neohuberia,* described in 1963, is based on a species of *Eschweilera;* and *Pachylecythis,* proposed in 1964 from a pyxidium only, is a *Lecythis.*

Pichon (1945) discussed the position of the genus *Combretodendron (=Petersianthus)* and, at the same time, proposed a new classification of the Lecythidaceae. He divided the family into 3 subfamilies and further split the subfamilies into tribes, as follows:

Subfamily I: Planchonioideae
  Tribus I$_1$: Planchonieae *(Planchonia)*
  Tribus I$_2$: Barringtonieae *(Careya, Barringtonia, Chydenanthus)*
  Tribus I$_3$: Combretodendreae *(Combretodendron)*
  Tribus I$_4$: Foetidieae *(Foetidia)*
Subfamily II: Lecythidoideae
  Tribus II$_1$: Griadeae *(Gustavia, Grias)*
  Tribus II$_2$: Couroupiteae *(Couroupita, Corythophora)*
  Tribus II$_3$: Lecythideae *(Lecythis)*
  Tribus II$_4$: Couratarieae *(Cariniana, Couratari, Cercophora)*
  Tribus II$_5$: Bertholletieae *(Allantoma, Sapucaya, Chytroma, Eschweilera, Jugastrum, Holopyxidium, Bertholletia)*
Subfamily III: Napoleonoideae
  Tribus III$_1$: Napoleoneae *(Napoleonaea)*
  Tribus III$_2$: Craterantheae *(Crateranthus)*
  Tribus III$_3$: Asterantheae *(Asteranthos)*

Pichon (1945) gives floral, fruit, seed, and embryo characteristics for each subfamily and tribe. Melchior (1964) follows Pichon without modification.

Embryological differences between the Myrtaceae and the Lecythidaceae were pointed out by Treub (1884), Mauritzon (1939), and Venkateswarla (1952). Mauritzon states "Personally I am unable to find with the aid of embryology any evident connecting link between any of the Lecythidaceae and any other family of Myrtles." The principal embryological differences bettween the Myrtaceae and Lecythidaceae are the large nucellus and thick integuments (2 cells thick) of the former and the scanty nucellus and thick integuments of the latter. Since these studies only include species of *Barringtonia, Gustavia, Couroupita* and *Napoleonaea* there is a great need for further embryological study of the family. Information on staminal development has been provided by John McLean Thompson (1921, 1927), who concluded that the stamens develop centrifugally. As has been demonstrated by Payens (1967), embryo structure differs between genera and hence is of taxonomic importance. Payens found that the embryo of *Barringtonia* lacks true cotyledons, possessing instead tiny scales at the apical end. Essentially the same structure is found in *Careya* (Thomson, 1858), *Chydenanthus* (Treub, 1884), *Abdulmajidia* (Whitmore, 1974), *Bertholletia* (Goebel, 1905; Payens, 1967), *Eschweilera* (Berg, 1858, Duke, 1969, Prance and Mori, 1978); and *Lecythis* (Duke, 1969; Prance and Mori, 1978). In contrast, well-developed cotyledons are found in *Cariniana* (Payens, 1967; Prance and Mori, 1978), *Petersianthus* (Pichon, 1945), *Couratari* (Poiteau, 1825; Knuth, 1939b, Duke, 1969), *Couroupita* (Poiteau, 1825; Knuth, 1939b; Payens, 1967), *Gustavia* (Poiteau, 1825; Woodson, 1958; Mori, 1974), and *Planchonia* (Knuth, 1939a; Kartawinata, 1965).

The palynologist Muller (1972) recognizes two types of pollen in the family, the *Planchonia* main type (syntricolpate) and the *Lecythis* main type (tricolpate). According to Muller, pollen morphology supports the division of the family into 4 subfamilies (Planchonioideae, Foetidioideae, Napoleonaeoideae, and the Lecythidoideae) as was done by Niedenzu in 1892. Walker and Doyle (1975) comment on the different positions of Lecythidaceae in the Cronquist and Takhtajan systems and indicate that pollen does not help answer the problem.

Preliminary evidence from cytology tends also to support the separation of the Lecythidaceae from the Myrtaceae. The subfamily Leptospermoideae of the Myrtaceae has a constant number of $2n=22$ while the subfamily Myrtoideae has $2n$ numbers ranging from 22-28 (Atchison, 1947). The known chromosome numbers also support recognition of at least 3 of Niedenzu's (1892) 4 subfamilies. The Planchonioideae are $x=13$ (Sobti and Singh, 1961; Roy and Jha, 1965, Mehra, 1972; Mangenot and Mangenot, 1962; Sarkar et al, 1976), the Napoleonaeoideae are $x=16$ (Mangenot and Mangenot, 1957, 1962), and the Lecythidoideae are $x=17$ (Mangenot and Mangenot, 1958, 1962; Kowal et al, 1977). There are no counts from the Foetidioideae. Raven (1975) has treated the three subfamilies as three families based on their constantly different base numbers. Kowal et al (1977) concluded that chromosome data do not help place the Lecythidaceae sensu lato in any definite order of the angiosperms.

Hegnauer (1966) concluded from phytochemistry that the Lecythidaceae are close to the Myrtaceae. He does add, however, that for a more exact phytochemical comparison of the family there have been too few observations. Kubitzki, of the University of Hamburg, has begun a more detailed analysis of the phytochemistry of the family but has not yet published any results.

Most modern phylogenists treat the Lecythidaceae as a single family which includes the Barringtoniaceae and Asteranthaceae (Hutchinson, 1959; Payens, 1967; Thorne, 1968; Cronquist, 1968; Takhtajan, 1969; Stebbins, 1974). However, Hutchinson (1969, 1973) later separated the group into the 3 families recognized by Knuth, and Airy-Shaw (1973) treated all four subfamilies of Niedenzu (1892) as families and also placed *Asteranthos* in a family of its own. In his monograph of *Barringtonia* Payens (1967) suggests that:

> Whatever subdivision to the Lecythidaceae should be given, there is in my opinion no argument to recognize more than one family, as the members are too intricately, and partly reticulately, knit together and furthermore have too much intrinsic structural characters in common.

There is, however, no agreement as to the position of the family among the Dicotyledons. Hutchinson (1959) and Takhtajan (1969) leave the family in the Myrtales, while Thorne (1968, 1976) places it in the Theales, and Cronquist (1968) in the Lecythidales, putting it somewhere between the Theales and Malvales. The large order Theales of Thorne (1976) includes the Lecythidineae as a suborder with one family Lecythidaceae which is divided into three subfamilies (Planchonioideae, Lecythidoideae and Napoleonaeoideae (including *Asteranthos*)). Thorne relates the Lecythidaceae to the Theales on account of their numerous stamens, showy imbricate petals, and centrifugal stamens. He

Table I.
Comparison of the differences between the Lecythidaceae and Myrtaceae

Character	Lecythidaceae	Myrtaceae	References
Flowers			
symmetry	actinomorphic or zygomorphic	actinomorphic	Lawrence (1951)
anthers	usually basifixed	usually versatile	Lawrence (1951)
stamen development	centrifugal	centripetal	Thompson (1921, 1927), Cronquist (1968), Leins (1972), Thorne (1976)
Leaves			
arrangement	alternate	usually opposite	Lindley (1853), Thorne (1976)
margins	often serrulate-serrate	entire	Lindley (1853)
stipules	minute or absent	absent	Pittier (1927), Weberling (1957), Lawrence (1951), Payens (1967)
pellucid dots	absent	present	Lindley (1853)
Stem			
secrectory cavities	absent	present	Costantin and Dufour (1885)
internal phloem	absent	present	Costantin and Dufour (1885), Thorne (1976)
cortical bundles	present	absent	Costantin and Dufour (1885), Lignier (1890)
vestured pitting	absent	present	Thorne (1976)
Wood			
pores	mostly solitary	mostly in multiples	Diehl (1935)
fiber pits	distinctly bordered	simple or indistinctly bordered	Diehl (1935)
parenchyma	paratracheal or diffuse	distinctly metatracheal	Diehl (1935)
Embryology			
nucellus	scanty	abundant	Mauritzon (1939)
integuments	thick, with vascular tissue, fused	2 cells thick, without vascular tissue, separate	Mauritzon (1939)
Chromosomes			
number	$n = 13$ for the Planchonioideae, $n = 16$ for the Napoleonaeoideae and $n = 17$ for the Lecythidodeae	$n = 11$ for the Leptospermoideae, $n = 11$-14 for the Myrtaceae	Atchison (1947), Banerjee (1950), Roy and Jha (1965), Kowal et al (1977)

Table II
A summary of the most important taxonomic treatments of the Lecythidaeceae

Jussieu, Antoine Laurent de
(1789)

- Myrtaceae (Ordo "Myrti")
  - *Butonica (= Barringtonia)*
  - *Stravadium (= Barringtonia)*
  - *Pirigara (= Gustavia)*
  - *Couroupita*
  - *Lecythis*

Poiteau
(1825)

- Lecythidaceae ("Lécythidées")
  - *Lecythis*
  - *Bertholletia*
  - *Couroupita*
  - *Gustavia*
  - *Couratari*

de Candolle
(1828)

- Myrtaceae
  - Tribe Barringtonieae
    - *Barringtonia*
    - *Stravadium (= Barringtonia)*
    - *Gustavia*
  - Tribe Lecythideae
    - *Lecythis*
    - *Eschweilera*
    - *Bertholletia*
    - *Couroupita*
    - *Couratari*

de Candolle
(1839)

- Napoleonaeaceae
  - *Napoleonaea*
  - *Asteranthos*

Lindley
(1846)

- Lecythidaceae
  - *Couratari*
  - *Cariniana*
  - *Lecythis*
  - *Eschweilera*
  - *Bertholletia*
  - *Couroupita*
- Barringtoniaceae
  - *Barringtonia*
  - *Stravadium (= Barringtonia)*
  - *Careya*
  - *Gustavia*
  - *Foetidia*
  - *Grias*
- Belvisiaceae
  - *Napoleonaea*
  - *Asteranthos*

Berg
(1858)

- Myrtaceae
  - Tribe Barringtonieae
    - *Gustavia*
  - Tribe Lecythideae
    - *Couroupita*
    - *Bertholletia*
    - *Lecythis* (including *Eschweilera)*
    - *Lecythopsis (= Couratari)*
    - *Couratari*

Bentham & Hooker
(1865)

- Myrtaceae
  - Tribe Lecythideae
    - Subtribe Barringtonieae
      - *Barringtonia*
      - *Petersia (= Petersianthus)*
      - *Careya*
      - *Planchonia*
      - *Grias*
      - *Gustavia*
    - Subtribe Eulecythideae
      - *Couratari*
      - *Couroupita*
      - *Lecythopsis (= Couratari)*
      - *Lecythis*
      - *Bertholletia*
    - Subtribe Napoleoneae
      - *Napoleonaea*
      - *Asteranthos*

Table II—continued
A summary of the most important taxonomic treatments of the Lecythidaceae

Le Maout and Decaisne
(1873)

- Myrtaceae
  - Tribe Barringtonieae
    - *Barringtonia*
    - *Careya*
    - *Planchonia*
    - *Grias*
    - *Gustavia*
  - Tribe Lecythideae
    - *Couratari*
    - *Couroupita*
    - *Lecythis*
    - *Bertholletia*
- Napoleonaeaceae
  - Napoleonaea
  - Asteranthos

Miers
(1874, 1875a, b)

- Lecythidaceae
  - *Gustavia*
  - *Couroupita*
  - *Bertholletia*
  - *Lecythis*
  - *Chytroma (= Lecythis* pro parte & *Eschweilera* pro parte)
  - *Eschweilera*
  - *Jugastrum (= Eschweilera)*
  - *Couratari*
  - *Cariniana*
  - *Allantoma*
  - *Grias*
  - *Cercophora (= Strailia)*
- Barringtoniaceae
  - *Barringtonia*
  - *Agasta (= Barringtonia)*
  - *Butonica (= Barringtonia)*
  - *Stravadium (= Barringtonia)*
  - *Planchonia*
  - *Careya*
  - *Doxomma (= Barringtonia)*
  - *Petersia (= Petersianthus)*
  - *Megadendron (= Barringtonia)*
  - *Chydenanthus*
- Belvisiaceae
  - *Napoleonaea*
- Rhododendreae (Ericaceae)
  - *Asteranthos*

Niedenzu
(1892)

- Lecythidaceae
  - Subfamily Foetidioideae
    - *Foetidia*
  - Subfamily Planchonioideae
    - *Planchonia*
    - *Petersia (= Petersianthus)*
    - *Careya*
    - *Barringtonia*
    - *Chydenanthus*
  - Subfamily Lecythidoideae
    - *Japarandiba (= Gustavia)*
    - *Grias*
    - *Couroupita*
    - *Lecythis*
    - *Eschweilera*
    - *Bertholletia*
    - *Cariniana*
    - *Cercophora (= Strailia)*
    - *Couratari*
    - *Allantoma*
  - Subfamily Napoleonaeoideae
    - *Asteranthos*
    - *Napoleonaea*

Table II—continued

A summary of the most important taxonomic treatments of the Lecythidaceae

Knuth
(1939a, b, c)

- Barringtoniaceae
  - Tribe Barringtonieae
    - *Barringtonia*
    - *Careya*
    - *Planchonia*
    - *Chydenanthus*
  - Tribe Combretodendreae
    - *Combretodendron* (= *Petersianthus*)
  - Tribe Foetidieae
    - *Foetidia*
  - Tribe Craterantheae
    - *Crateranthus*
  - Tribe Napoleoneae
    - *Napoleonaea*
- Lecythidaceae
  - *Gustavia*
  - *Grias*
  - *Cariniana*
  - *Allantoma*
  - *Couroupita*
  - *Corythophora*
  - *Lecythis*
  - *Holopyxidium* (= *Lecythis*)
  - *Sapucaya* (= *Lecythis*)
  - *Chytroma* (= *Lecythis* pro parte & *Eschweilera* pro parte)
  - *Eschweilera*
  - *Jugastrum* (= *Eschweilera*)
  - *Bertholletia*
  - *Cercophora*
  - *Couratari*
- Asteranthaceae
  - *Asteranthos*

Pichon
(1945)

- Lecythidaceae
  - Subfamily Planchonioideae
    - Tribe Planchonieae
      - *Planchonia*
    - Tribe Barringtonieae
      - *Careya*
      - *Barringtonia*
      - *Chydenanthus*
    - Tribe Combretodendreae
      - *Combretodendron* (= *Petersianthus*)
    - Tribe Foetidieae
      - *Foetidia*
  - Subfamily Lecythidoideae
    - Tribe Griadeae
      - *Gustavia*
      - *Grias*
    - Tribe Couroupiteae
      - *Couroupita*
      - *Corythophora*
    - Tribe Lecythideae
      - *Lecythis*
    - Tribe Couratarieae
      - *Cariniana*
      - *Couratari*
      - *Cercophora* (= *Strailia*)
    - Tribe Bertholletieae
      - *Allantoma*
      - *Sapucaya* (= *Lecythis*)
      - *Chytroma* (= *Lecythis* pro parte & *Eschweilera* pro parte)
      - *Jugastrum* (= *Eschweilera*)
      - *Holopyxidium* (= *Lecythis*)
      - *Bertholletia*
  - Subfamily Napoleonoideae
    - Tribe Napoleoneae
      - *Napoleonaea*
    - Tribe Craterantheae
      - *Crateranthus*
    - Tribe Asterantheae
      - *Asteranthus*

Table II—continued

A summary of the most important taxonomic treatments of the Lecythidaceae

Airy-Shaw (1973)
Foetidiaceae
Foetidia
Barringtoniaceae
Barringtonia
Careya
Planchonia
Chydenanthus
Combretodendron (= Petersianthus)
Lecythidaceae
Gustavia
Grias
Allantoma
Cariniana
Couroupita
Lecythis
Corythophora
Holopyxidium (= Lecythis)
Chytroma (= Lecythis pro parte & *Eschweilera* pro parte)
Eschweilera
Bertholletia
Couratari
Asteranthaceae
Asteranthos
Napoleonaeaceae
Napoleonaea
Crateranthus

places them in a suborder on account of their often valvate sepals, presence of a staminal corona, inferior ovary, large baccate or woody fruit, and the exalbuminous seeds. Stebbins (1974), places his order Lecythidales between the Urticales and Violales, but with some doubt. There is a need for a comparative study of the Theales and Malvales with the Lecythidaceae to determine if the family is more closely related to them or to the Myrtal alliance where it has been traditionally placed since the time of Jussieu.

Recently the authors of this volume have begun a series of papers dealing with the biology of the Lecythidaceae based on extensive field studies (Mori and Kallunki, 1976; Mori et al, 1978; Prance, 1976; Prance and Mori, 1978). These studies include observations on the floral biology and pollination ecology which are helping to interpret the complex floral structure of the family. There are few previous papers based on field observations. Greenhall (1965) reported bat dispersal of the seeds of *Lecythis usitata,* Huber (1909) reported agouti dispersal of the seeds of *Bertholletia,* and Jackson and Salas (1965) reported the pollination of *Lecythis elliptica (= L. minor)* by bees.

Other recent work on the Lecythidaceae includes that of Monteiro-Scanavacca (1974, 1975a, b, 1977) who studied the floral vascular system of most genera of neotropical Lecythidaceae. She provided good descriptions of

Table III
Number of Species and Distribution of Genera of Lecythidaceae by Subfamily

Subfamily	Genus	Number of species	Distribution	References
Planchonioideae		(55)		
	Abdulmajidia	2	Malaysia	Whitmore, 1974
	Barringtonia	40	E. Afr. (1 sp), Madag. (2 sp), trop. Asia, Aust. & Pacif.	Payens, 1967; Kochummen and Whitmore, 1973
	Careya	4	Trop. Asia	Knuth, 1939a
	Chydenanthus	2	S.E. Asia & Malaysia	Knuth 1939a
	Petersianthus[a]	2	Trop. W. Afr (1 sp) & Philipp. Is. (1 sp)	Knuth, 1939a; Liben, 1968, 1971b
	Planchonia	5	Andaman Is. to N. Austr.	Kartawinata, 1965
Foetidioideae		(5)		
	Foetidia	5	Pemba Is. & Madagascar to India & Malaya	Knuth, 1939a
Napoleonaeoideae		(12)		
	Asteranthos	1	N. Brazil	Knuth, 1939c
	Crateranthus	3	Trop. W. Afr.	Knuth, 1939a
	Napoleonaea	8	Trop. W. Afr.	Liben, 1971a
Lecythidoideae		(ca 212)		
	Allantoma	1	Guiana & Brazil	
	Bertholletia	1	Trop. S. Am.	
	Cariniana	15	Trop. S. Am.	
	Corythophora	4	Brazil	
	Couratari[b]	15	Trop. S. Am.	
	Couroupita	4	Trop. Am. & W.I.	
	Eschweilera[c]	ca 100	Trop. Am.	
	Grias	6	Panama to Peru	
	Gustavia	41	Trop. Am.	
	Lecythis[d]	ca 25	Trop. Am.	

[a] *Combretodendron* is a widely used synonym of *Petersianthus*. See Liben (1968)
[b] Including *Lecythopsis*
[c] Including *Neohuberia, Jugastrum* and *Chytroma* pro parte. See Prance and Mori (1977)
[d] Including *Chytroma* pro parte, *Holopyxidium, Pachylecythis, Sapucaya,* and *Cercophora*. See Prance and Mori (1977).

the vascular trace anatomy of the androecium and gynoecium and of the placentation. Her study is based on one species of each genus and should be expanded.

New taxa are still being discovered in the family. Within the last ten years Whitmore (1974) described a new Malaysian genus *(Abdulmajidia),* Mori (1971, 1976, 1978) and Mori and García-Barriga (1975) described new species of *Lecythis* and *Gustavia,* Prance and Anderson (1976) described new species of *Cariniana* and *Couratari,* Rodrigues (1974) described new species of *Corythophora, Couratari* and *Cariniana,* and Rizzini (1976) described new species of *Couratari.*

The taxonomic history of the Lecythidaceae may be summarized as follows:

1. Period of discovery and description of new genera beginning with the work of Christovão, Marcgrave, and Linnaeus.
2. Alignment with the Myrtaceae, first proposed by Jussieu in 1789, followed by de Candolle (1828), Bentham and Hooker (1865) and many others.
3. Separation from the Myrtaceae into a separate family, first suggested by Poiteau (1825) and followed by Don (1832), Lindley (1846), Miers (1874), and all workers after Miers.
4. Continued accumulation of evidence for the segregation of the Lecythidaceae from the Myrtaceae (Table I summarizes the known differences).
5. Segregation of Asteranthaceae, Belvisiaceae, Napoleonaeaceae, and Barringtoniaceae from the Lecythidaceae, suggested in various combinations by Lindley (1846), Miers (1874), Knuth (1939a, b, c), Hutchinson (1969, 1973), and Raven (1976).
6. Lumping of the segregate families back into the Lecythidaceae by Hutchinson (1959), Payens (1967), Thorne (1968), Cronquist (1968) and Takhtajan (1969).
7. Placement in an order other than the Myrtales, the Theales as suggested by Thorne (1968, 1976), the Lecythidales by Cronquist (1968), and Stebbins (1974).
8. Accumulation of information to determine the proper place for the Lecythidaceae among the angiosperms, and studies of the biology of Lecythidaceae, both steps in their initial phases.

III. SUBDIVISIONS OF LECYTHIDACEAE

Table II summarizes the way in which the Lecythidaceae has been subdivided in the most important taxonomic treatments. Details of other minor variations have been given in the taxonomic history in Chapter II. The Lecythidaceae has been placed within the Myrtaceae in most historic treatments such as those of de Candolle (1828) and Bentham and Hooker (1865) or it has been regarded as a separate family or split into several families in more recent classifications. The Asteranthaceae, Belvisiaceae, Foetidiaceae, Napoleonaeaceae, Barringtoniaceae, and Lecythidaceae have all been regarded as separate families in various combinations by different authors (Lindley, 1846; Miers, 1874, 1875a; Knuth, 1939a, b, c; Hutchinson, 1973; Airy-Shaw, 1973; etc.). These segregate families, or some of them, have also been treated as subfamilies of Lecythidaceae (Niedenzu, 1892; Pichon, 1945) or tribes of Myrtaceae (de Candolle, 1828; Berg, 1858; Bentham and Hooker, 1865; etc.).

In our opinion these taxa are closely related and belong together regardless of what taxonomic rank they are given. We agree with Payens (1967) that there is no strong argument to recognize more than one family as the members are too intricately and reticulately knit together (see Table IV). There are, however, some important differences in pollen, chromosome number, anatomy, etc. and so we follow the classification first suggested by Niedenzu

(1892) in which these differences are recognized at the subfamilial level. The neotropical Lecythidaceae, with the exception of the monotypic *Asteranthos* of the Napoleonaeoideae, all belong to the subfamily Lecythidoideae. However, our placement of *Asteranthos* is open to question since the seeds of this genus are unique in the family (see Chapter IV, Part 5). Consequently, its position must be considered provisional until further evidence is accumulated, especially from cytology and the comparative anatomy of *Asteranthos, Crateranthus,* and *Napoleonaea.* Our current conspectus of the number of species and distribution of genera of all subfamilies of Lecythidaceae is given in Table III. Descriptions of each subfamily and a key to the subfamilies are provided at the beginning of the systematic treatment of the family (Chapter XII).

IV. MORPHOLOGY AND ANATOMY

1. Habit and Bark

Neotropical Lecythidaceae are small to very large trees which are most abundant in the upper strata of lowland tropical forests (see Chapter VI). Schulz (1960) has divided the woody plant species of the forests of northern Surinam into four groups, i e upper story, middle story, lower story and undergrowth. Upper story species are generally 28-45 meters tall (Schulz, 1960) but may reach 55 meters (e g *Terminalia amazonica,* Fig 42 in Oldeman, 1974). Because these species do not form a closed canopy and because their crowns project above those of most other woody species, they are often called emergents. Middle story species attain a height of 25 meters and their crowns usually form a continuous canopy, whereas lower story species reach heights of between 8 and 18 meters and do not form a closed canopy (Schulz, 1960). Undergrowth species are mostly small trees, tall shrubs and stemless palms, all of which reach a maximum height of 3-10 meters (Schulz, 1960). In the forests of northern Surinam, the Lecythidaceae are most common in the middle story, where they often form the majority of the trees, less common in the upper story, and essentially absent from the undergrowth (Schulz, 1960). Representative species of Lecythidaceae occupying these strata are *Couratari stellata* of the upper story (reaching 45 m × 112 cm DBH, see fig 60 in Schulz, 1960), *Eschweilera odora* of the middle story (reaching 25 m × 50 cm DBH, see fig 60 in Schulz, 1960), and *Gustavia hexapetala* of the lower story (reaching 20 meters but usually smaller, pers. obs.). Height/diameter diagrams for all species of Lecythidaceae in forests rich in species of this family are needed for a proper evaluation of intrafamilial stratification.

Two principal growth forms are found in the Lecythidaceae. At one extreme are those species with well defined trunks, relatively small leaves, and a much-branched crown in which the branches are much smaller in diameter than the trunk. We refer to this growth form as leptocaul (Figs 1C, D). The leptocaul form is prevalent in the family as a whole, and it is the only growth form found in *Asteranthos, Allantoma, Cariniana, Couroupita, Corythophora, Bertholletia, Couratari, Eschweilera,* and *Lecythis.* At the

Table IV

A comparison of the characteristics used in the classification of the 4 subfamilies of Lecythidaceae

Character	**Planchonioideae**	**Foetidioideae**	**Napoleonaeoideae**	**Lecythidoideae**
Symmetry of Flowers	actinomorphic	actinomorphic	actinomorphic	Zygomorphic or actinomorphic in *Allantoma, Grias,* and *Gustavia*
Petals	present	absent	absent	present
Corona of staminal origin	absent	absent	present	absent
Staminodes	mostly present	none	present *(Napoleonaea)* absent *(Crateranthus, Asteranthos)*	present or absent in *Gustavia, Grias, Allantoma* and *Cariniana*
Pollen	syntricolpate	tricolpate	tricolpate	tricolpate
Fruit	indehiscent—berry or drupe	indehiscent	indehiscent—berry, drupe or possibly a septacidel capsule in *Asteranthos*	dehiscent pyxidium, or indehiscent in *Gustavia, Grias* and *Couroupita*
Fusion of filaments	fused at base into distinct staminal ring except *Petersianthus* which is weakly fused	weakly fused	fused at base into distinct annular ring except in *Asteranthos* which is weakly fused	fused at base into distinct staminal ring
Intrastaminal disk	present except in *Careya*	present	present in *Napoleonaea,* absent in *Crateranthus* and *Asteranthos*	absent
Placenta	columnar	peltate	columnar	columnar
Cotyledons	absent: *Barringtonia, Careya, Chydenanthus* present: *Petersianthus, Planchonia*	unknown	present in *Napoleonaea* and *Asteranthos*	absent in *Grias, Allantoma, Bertholletia, Lecythis, Corythophora* and *Eschweilera* present in *Gustavia, Cariniana, Couroupita* and *Couratari*
Cortical bundle orientation	reversed	reversed	normal	normal
Wood	without crystal chains	with crystal chains	without crystal chains	with crystal chains
Chromosome numbers	$x = 13$	unknown	$x = 16$ *(Asteranthos* unknown)	$x = 17$

other extreme are species with very large leaves clustered at the ends of stout branches and with unbranched or few branched trunks (Figs 1A, B). We refer to this growth form as pachycaul, a term which includes the *Modèle de Corner* and *Modèle de Schoute* of Hallé and Oldeman (1970) or the lamp post form of D'Arcy (1973). All species of *Grias* and several species of *Gustavia* have this growth form.

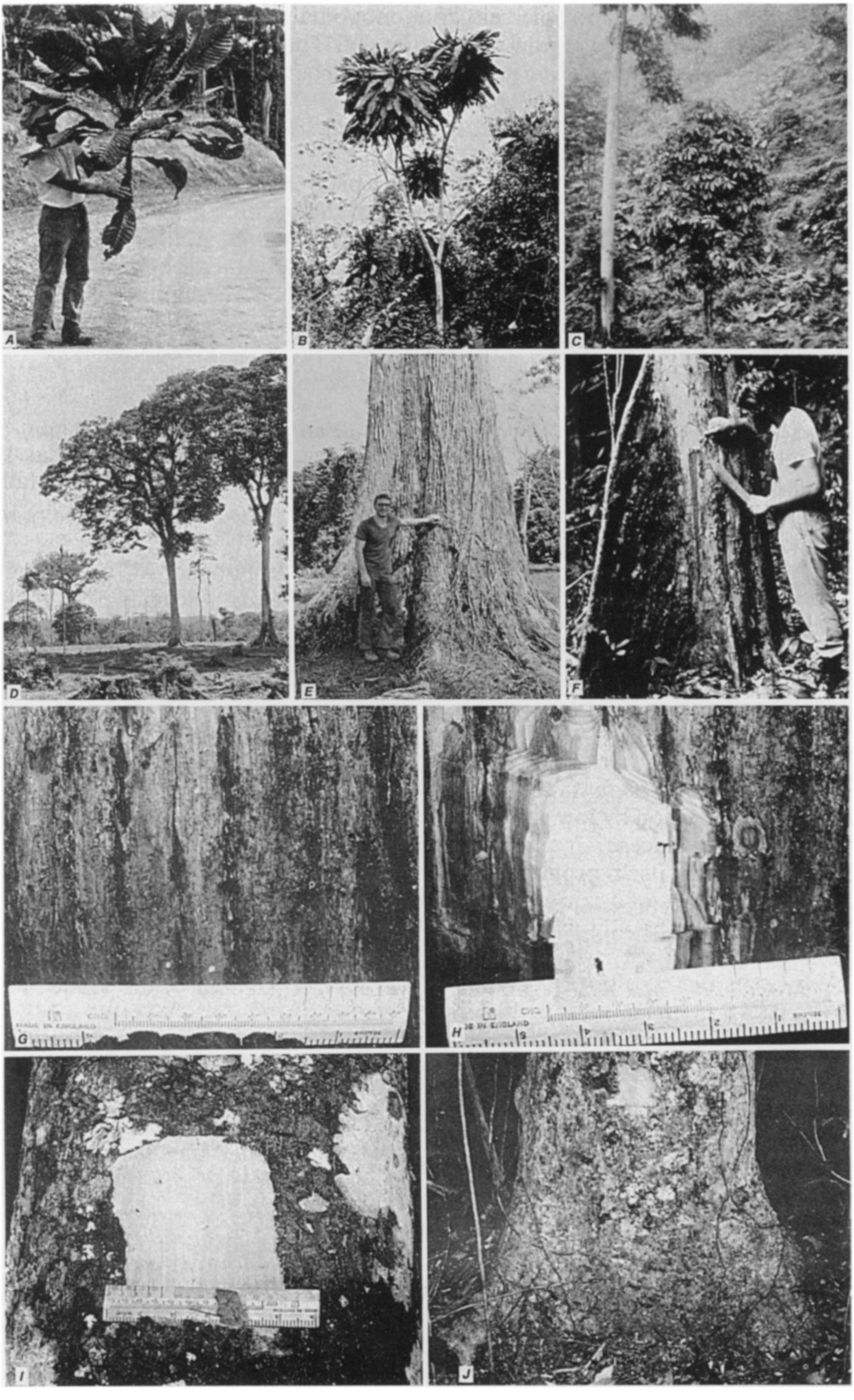
The classification of Lecythidaceae into pachycaul and leptocaul species is an oversimplification. For example, studies of the architecture of tropical trees by Hallé and Oldeman (1970) have revealed that our pachycaul category corresponds to two of their models and that our leptocaul group is more complex, including at least five of their architectural types. A summary of the architectural types of Hallé and Oldeman (1970) found in our two categories is as follows:

I. Pachycaul

1. *Modèle de Corner* (examples: *Gustavia grandibracteata, G. monocaulis).* Includes species with unbranched trunks, monopodial growth, and lateral inflorescences (Fig 1A).
2. *Modèle de Schoute* (examples: all species of *Grias, Gustavia grandibracteata, G. superba).*
   Includes species with branched trunks, axes with monopodial, orthotropic growth, and lateral inflorescences (Fig 1B). Hallé and Oldeman (1970) and Hallé and Mabberley (1976) state that a "*Grias* sp. Brésil. J. B. Rio de Janeiro" belongs to their *Modèle de Corner* rather than here. However, this species is probably *G. neuberthii* (see Prance 16572) which, as in all other species of *Grias* known to us, is usually branched and therefore does not fit the description of the *Modèle de Corner.*

II. Leptocaul

3. *Modèle de Rauh* (example: *Couroupita guianensis)*
   Includes species with branched trunks, monopodial, orthotropic, and rhythmic growth, the latter resulting in verticillate or subverticillate branches. The branches are morphologically identical to the trunk, and the inflorescences are lateral. In the case of *C. guianensis* the inflorescences arise from the trunk and often have indeterminate growth (see Chapter IV, Part 3).
4. *Modèle de Massart* (example: *Couratari* cf *stellata,* fide Hallé and Oldeman, 1970).
   Includes species with monopodial, orthotropic trunks with spiral phyllotaxy and rhythmic growth, of which the latter results in a verticillate or subverticillate branch arrangement. The lateral branches are plagiotropic, generally floriferous, and with distichous or nearly distichous phyllotaxy. Extension growth of the lateral branches may be monopodial or sympodial. This type differs from the *Modèle de Rauh* mainly in the plagiotropic rather than orthotropic branches.
5. *Modèle de Roux* (example: *Bertholletia excelsa).*
   Includes species with monopodial, orthotropic trunks with spiral phyllotaxy and continuous growth. The continuous growth results in branches that are alternately arranged rather than verticillate. The


A
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branches are plagiotropic, either monopodial or sympodial, and with distichous or nearly distichous phyllotaxy. The *Modèle de Roux* differs differs from the *Modèle de Massart* by having continuous instead of rhythmic growth.

6. *Modèle de Troll (Eschweilera* sp, *Oldeman & Sastre 183, Lecythis* cf *pisonis,* fide Hallé and Oldeman, 1970).
   Includes species with entirely plagiotrophic composite axes. This model is characterized by all the axes being more or less equal.

The presence of 6 architectural types in the approximately 207 species of New World Lecythidaceae gives a number of species to architectural type ratio of 34.5. Hallé and Mabberly (1976) reported that the New Guinea species *Barringtonia calyptrocalyx* K. Schum. has Corner's architectural model. An additional model, that of *Kwan Koribu,* is found in *Petersianthus africanum* of the Old World Planchonioideae (Hallé and Oldeman, 1970), making a grand total of 7 models in 278 species or 39.7 species per model. The Euphorbiaceae has 13 types among its 10,000 species and the Icacinaceae 5 types in 250 species (Hallé and Oldeman, 1970), giving ratios of 769.2 and 50 respectively. These data demonstrate the relative richness of architectural models in Lecythidaceae and suggest that further study of the architecture of the family may be useful to the understanding of the taxonomy and evolution of Lecythidaceae as well as the evolution of architectural types.

An examination of architectural types and habitats of Lecythidaceae demonstrates that the family consists almost exclusively of species of large trees of varied architecture which occur in the upper three strata of tropical forests. Shrubby habit is extremely rare, occurring only in *Eschweilera nana* (Berg) Miers of the cerrado of Central Brazil. Unlike various other predominantly woody families of Amazonia it is not represented in the Cerrado vegetation by low suffruteces such as *Parinari obtusifolia* Hook. f. of the Chrysobalanaceae.

The trunk itself provides useful but infrequently observed taxonomic characters. Depending on the species, the trunk may be cylindric, buttressed (Figs 1E, F), or basally swollen (Fig 1J). The buttresses vary in height, width, and thickness. For example, the buttresses of *Couratari guianensis* are high, relatively narrow, and thick, whereas those of other species in other genera may be high, narrow, and thin (Fig 1F) or with various combinations of

Fig 1. Habit and bark of selected species of neotropical Lecythidaceae. A, *Gustavia monocaulis (Mori & Kallunki 5600),* note pachycaul growth form of type corresponding to the *Modèle de Corner;* B, *Gustavia superba* (unvouchered), note pachycaul growth form of type corresponding to the *Modèle de Schoute;* C, *Gustavia macarenensis* subsp. *paucisperma (Nee & Mori 4156),* small tree in center of photograph, note leptocaul growth form; D, *Lecythis ampla* (unvouchered), large tree to right of center, note leptocaul growth form; E, Trunk of *Lecythis ampla* (unvouchered), note furrowed bark and low, thick buttresses; F, *Eschweilera* cf. *subglandulosa (Mori & Bolten 8630),* note high, thin, relatively narrow buttresses; G, *Lecythis davisii (Mori & Bolten 8106),* note furrowed bark which is typical of many species of *Lecythis;* H, Slash of *Lecythis davisii (Mori & Bolten 8106),* note the thick, stratified outer bark which is characteristic of this and several related species of *Lecythis;* I, *Eschweilera* sp *(Mori & Bolten 8441),* note the unfurrowed, relatively thin outer bark which is characteristic of most species of *Eschweilera;* J, *Lecythis* aff *chartacea (Mori & Bolten 8595),* note basally swollen trunk.

height, width, and thickness. *Lecythis idatimon* has a cylindrical bole, and *Lecythis* cf *chartacea* (Mori & Bolten 8595, Fig 1J) has a basally swollen trunk. We have seen no examples of species with prop roots, but an undertermined species of *Eschweilera* is reported to have pneumatophores (Oldeman, 1971). Of the genera treated in this monograph, all species of *Gustavia* and *Grias, Asteranthos brasiliensis* and *Allantoma lineata* have relatively slender, cylindric trunks whereas most species of *Cariniana* have buttressed trunks.

The barks of tropical trees are amazingly diverse. Whitmore (1962) has demonstrated that the wide range of bark types found in the Dipterocarpaceae provides useful taxonomic characters. Likewise, the bark of Lecythidaceae is useful in separating species and possibly in helping to distinguish genera. For example, two closely related sympatric species of *Corythophora, C. alta* and *C. rimosa,* are easily distinguished in the field by the relatively smooth bark of the former and the deeply fissured bark of the latter (Figs 2C, D). There is also some indication that the barks of species of *Eschweilera* are fundamentally different from those of *Lecythis,* the former having relatively smooth bark, often with shallow irregular depressions (splotch marks) and thin outer bark (Figs 2E, F) and the later having furrowed, thick outer bark, with no irregular depressions (Figs 1G, 2A, B). There are exceptions to these generalizations; for example, the bark of *L. idatimon* is without distinctive furrows. Nevertheless, the apparent difference in the barks of *Eschweilera* and *Lecythis* merits further study.

Characteristics of the slash (an oblique cut made with a machete through the outer and inner bark) are taxonomically useful. For example, the slash of the inner bark of *Lecythis poiteaui* is bright yellow, and the outer bark of *Lecythis* is generally much thicker than that of *Eschweilera* (Fig 1H, I).

Roth's study (1969) of the anatomy of the bark of 11 species of Venezuelan Lecythidaceae is the only detailed anatomical study of the bark of this family. She concluded that the New World Lecythidaceae has a characteristic, homogeneous bark with the following properties:

1. a fibrous structure caused by fibers in the phloem,
2. lamination of the phloem caused by thin, short layers of superimposed phloem fibers,
3. straight and thin but multiseriate medullary rays,
4. a pattern of squares caused by the regular intersection of the phloem fibers and the medullary rays at 90° to one another,
5. failure of the medullary rays to form expansion tissue except in *Eschweilera trinitensis* and *Gustavia augusta,*
6. lack of stone cells except in the phelloderm of *Eschweilera subglandulosa,*
7. frequent formation of a stratified phelloderm,
8. eventual formation of stratified phellum or cork (see Fig 1H which shows the stratified outer bark of *Lecythis davisii),*
9. lack of a secretory system,
10. formation of "U-shaped" cell walls in the peridermis,
11. the general lack of differentiation in the phloem of the bark,

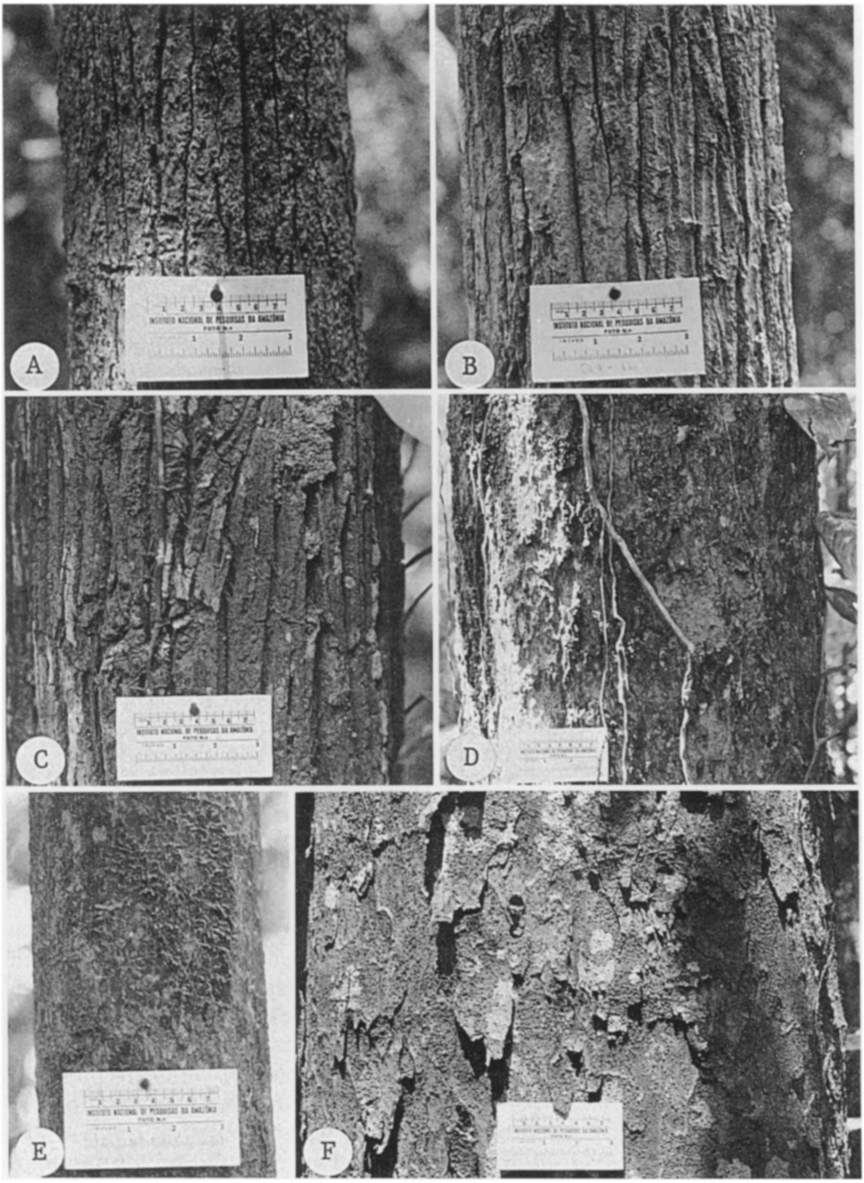


FIG 2. Barks of selected species of *Lecythis, Corythophora,* and *Eschweilera.* A, *Lecythis* sp 1 *(Prance 23124);* B, *Lecythis* sp 2 *(Prance 23119),* note the furrowed barks of these two species of *Lecythis;* C, *Corythophora rimosa (Prance 23146);* D, *Corythophora alta (Prance 23095),* note the difference in barks of these two species of *Corythophora;* E, *Eschweilera odora (Prance 23075);* young tree; F, *Eschweilera odora (Prance 23096),* older tree with the bark peeling in flakes.

12. formation of an annular rhytidome as well as a squamose rhytidome, and
13. stratification in the majority of the tissues of the bark.

Roth (1969) provides detailed illustrations of the cross section of the 11 species of Lecythidaceae studied. Her observations and figures provide the basis for extending the study of bark to other members of the family.

The regular, laminated structure of the bark of Lecythidaceae, according to Roth (1969), suggests that the bark of this family is phylogenetically advanced.

In summary, species of New World Lecythidaceae are trees which are most abundant in the upper three strata of tropical forests. Two principal growth forms, pachycaul and leptocaul, are found in the family but the pachycaul group includes two and the leptocaul group five of the architectural models of Hallé and Oldeman (1970). Characteristics of the trunk and bark are also taxonomically useful but in need of more detailed study.

2. Leaves and Stems

The terminology used to describe leaves in this monograph follows Hickey (1973) and to a lesser extent Lawrence (1951).

The leaves of neotropical Lecythidaceae are simple, alternate, usually petiolate, and pinnately veined. The secondary veins depart at an acute angle from the mid-vein, curve apically toward the margin, and either join the superadjacent secondary to form marginal loops (brochidodromous type of Hickey, 1973) or do not form prominent marginal loops (eucamptodromous type of Hickey, 1973). In many species the basal secondaries are eucamptodromous and the apical ones are brochidodromous in the same leaf. The junction of the secondary vein with the mid-vein is thickened in *Cariniana pyriformis, C. domestica, C. rubra,* and *C. penduliflora.* These thickenings are hollow and the opening into the cavity is lined with hairs. We refer to these cavities as domatia because they appear to be frequented by mites. The tertiary veins generally form a reticulum that is longitudinally or obliquely oriented to the mid-vein. However, *Allantoma* and *Cariniana* have tertiary veins that are not as reticulate and that are oriented more or less perpendicularly to the mid-vein. Areoles are well developed or imperfect in species of all genera except *Grias* which lacks or has incomplete areoles (see Hickey, 1973 for definitions and illustrations of areole types).

Longitudinal striations, which run parallel to the mid-vein, are present in *Couratari stellata, C. macrosperma,* and *Lecythis rosea.* The striations are probably pressure marks caused by the way the leaf is folded in the bud. The mesophyll of leaves of *Asteranthos brasiliensis* is penetrated by a unique network of sclereids (Lignier, 1890).

Weberling (1957), Pittier (1927), and Mori (1974) have reported minute, caducous stipules in species of *Asteranthos, Gustavia, Cariniana, Couroupita, Lecythis, Eschweilera,* and *Couratari.* However, stipules are never present in mature leaves and never leave an easily detectable scar. Mori (1974) has pointed out that stipules are most easily observed in species of *Gustavia* on the cataphylls and first leaves of seedlings.

Leaf size is sometimes useful in placing a collection of Lecythidaceae to genus for all species of *Grias* and many, but not all, species of *Gustavia* have very large leaves (up to 170 × 50 cm) clustered at the ends of the branches (Figs 1A, B). Nevertheless, there are no species of Lecythidaceae with really small leaves, i e all fall into the mesophyll, macrophyll, or megaphyll size classes of Raunkiaer (1934).

Leaf surfaces are glabrous in most species, but in a few species *Gustavia angustifolia* (Fig 3H), *G. petiolata, G. grandibracteata* (Fig 3C), *G. pubescens,* and *Grias multinervia* (Fig 3M) they are pubescent. The abaxial leaf surface of species of *Grias* often has reddish-brown punctae which probably are the scars of caducous papillae or epidermal hairs. Likewise, the margins of almost all species of neotropical Lecythidaceae have scars left by caducous hairs.

As viewed with the SEM, the cuticle of the abaxial surface is more or less smooth in the genera treated in this revision (Fig 3). In contrast, it is distinctly papillate, in some species of *Lecythis* and in *Bertholletia excelsa* (Fig 4). The stomates are often sunken within stomatal crypts and/or surrounded by papillae, both apparently adaptations for reducing evapotranspiration (Figs 3, 4).

Lignier (1890) was the first to stress the value of stem and petiole anatomy in the subfamilial classification of Lecythidaceae. The presence of cortical bundles helps to characterize the family, and their arrangement (inversely vs normally oriented) is a useful diagnostic character at the subfamilial level. The cortical bundles are inversely oriented (i e xylem outside, phloem inside) in the subfamilies Planchonioideae and Foetidioideae and normally oriented (i e phloem outside, xylem inside) in the Napoleonaeoideae and Lecythidoideae (Lignier, 1890; see Table 2 in Mori, 1974). There are numerous cortical bundles in the Planchonioideae, Foetidioideae, and Lecythidoideae and only 4 in the Napoleonaeoideae. A comparative anatomical study of the Lecythidaceae and the 36 other families of dicotyledons with cortical bundles (Metcalfe and Chalk, 1957) may shed light on the still unsolved phylogenetic position of the family.

Variation in the number and position of vascular traces in the petiole is also useful in classification at the subfamilial level (Lignier, 1890). In order to minimize positional differences our sections were made near the junction of the petiole and the blade. However, we found little change in the cross-sectional arrangement of the vascular traces throughout the length of the petiole. The most striking difference in petioles is the reduced number of traces in *Napoleonaea.* Here, there is one major bundle and two minor adaxial bundles see (Fig. 10B in Lignier, 1890). In contrast, the petioles of species of other genera have numerous traces (Figs 5, 6, 7). Because we have not yet studied petioles of species of Planchonioideae, we are not able to confirm Lignier's (1890) report that the traces of the Planchonioideae are inversely oriented whereas those of the Napoleonaeoideae and Lecythidoideae are normally oriented. Lignier also noted that the arrangement of the traces of *Gustavia* and *Grias* differs from those of the remaining New World genera. Species of *Gustavia* and *Grias* have a principal arc of traces with secondary traces adaxially and abaxially to it (Fig 6). In contrast, species of the remaining

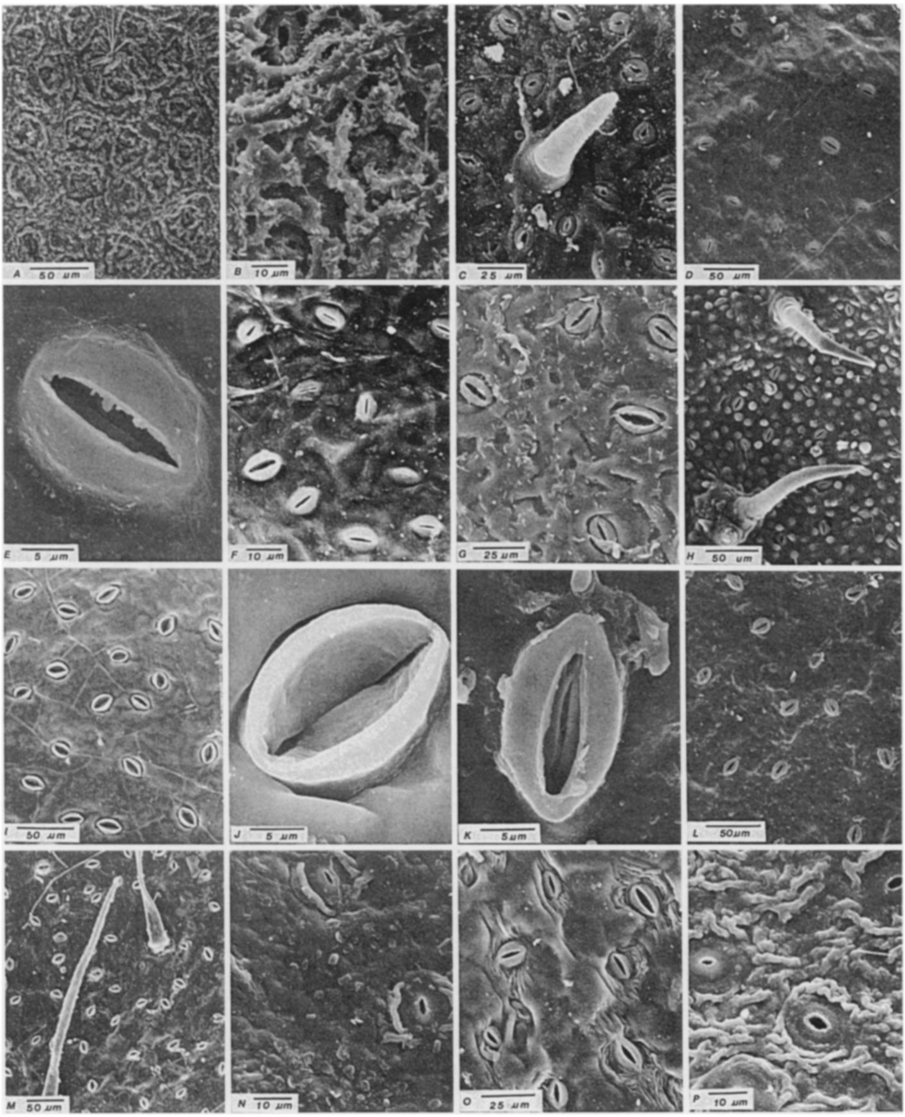


FIG 3. SEM photomicrographs of the abaxial leaf surface of selected species of *Asteranthos, Gustavia, Grias, Allantoma,* and *Cariniana.* A-B, *Asteranthos brasiliensis (Prance et al 15481);* C, *Gustavia grandibracteata (Gentry 7457);* D-E, *G. monocaulis (Mori & Kallunki 5598);* F, *G. superba (Mori et al 6837);* G, *G. dubia (Mori 7704);* H, *G. angustifolia (Rose & Rose 23503);* I-J, *Grias neuberthii (Croat 18331);* K-L, *G. cauliflora (Mori & Kallunki 5404);* M, *G. multinervia (Cuatrecasas 14208);* N, *Allantoma lineata (Ramos P20232);* O, *Cariniana estrellensis (Irwin et al 8885);* P, *C. pauciramosa (Prance et al 17516).* All prepared from dried specimens.

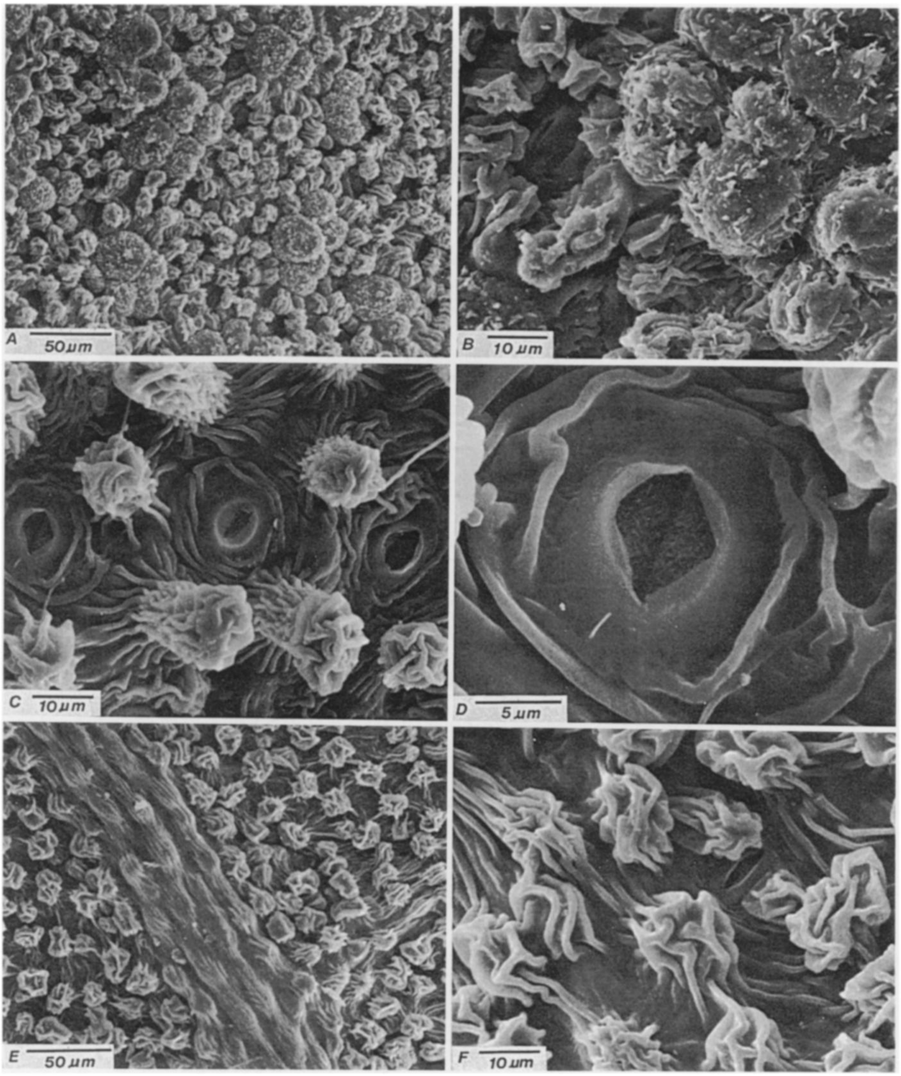


FIG 4. SEM photomicrographs of the abaxial leaf surface of selected species of *Bertholletia* and *Lecythis*. A-B, *Bertholletia excelsa (Ramos* P*20205);* C-D, *Lecythis* sp *(Oldeman 2245);* E-F, *Lecythis poiteaui (Oldeman B893).* All prepared from dried specimens.

genera have only the principal arc and adaxial traces, i e there are no abaxial traces (Fig 7). Most of our observations confirm those of Lignier (1890). However, we have also detected a major dichotomy in petiole structure within

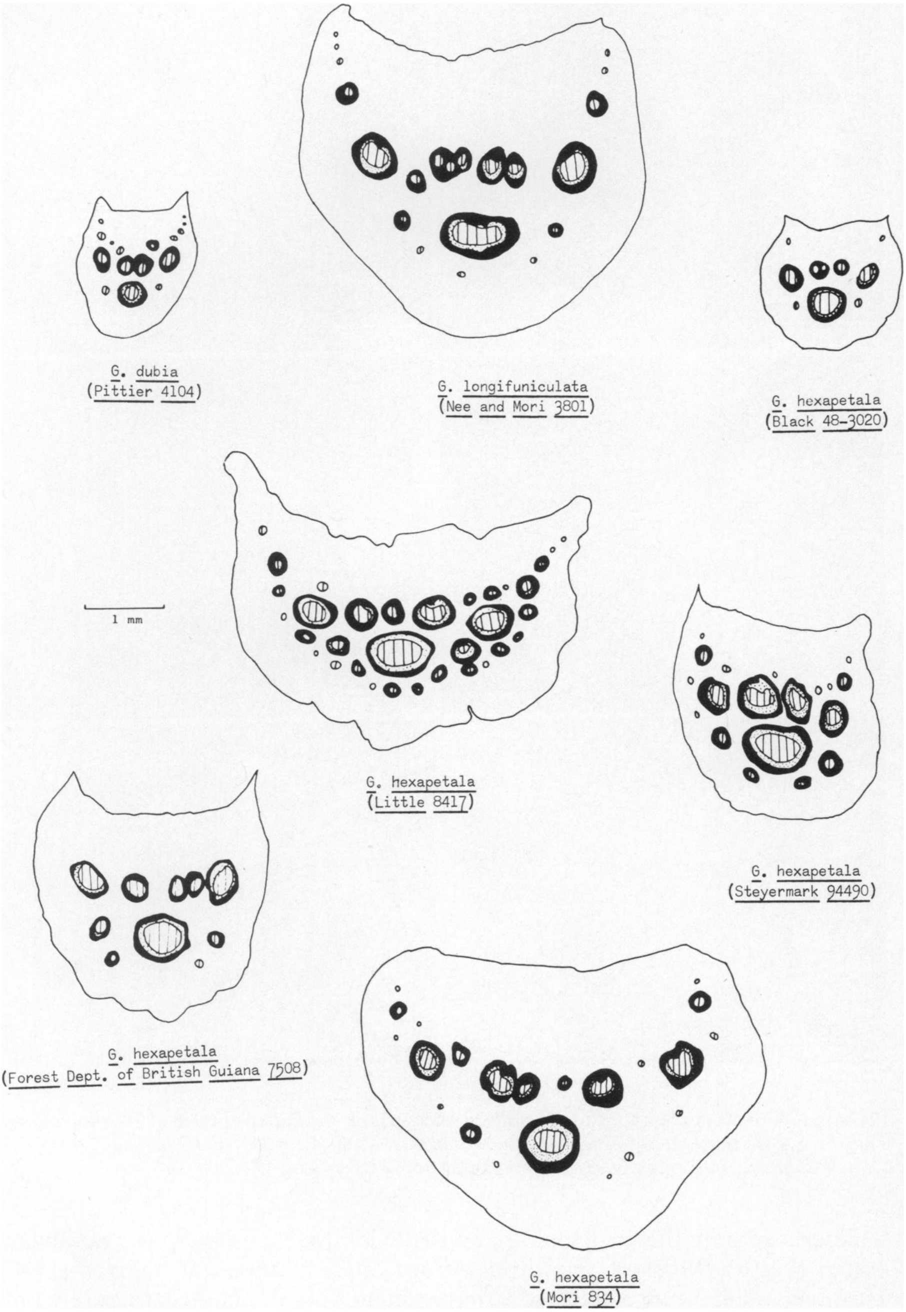


FIG 5. Petiole cross section of species of *Gustavia* section *Hexapetala*. Sections made near junction of the petiole and blade, solid = sclerenchyma, stippled = phloem; vertical lines = xylem.

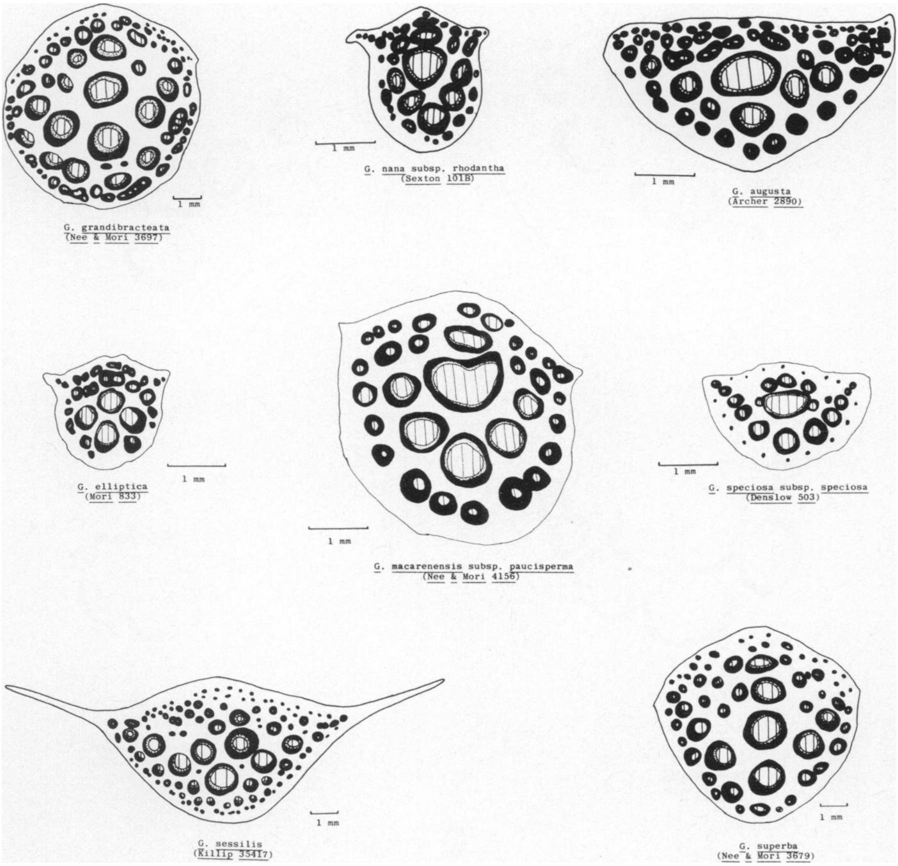
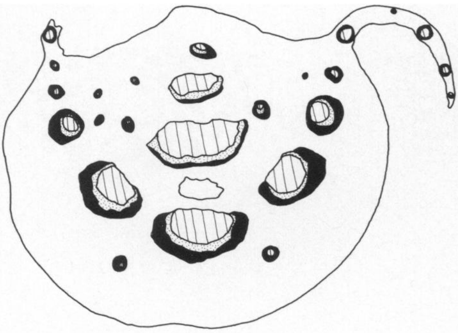


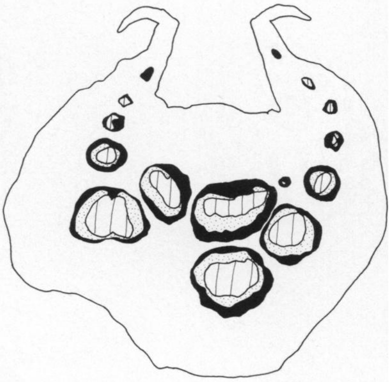
FIG 6. Petiole cross section of selected species of *Gustavia*. Sections made near junction of the petiole and blade, solid = sclerenchyma; stippled = phloem; vertical lines = xylem.

Gustavia. Most species of *Gustavia* are as Lignier described, i e with a principal trace or group of traces and both adaxial and abaxial traces. In addition, the bundles penetrate the entire cross section of the petiole (Fig 6). The exception to this structure is found in species of *Gustavia* section *Hexapetala*. Here, there is one principal trace with the secondary traces mostly adaxial to it, and the traces do not occupy the entire cross sectional area of the petiole (Fig 5). In fact, the adaxial part of the petiole is occupied by a characteristic region of parenchyma, the cells of which are arranged in vertical columns. The structure of the petiole of species of *Gustavia* section *Hexapetala* more closely resembles that of species of genera other than *Gustavia* and *Grias*.

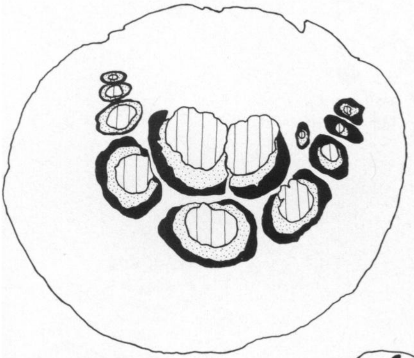
Lignier (1890) includes a large canal in his illustrations of the petiole cross section of *Couratari guianensis* (see his Fig 4, page 348). Our sections of *Couroupita*



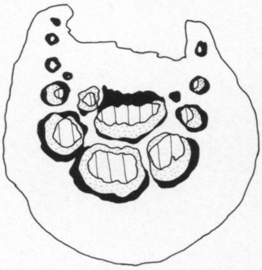
Couroupita guianensis
unvouchered



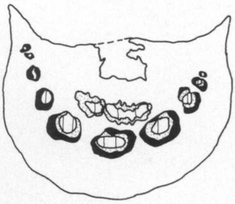
Corythophora sp.
Mori 8783



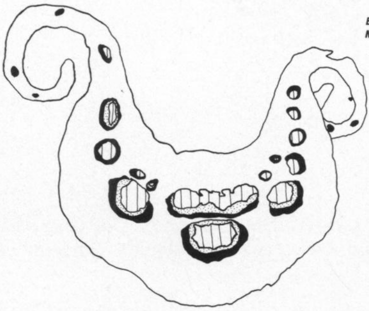
Eschweilera sp.
unvouchered



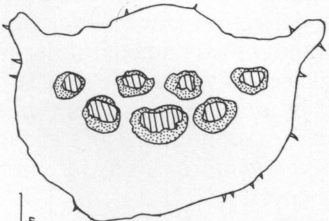
Eschweilera odora
Mori & Bolten 8727



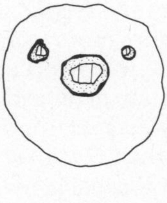
Lecythis sp.
Mori 8896



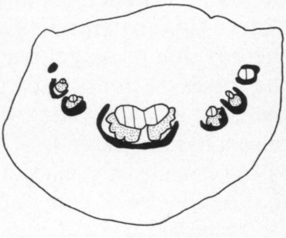
Couratari stellata
Prance 24298



Cariniana legalis
Prance 23705



Napoleonaea sp.
unvouchered



Asteranthos brasiliensis
Osmarino 7

guianensis (Fig 7) show the same structure illustrated by Lignier for *Couratari guianensis.* Because we have not observed canals in species of *Couratari* and because of the similarity of our section of *Couroupita guianensis* to Lignier's illustration of *Couratari guianensis* we conclude that Lignier's illustration was actually of *Couroupita guianensis.*

The following key summarizes our knowledge of the stem and petiole anatomy of Lecythidaceae. It illustrates the utility of anatomical features for classification of the family and at the same time points out the incompleteness of our observations.

Key to Taxa of Lecythidaceae Based on Stem and Petiole Anatomy

1\. Cortical bundles 4; petiole with one principal trace and two smaller adaxial traces.
Napoleonaea.
1\. Cortical bundles more than 4; petiole with numerous traces.
  2\. Cortical bundles with xylem outside, phloem inside (inversely oriented).
  Planchonioideae and *Foetidioideae.*
  2\. Cortical bundles with phloem outside, xylem inside (normally oriented).
  Lecythidoideae, *Asteranthos,* and *Crateranthus.*
    3\. Cross section of petiole with a principal arc or trace and both adaxial and abaxial traces, the traces occupying nearly the entire cross section of the petiole (Fig 6).
    Grias spp and all *Gustavia* spp except spp of section *Hexapetala.*
    3\. Cross section of petiole with a principal arc or trace and only adaxial traces, the traces not occupying the entire cross section of the petiole (Fig 5).
    Gustavia section *Hexapetala* and spp of remaining genera.
      4\. Cross section of petiole with an obvious canal.
      Couroupita guianensis and some species of *Lecythis.*
      4\. Cross section of petiole without canals. All remaining species examined.

3. Inflorescences

In this monograph the flower-bearing stalk is considered the pedicel. It is always subtended by a *bract* and bears two *bracteoles* variously inserted along its length. The bract and bracteoles completely enclose the young bud and probably function to protect it from water loss and/or physical injury. The bracts and bracteoles are variously modified, being large and persistent in some species and small and caducous in others.

The point at which the pedicel dehisces from the inflorescence is the *articulation.* In some species the articulation is at the junction of the pedicel with a branch of the inflorescence, and in other species it is above the point of attachment, i e on the pedicel itself. In the latter case the pedicel is divided into two segments, the *supra-articular* region, i e the segment that falls with the flower or fruit, and the *subarticular* region, i e the segment that remains attached to the rachis of the inflorescence. Bracteole position in relation to the articulation is a useful taxonomic character at the generic level. The bracteoles may be inserted above the articulation *(Gustavia, Grias)* or just below the articulation (all other genera).

FIG 7. Petiole cross section of selected species of Lecythidaceae. Sections made near junction of the petiole and blade, solid = sclerenchyma; stippled = phloem; vertical lines = xylem.

In this monograph *peduncle* denotes the region between the base and the first flower of racemose inflorescences or that between the base and the first branch of branched inflorescences.

There are relatively few inflorescence types in the family. We recognize: 1) solitary flowers in the axils of leaves or leaf-like bracts, 2) racemes, 3) fascicles, and 4) panicles. In this treatment we consider all branched inflorescences to be panicles and indicate their complexity by the number of branches. An inflorescence with one order of branching is a raceme, with two orders a once-branched panicle, etc. In the Lecythidaceae, panicles are composed of spicate or racemose branches and usually have two to three orders of branching. Fascicles are clusters of flowers which probably have been derived from racemes via contraction of the rachis.

Inflorescence position is of taxonomic value in the family. The inflorescences are classified as *suprafoliar* if they arise on the upper part of the stem above the leaves, as *axillary* if they arise from the leaf axils, and as *cauline* if they arise from the branches or the trunk. Some caution must be used to determine position because a suprafoliar inflorescence may become a cauline infructescence after continued extension growth of the stem apex (see comments on *Gustavia grandibracteata*). Suprafoliar inflorescences are *terminal* if they terminate extension growth and *subterminal* if extension growth continues from the terminal bud after flowering.

The inflorescences of *Couroupita* spp and *Grias neuberthii* continue to elongate over many flowering periods. This *indeterminate* inflorescence growth contrasts with the more usual condition in the family (and in other Angiosperms) in which an inflorescence produces flowers for a single flowering period (i e determinate growth).

The density of inflorescences and inflorescence position in the canopy have evolved in response to the selective pressures of specific pollinators. For example, mass-flowering species, such as *Bertholletia excelsa, Lecythis idatimon,* and *Couratari* spp, are canopy trees with many inflorescences produced at the periphery of the crown. In some mass-flowering species (e g *Couratari guianensis, C. oligantha*), the flowers are even more attractive to pollinators because they appear when the tree is leafless. In contrast, steady-state flowering species, such as *Eschweilera grandiflora,* are understory trees which produce fewer inflorescences spaced throughout the crown. Mass-flowering species are pollinated by a greater variety of bees than are steady-state flowers; the latter are visited mainly by Euglossine bees. A more specific example of inflorescence adaptation to a specific pollinator is that of *Lecythis poiteaui* and its bat pollinators. This species produces its inflorescences in elongated racemes which project above the crown and, consequently are free from the foliage and more accessible to bats.

In zygomorphic-flowered species the position of the inflorescence and orientation of the flower generally place the androecial hood in position to serve as a landing platform. For example, in *Couroupita subsessilis,* a species with a long racemose inflorescence, the inflorescence emerges from the trunk at about a 45° angle, but the flowering apex of the raceme curves upward, placing the hood at the proper angle to serve as a landing platform (Fig 10C).

The hood of *Lecythis idatimon* is brought into position to serve as a landing platform by the flower's strongly curved pedicel (Fig 12H-J).

Flowering strategies and floral position in relation to pollinators are discussed in more detail in the section on floral biology (Chapter VIII).

The generic descriptions below summarize our knowledge of the inflorescences of all genera of New World Lecythidaceae and includes a discussion of the evolutionary trends of each genus.

Asteranthos

The single species of this genus, *A. brasiliensis,* has solitary, axillary flowers (Fig 40). The pedicel bears two, opposite, unequal bracteoles inserted below the articulation, the bracteoles are in turn subtended by several caducous bracts. The first bract below the bracteoles is the bract of the extant flower, and the remaining vestigial bracts represent the bracts of aborted flowers. The area between the bract of the extant flower and the stem is about 5 mm long and represents the peduncle. We interpret the solitary flower of *Asteranthos* as being derived from a more complex inflorescence that has contracted and lost all but one flower.

Gustavia

The pedicels of all species of *Gustavia* are subtended by a bract and bear two bracteoles above the point of articulation. The inflorescences are of two types, solitary and racemose. However, solitary inflorescences have two origins. For example, the solitary flowers of *G. grandibracteata* are single flowers subtended by leaf-like bracts, whereas those of *G. poeppigiana* arise from a reduced rachis which bears the vestigial bracts of aborted flowers.

Each year in *G. grandibracteata* a fertile stem produces sequentially clusters of: 1) tightly compacted, large, petiolate leaves; 2) sessile, sterile, foliaceous bracts; and 3) solitary flowers each subtended by a leaf-like bract (Fig 42C). After flowering the terminal bud resumes vegetative growth, producing the next flush of leaves. Consequently, the developing fruits assume a lateral position. In this species there is no separation of vegetative and reproductive axes. In addition, the subtending floral bracts and pedicellary bracteoles are larger and more leaf-like than in any other species of Lecythidaceae. Therefore, we consider this type inflorescence to be the most primitive of the family.

From this primitive type, evolution of the inflorescence of *Gustavia* has involved: 1) loss of the sterile, foliaceous bracts subtending the flower-producing region of the stem; 2) differentiation and reduction in size of the floral bracts and pedicellary bracteoles; 3) separation of the vegetative and reproductive axes; 4) transfer of position from subterminal, to axillary, to cauline; 5) elongation or contraction of the rachis, and 6) reduction or increase in numbers of flowers.

In most other species of *Gustavia,* the leaf-like, sterile bracts present in *G. grandibracteata* are missing, and the bracts and bracteoles are reduced to small scales. *Gustavia monocaulis* alternates vegetative and reproductive phases on the same axis as does *G. grandibracteata,* but all other species have more or less well defined inflorescences which terminate growth of their axes. The racemose inflorescences of most species arise from leaf axils or from the branches or trunk in the axils of leaf scars. Consequently, inflorescence position in the genus may be suprafoliar (both terminal and subterminal), axillary, or cauline.

The racemes of *Gustavia* may be relatively short as in *G. augusta* or greatly elongated as in *G. flagellata,* which has inflorescences to 105 cm long. In *G. poeppigiana,* the rachis is so contracted that only one or infrequently two, flowers are produced.

Grias

The pedicels of all species of *Grias* are subtended by a bract. The bracteoles may be strongly developed *(G. neuberthii)* or reduced to very minute scales (all other species) and in all species are inserted above the point of articulation. In this genus the inflorescences are either fascicles or racemes. The fascicles arise from the leaf axils *(G. colombiana)* or from the axils of leaf scars on the branches or trunk *(G. colombiana, G. cauliflora).* In all species with racemes the inflorescences are cauliflorous. Fascicles and racemes may be produced from the same position on the trunk year after year and, thus, cause warty or knobby outgrowths at that position.

Grias neuberthii, considered by us to be the species most closely related to *Gustavia,* has well developed, keeled bracteoles. All other species have very reduced, inconspicuous bracteoles. The racemes of this species may continue to produce flowers through several growing seasons and, therefore are considered to have indeterminate growth.

Allantoma

The single species in this genus, *A. lineata,* has small, membranous and scale-like bracts and bracteoles which arise below the articulation. Both are caducous and can be observed only below the youngest flower buds. The only difference between the bract and the bracteoles is the larger size of the former. The inflorescence is a raceme or more frequently a once-branched panicle with the secondary branches arising from near the base of the primary branch. The inflorescences are suprafoliar in position (Fig 62).

Cariniana

The bracts and bracteoles are small and caducous, and can be seen below only the smallest flower buds. The pedicel may be absent (e g *C. decandra*) or relatively long and slender (e g *C. estrellensis*). In all species the articulation occurs at the junction of the pedicel and rachis of the inflorescence, and the bracteoles are inserted directly below it. The inflorescences are racemes *(C.*

estrellensis) or in all other species panicles with two to three orders of branching. In most species the inflorescences are suprafoliar, but those of *C. estrellensis* arise from the branches and occasionally axillary inflorescences are found in those species with predominantly suprafoliar inflorescences.

Couroupita

In this genus articulation of the flower is on the pedicel immediately below the hypanthium, and when the flower falls it leaves part of the pedicel attached to the rachis of the inflorescence. In all previous genera *(Asteranthos, Gustavia, Grias, Allantoma, Cariniana)* the articulation is at the junction of the pedicel and the rachis of the inflorescence. In *Couroupita* the bract is inserted at the base of the pedicel and the bracteoles are inserted just below the articulation. The inflorescence of *Couroupita* is racemose and arises from the trunk or large branches. An inflorescence-bearing region of the trunk or branches often remains meristematic through many growing seasons and becomes warty or knobby because of persistent inflorescence bases. In addition, a given raceme has indeterminate growth and may produce flowers through many growing seasons. We have also observed that some racemes produce normal leaves between flowering periods.

Corythophora

In this genus, articulation occurs above the point of attachment of the pedicel to the rachis of the inflorescence and directly below the hypanthium. Therefore the subarticular region accounts for most of the pedicel's length. Because the whole pedicel is very short, the flowers of *Corythophora* are subsessile. The inflorescences are panicles with two to three orders of branching and are usually suprafoliar.

Lecythis

The articulation of the pedicel in this genus is variable. In some species articulation occurs at the junction of the pedicel with the rachis of the inflorescence (e g *L. poiteaui, L. pisonis*) and in others above the point of attachment (e g *L. minor, L. idatimon*). The inflorescences are racemose (e g *L. pisonis. L. poiteaui*) or panicles with two or three orders of branching (e g *L. minor, L. idatimon*). The inflorescences in most species are suprafoliar but in others are axillary or cauline (e g *L. pisonis*).

Bertholletia

The single species of this genus, *B. excelsa,* has pedicels which articulate directly below the hypanthium. The whole pedicel is very short or nearly absent and, therefore, the flowers are subsessile. The inflorescences are suprafoliar panicles with two or three orders of branching.

Eschweilera

In this genus the articulation of the pedicel occurs either at or above the junction of the pedicel with the branch of the inflorescence. In some species the flowers are sessile (e g *Eschweilera gigantea, E. congestiflora*), while in others the pedicels are well developed *(E. grandiflora).* The inflorescences are racemes or panicles with two to three orders of branching and may be suprafoliar, axillary, or infrequently cauline.

Couratari

The articulation of the pedicel occurs at or slightly above the junction of the pedicel with the rachis of the inflorescence. All species have relatively long, slender pedicels. The inflorescences are racemes or panicles with two to three orders of branching and are suprafoliar. Several species (e g *C. guianensis, C. oligantha*) flower in a leafless condition.

The inflorescences of Lecythidaceae exhibit several interesting evolutionary trends. The most primitive inflorescences are found in *Gustavia,* especially in *G. grandibracteata.* Here, the flowers are solitary in the axils of leaf-like bracts, the pedicel is articulate at its junction with the stem, the bracteoles are inserted above the articulation, and there is no differentiation between vegetative and reproductive axes. *Gustavia* is the only genus of New World Lecythidaceae to have species *(G. grandibracteata* and *G. monocaulis)* with undifferentiated vegetative and reproductive axes. In other species of *Gustavia* (e g *G. augusta, G. superba*), the bracts and bracteoles are greatly reduced and the reproductive and vegetative axes are differentiated. The position of the articulation and the position of the bracteoles in relation to the articulation are the same in all species of *Gustavia.*

The inflorescence of *Grias neuberthii* is identical to that of a racemose, cauliflorous *Gustavia* species. Indeed, in all respects *G. neuberthii* is more closely related to *Gustavia* than is any other species of *Grias.* Other species of *Grias* (e g *G. cauliflora, G. colombiana*) have very reduced bracteoles and have fasciculate inflorescences. Nevertheless, the position of the articulation and of the bracteoles in relation to the articulation are the same in *Gustavia* and *Grias.*

In genera other than *Gustavia* and *Grias,* there is a definite trend for the articulation of the pedicel to be on the pedicel itself instead of at the base. Consequently, when the flower falls the subarticular region of the pedicel remains as a stub on the rachis of the inflorescence. With the change in position of the articulation there is also a change in position of the bracteoles in relation to the articulation. In all genera, except *Gustavia* and *Grias,* the bracteoles are inserted just below the articulation rather than above it. For example, in *Couroupita guianensis* articulation occurs on the pedicel itself, and the bracteoles are inserted just below the articulation. In genera other than *Gustavia* and *Grias,* articulation occurs above the base of the pedicel in most species and the bracteoles are inserted below the articulation in all species.

Another trend in inflorescence evolution is increased branching. The flowers of all species of *Gustavia, Grias,* and *Couroupita* are either solitary or in simple racemes. In the remaining genera, branched inflorescences, which we term panicles, are common.

Cauliflory is common in *Gustavia, Grias,* and *Couroupita* but absent in all other genera except three of ca 100 species of *Eschweilera.* In all genera except *Gustavia, Grias* and *Couroupita* the most common inflorescence position is terminal.

In summary, general inflorescence trends in the New World Lecythidaceae are: 1) change of pedicel articulation from its base to above its base, 2) change of bracteole insertion from above to below the articulation, 3) increase in branching, and 4) change in position from cauline to terminal.

4. Flowers

The flowers of Lecythidaceae subfamily Lecythidoideae are characterized by: 1) many stamens fused at their bases into a connate ring which is either symmetrical or asymmetrical, and 2) the inferior to half-inferior ovaries.

The calyx is either entire or distinctly lobed. The calyces of *Asteranthos,* and some species of *Gustavia,* and *Grias* are entire whereas those of the remaining genera are distinctly lobed. The calyces of species of *Gustavia* range from entire to distinctly 4- or 6-lobed. All species of Lecythidaceae with zygomorphic flowers have 6 calyx lobes, except *Bertholletia excelsa* which has 2. The actinomorphic flowered, monotypic genus *Allantoma (A. lineata)* has a 5-lobed calyx. In some species of *Grias* and in *Bertholletia excelsa,* the calyces either enclose or nearly enclose the bud. Among these species the calyces of *Grias multinervia, G. colombiana, G. peruviana,* (Fig 11L) and *G. haughtii* completely enclose the bud and open circumscissilely or irregularly, whereas the calyx of *G. cauliflora* has a small apical pore, and that of *B. excelsa* a vertical slit. Only one species of *Grias, G. neuberthii* (Fig 11K), has 4 separate calyx lobes which do not enclose the bud.

The petals of New World Lecythidaceae offer few taxonomic characters. Only petal number has diagnostic value and that to a limited degree. *Asteranthos brasiliensis* lacks petals and has a petaloid corona instead. *Grias* species have 4 petals, *Allantoma lineata* has 5 petals, and *Gustavia* species generally have 6 or 8 petals. All species with zygomorphic androecia have 6 petals which are often arranged to direct pollinators to the anterior end of the flowers.

Floral evolution in the Lecythidoideae has occurred, for the most part, in the androecium. Mirbel (1815) originally coined the term androphorum for what is now generally called the androecium of flowering plants. In 1874, Miers restricted Mirbel's use of androphorum to that "peculiar system of male organs found only in the Lecythidaceae." Since then androphorum or androphore has been used in most treatments of New World Lecythidaceae (Knuth, 1939b; Pittier, 1912, 1927; Macbride, 1941; Woodson, 1958; Mori, 1968; Prance and Mori, 1977; Mori et al, 1978). The androecium readily serves to distinguish the zygomorphic flowered genera of Lecythidaceae from all other plant families.

Monteiro-Scanavacca (1975a), in a study of the vascular supply of the androecium of New World Lecythidaceae, does not use the term androphore. She points out that the term gynophore is used for an elongation of the floral axis which bears the gynoecium. Androphore, she adds, should be used for a similar structure bearing the androecium. Examples of gynophores are found in the Simaroubaceae and in all species of *Scleria* and most species of *Fimbristylis* (Koyama 1965, 1971, pers. comm.). The Passifloraceae and Capparaceae are well known examples of families with true androgynophores. Monteiro-Scanavacca's studies (1975a) have demonstrated that the unique androecium of the New World Lecythidaceae is the product of staminal fusion. Therefore, the term androphore can not be applied to the androecium of the Lecythidaceae in the same sense as gynophore and androgynophore are used in other families.

As used by previous students (Miers, 1874; Knuth, 1939b; Pittier, 1912, 1927; Macbride, 1941; Woodson and Schery, 1958; Mori, 1968; Prance and Mori, 1977), the term androphore is equivalent to androecium. In this monograph we use androecium rather than androphore to be more consistent with the use of gynophore and androgynophore in other families. This term also indicates the staminal origin of the entire organ of Lecythidaceae, whereas use of the term androphore incorrectly implies that at least part of the male organ is extrastaminal in origin.

The androecium is actinomorphic in *Asteranthos, Gustavia, Grias,* and *Allantoma* and zygomorphic in *Cariniana, Couroupita, Corythophora, Lecythis, Bertholletia, Eschweilera,* and *Couratari.* The actinomorphic androecium consists of a fused basal portion called the staminal ring and of free stamens, which arise either from the upper margin of the ring *(Gustavia, Grias)* or from the inner surface of the ring *(Allantoma).* The androecium of *Cariniana* is only slightly prolonged on one side and therefore falls between the actinomorphic and highly zygomorphic genera. We include *Cariniana* with the actinomorphic genera in this volume of the monograph because its zygomorphy is slight compared to that of the remaining genera.

The actinomorphic flowers of *Asteranthos brasiliensis,* which belongs to subfamily Napoleonaeoideae, are structurally different from those of the other actinomorphic-flowered New World genera. It is discussed in more detail in the Systematic Treatment of the genus.

Androecial structure of the zygomorphic-flowered genera is more complicated than that of the actinomorphic-flowered genera. Miers (1874, p 159) described the androecium of *Couroupita* as follows:

> "The androphorum is large, with a shallow, cup-shaped annular ring at its base, covered by numerous short appendages, each bearing a stamen; but this ring does not expand equally all around as in *Gustavia;* on the contrary, its enlargement takes place on one side only, under the form of a ligular fleshy plate, twice the length and as broad as the basal staminiferous ring, bare between its parallel margins, coiling gradually inwards, and considerably at its extremity, where it forms an inverted globular hood, concealing the ovary and basal ring; the interior of this hood is densely echinated by numerous subterete appendages, truncated at their summit, where each bears a stamen, consisting of a short thread-like filament, supporting a small anther of 2 collateral oval cells, bursting outwardly and longitudinally. The staminiferous appendages of the basal ring differ from the others only in being much shorter."

Miers' (1874, p 163) description of *Lecythis* further illustrates the structure of the androecium of zygomorphic-flowered Lecythidaceae:

> . . . ". . . the androphorum is large and conspicuous, attached to the claws of the petals and to the disk by its basal annular ring, which is densely covered with short staminif-

> erous appendages; it is expanded on one side into an incurving bare ligula, terminating in an inverted hood, similar to that of *Bertholletia,* and, in like manner, densely echinated with innumerable imbricated appendages, which are terete, bearing in all the lower series, on their clavated summits, each a fertile stamen; but the upper ones longer, incurved, are mostly bare of stamens; the stamens consist of a short slender filament, supporting a small anther, formed of 2 oval, collateral cells, without connective, which burst along the margin by a longitudinal suture, when they expand into 2 parallel plates."

The androecium of the zygomorphic-flowered species can almost always be divided into the following regions (Fig 8):

1. the staminal ring;
2. the ligule, a stamen-free area between the staminal ring and the hood, and;
3. the hood and associated appendages, the latter with or without anthers.

The staminal ring may possess as many as 1000 *(Lecythis poiteaui)* or as few as 10 *(Couratari oblongifolia)* fertile stamens. Although the ligule is usually free of stamens, in one species *(Couroupita darienensis),* fertile stamens are continuous between the staminal ring and the hood. As Eyma (1932) has pointed out, the hood exhibits remarkable variation. It may be essentially flat as in *L. alba, L. idatimon* (Fig 12H-J) and *L. pisonis* (Fig 9), dorsiventrally expanded as in *L. corrugata* and *Corythophora* spp (Figs 9, 12M), coiled inwards once as in *Eschweilera collina* (Fig 9), coiled inwards twice as in *E. longipes* (Fig 9), or coiled inwards with an outwardly extended flap at the apex of the coil as in all species of *Couratari* (Figs 9, 13N-O). The hood appendages may all bear fertile anthers as in *Couroupita* spp. (Figs 9, 12A); the distal appendages may be sterile and the proximal ones may bear anthers as in certain species of *Lecythis* (e g *L. ampla, L. pisonis,* (Fig 9), *L. usitata*); or all the appendages may be sterile as in all species of *Eschweilera* (Figs 9,13F, M). Hood structure is best studied by making a medial section of the androecium using fresh or pickled flowers (fig 9).

Accessibility of pollen and/or nectar to prospective pollinators is determined by the structure of the androecium. In actinomorphic-flowered species with large flowers (*Gustavia* spp), many kinds of insects are able to enter the flower. Species with smaller actinomorphic flowers, such as species of *Grias* and *Allantoma lineata,* are probably visited by smaller insects. In species with zygomorphic flowers, accessibility to the flower is determined by the degree of appression of the hood to the staminal ring. Some species (e g *Couroupita guianensis, L. alba, L. pisonis*) have a space between the hood and staminal ring (Figs 9, 10D, E), whereas other species (*L. corrugata, Corythophora* spp, *Bertholletia excelsa, Eschweilera* spp, *Couratari* spp) have the hood tightly appressed against the staminal ring. (Figs 9, 10F-H). Flowers with actinomorphic androecia or zygomorphic flowers with non-appressed hoods are therefore *open* to non-pollinators as well as pollinators. On the contrary, species with zygomorphic androecia and tightly appressed hoods can be entered only by those insects with enough strength to force the hood open. We consider the latter group of species to have a *closed* androecium.

Flower orientation on the tree is important in interpreting floral structure in relation to pollination systems. Actinomorphic-flowered species have erect flowers which are usually oriented by their upward curving pedicels into a

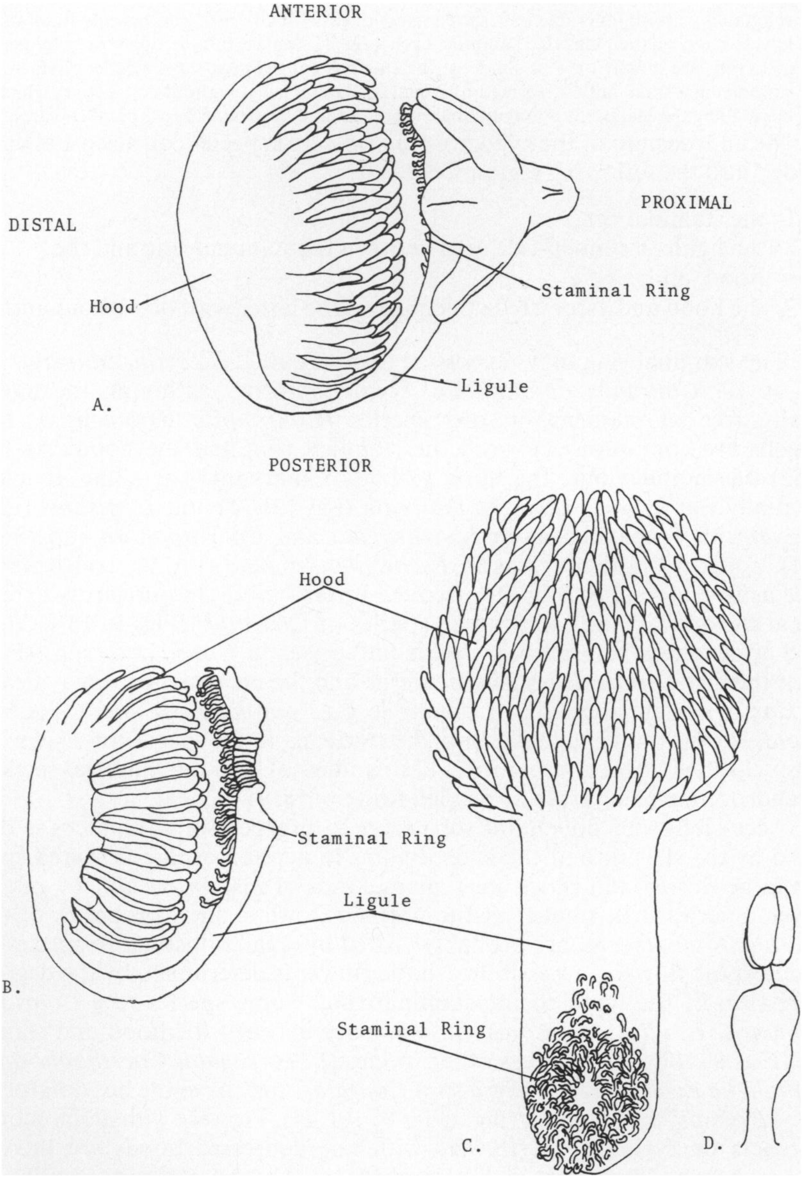


FIG 8. Schematic drawing of the androecium of *Lecythis minor,* illustrating the terminology used for Lecythidaceae with zygomorphic flowers. A, Androecium in natural position at the summit of the ovary (petals removed); B, Medial section of the androecium; C, Androecium artificially opened; D, Close-up of a stamen from the staminal ring, note the constriction at the apex of the filament.

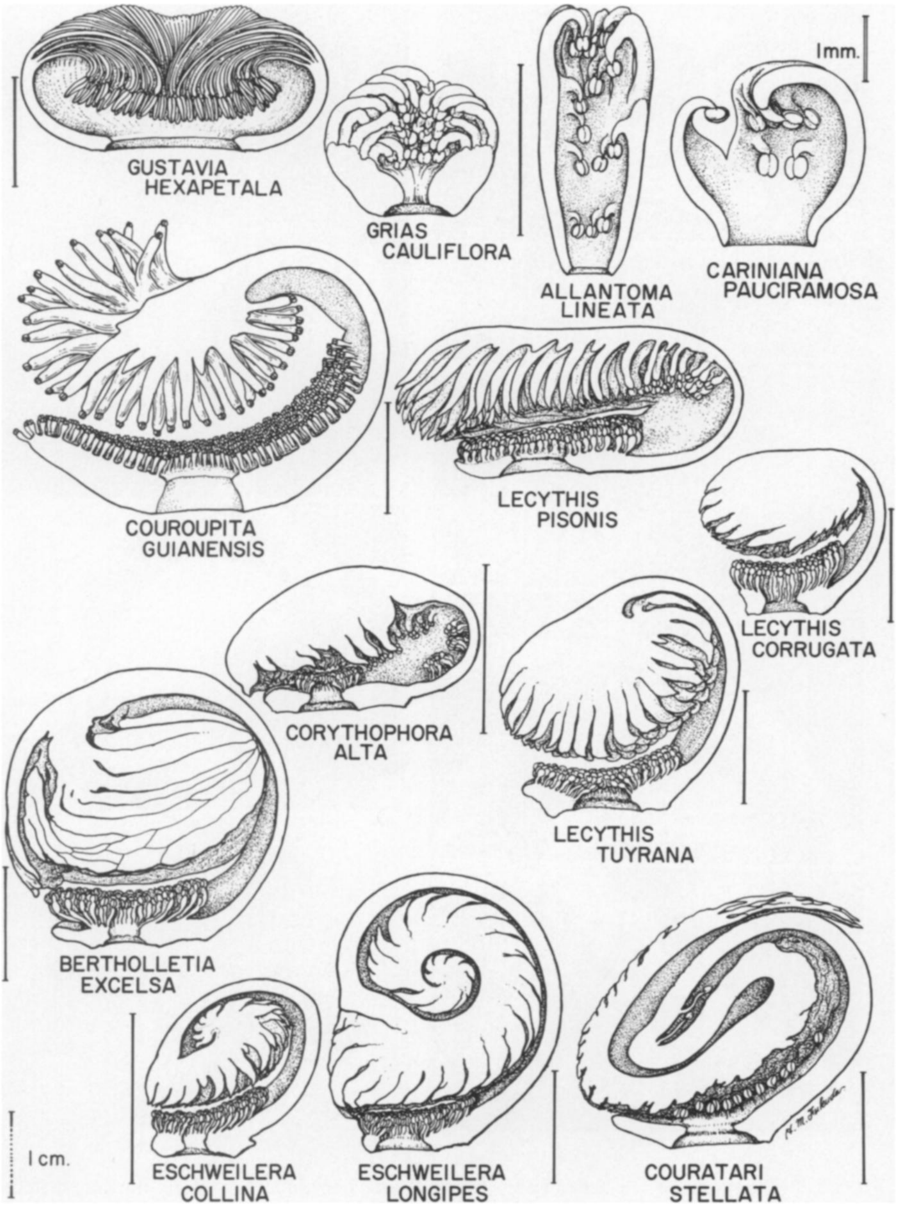


FIG 9. Medial sections of the androecia of selected species of New World Lecythidaceae. Note different degrees of zygomorphy, increase in staminal sterilization, and increasing complexity of the hood.

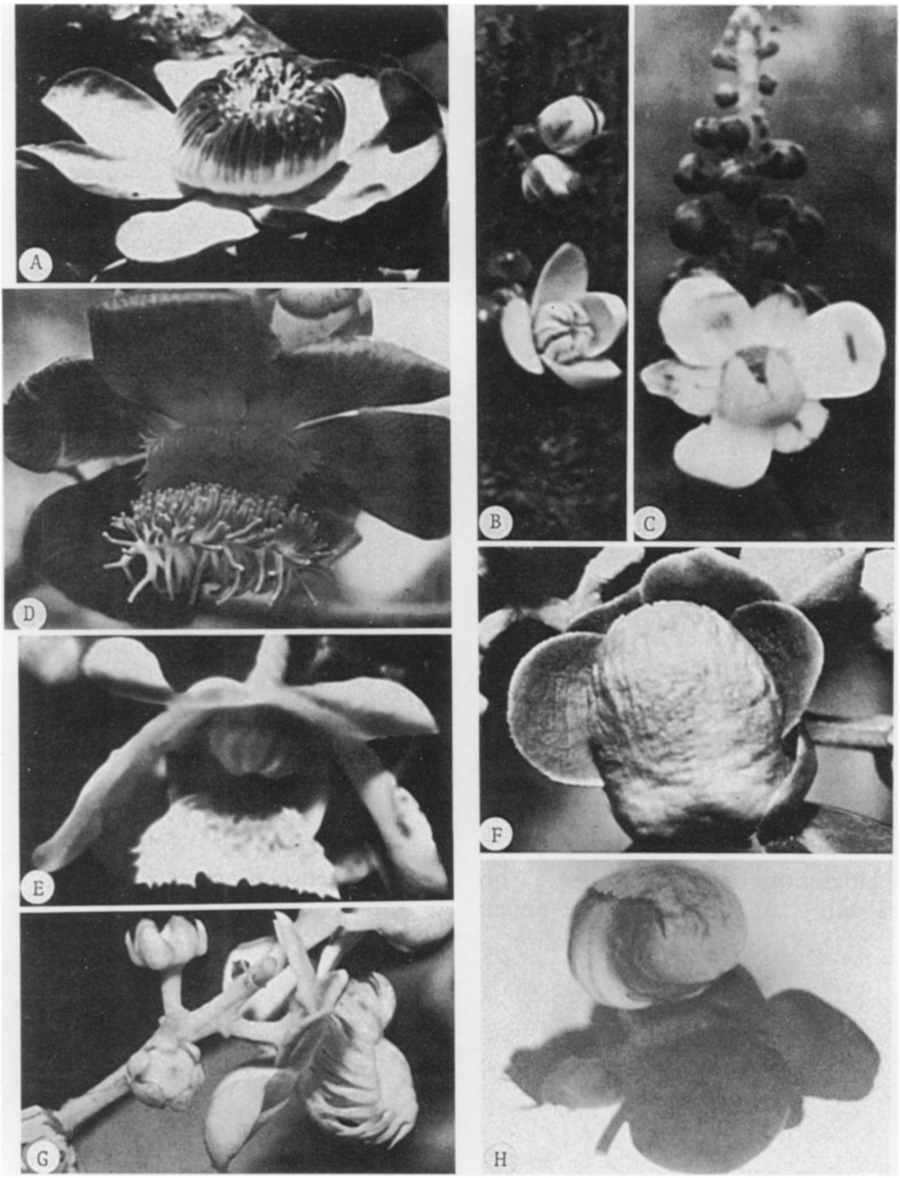


FIG 10. Photographs of selected species of New World Lecythidaceae which illustrate different structures of the androecium. A, *Gustavia superba* (unvouchered), note the actinomorphic androecium with many stamens; B, *Grias neuberthii (Prance 16572),* note the actinomorphic androecium with fewer stamens; C, *Couroupita subsessilis (Prance et al 24382),* note the zygomorphic androecium and the notch in the hood; D, *Couroupita guianensis (Mori & Kallunki 2992),* note the zygomorphic, open androecium and the anthers on the hood appendages; E, *Lecythis alba (Mori & Bolten 8688),* note the zygomorphic, open androecium and the anthers on the

position which makes them more readily accessible to insects (Fig 10A). Zygomorphic-flowered species usually have the hood arranged in such a way that it serves as a landing platform for the pollinators (Fig 10C, F, G). In order to facilitate our discussion of flower orientation and insect visitation we have used the following terms (Fig 8):

Proximal—the bottom of the flower, i e the end attached to the pedicel;
distal—the top of the flower, i e the end furthest removed from the pedicel;
posterior—the ligular side of the flower;
anterior—the side of the flower opposite the ligule, i e the open side of the flower through which the pollinator usually enters;
lateral—the remaining two sides of the flower, these are often blocked to insect entry by the petals.

The hood of the androecium almost always serves as a landing platform for pollinators. Consequently, the anterior end either points upwards so that insects can land on the upper edge (Fig 10F), or the distal end of the flower faces the ground so that the entire inner surface of the hood acts as the landing platform (Fig 10D, E). In species with closed flowers, the hood also acts as a spring which forces the insect's back against the anthers of the staminal ring and, at the same time, against the stigma, which protrudes through the center of the staminal ring.

According to Miers (1874) and Knuth (1939b), the stamens of the Lecythidaceae arise at the tips of swollen structures called stamen appendages. These authors restrict the term filament to the minute constriction between the stamen appendage and the anther (Fig 8D). In his study of the staminal zygomorphy of *Couroupita guianensis,* Thompson (1921, p 3) considered each inner stamen (i e stamen of the staminal ring) to consist of "a short upright clavate and fleshy filament of pale yellow color (text-fig 2, and figs, 7 and 9). Distally it is continued into a short thread-like connective surmounted by a subglobose basifixed anther." Thompson, therefore disagrees with Miers and Knuth, calling the stamen appendage and filament of the other two investigators the filament and connective respectively. Thompson (1921, p 9) further adds that "there is no structural evidence in support of the view taken by Miers regarding these stamens, according to which the anther and the short connective—which has not yet arisen—are alone component parts of the stamen." We also agree with Thompson that the small attenuation subtending the anther is part of the filament. It is a connective between the filament proper and the anther.

Evolution of the gynoecium has occurred in the position of the ovary in relation to the other floral parts, in the number of locules, and in the position of the placenta within the locule. The ovary may be completely inferior, i e truncate at the summit (e g all species of *Gustavia, Grias, Bertholletia,* and

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hood appendages; F, *Lecythis corrugata (Mori & Bolten 8682),* note the zygomorphic, closed androecium; G, *Eschweilera* sp *(Mori & Bolten 8637),* note the zygomorphic, closed androecium; H, *Couratari atrovinosa (Prance et al 23444),* note the zygomorphic, closed androecium with the extra flap at the summit of the hood.

Lecythis) or it may be half-inferior, i e bulged upward at the summit (e g all species of *Couroupita* and many species of *Eschweilera*).

The number of locules per ovary is relatively constant in most genera and is a useful generic character. However, there is some intraspecific variation and therefore several flowers should be examined to determine the most frequent locule number. *Eschweilera* and *Corythophora* are characterized by 2-locular ovaries, *Cariniana* and *Couratari* by 3-locular ovaries, *Grias, Allantoma, Bertholletia,* and *Lecythis* by 4-locular ovaries, and *Couroupita* by 6-locular ovaries. Ovaries of species of *Gustavia* have 4 or 6 locules and those of *Asteranthos* have 5 to 8 locules. *Sapucaya* and *Pachylecythis* have been segregated from *Lecythis* on the basis of locule number. However, we feel that the 6 locules of the former and the 5 locules of the latter are variants on the usual number of 4 in *Lecythis* and therefore these genera do not merit taxonomic recognition.

The ovules may be attached to a swollen placenta at the apex of the septum as in species of *Gustavia,* at the apex of the septum without a swollen placenta as in species of *Grias,* to a bilamellar placenta which runs the length of the septum as in species of *Couroupita,* to a bilamellar placenta at the base of the septum as in *Lecythis pisonis,* or to a placenta at the base of the locule itself as in species of *Eschweilera.*

The following descriptions and illustrations summarize our understanding of the diagnostic floral characteristics of each genus of New World Lecythidaceae.

Asteranthos (Fig 40)

The actinomorphic flowers of *A. brasiliensis* are apetalous. The showy, corolla-like structure is a corona of staminal origin. The calyx is also unique, being a circular rim with a crenate margin and marginal, widely separated, caducous teeth. Most New World Lecythidaceae have lobed calyces or, if the calyces are circular rims, as in some species of *Gustavia* and *Grias,* they are without marginal teeth. The anthers and filaments of *A. brasiliensis* are also diagnostic of the genus. The former are linear with longitudinal dehiscence, and the latter are without the apical constrictions so characteristic of other New World Lecythidaceae. The only other neotropical genus of Lecythidaceae with linear anthers is *Gustavia,* but in this genus anther dehiscence is apical rather than longitudinal. The ovary of *A. brasiliensis* is half-inferior, and the style is terminated by a capitate stigma with 5-8 radiate lobes.

Asteranthos has traditionally been related to *Napoleonaea* because both genera lack petals and possess coronas of staminal origin. Nonetheless, a careful morphological comparison of the flowers of the two genera is needed to determine whether these features result from common ancestry or convergent evolution.

Gustavia (Figs 9, 11A-E)

The flowers of this genus are actinomorphic. The staminal ring is well developed and ranges from 4 to 20 mm high. The stamens are borne on the

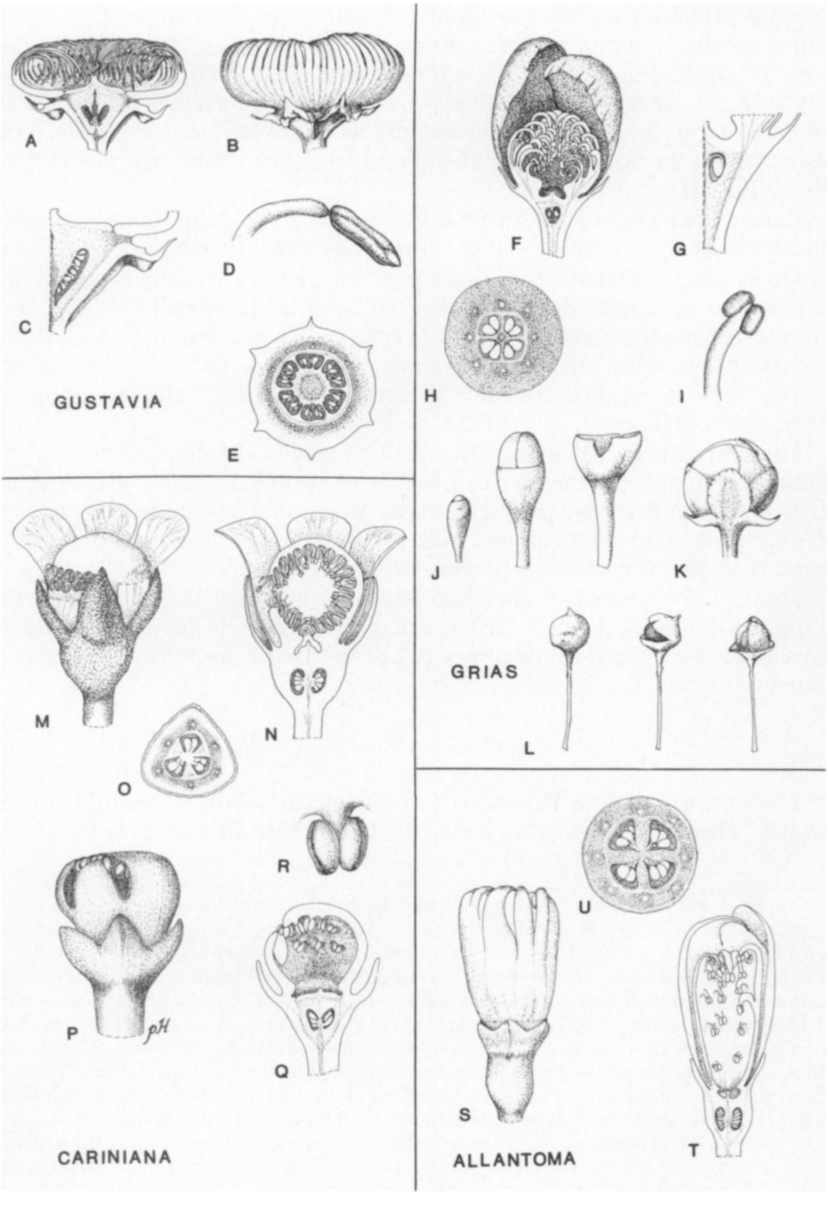

FIG 11. Floral characteristics of *Gustavia, Grias, Cariniana,* and *Allantoma* A-E, *Gustavia hexapetala (Prance 23413);* A, Flower viewed in longitudinal section, the petals have been removed. ×0.7; B, Flower with petals removed, note the symmetrical androecium. ×0.7; C, Longitudinal section of 1/2 of the ovary showing the expanded placenta on the upper part of the septum. ×0.96;

margin of the ring in several concentric series with the stamens of each series becoming progressively shorter from the outside to the inside of the flower. Among species, stamen number ranges from 500 to 1200. Although some species of other genera (e g *Lecythis poiteaui* with 1000 stamens) have this many stamens, species of no other genus of neotropical Lecythidaceae have such consistently high stamen numbers. The connective consists of a narrow constriction at the apex of the filament and bears the linear, apically dehiscent anthers (Fig 11D).

Various features of the calyx are useful for the delimitation of species. The calyces of some species (e g *G. superba* and *G. augusta*) are rim-like with only slight lobes, others (e g *G. romeroi*) have distinct apically rounded lobes, and others (e g *G. pulchra*) have distinct apically pointed lobes. Species of *Gustavia* section *Hexapetala, G. pubescens,* and *G. pulchra* have six lobes and all other species with lobed calyces have four lobes. The lobes of species of *Gustavia* section *Hexapetala* have inverted "Y-shaped" thickenings on the adaxial surfaces (Fig 43).

There appear to be no significant interspecific differences in petal morphology. However, the number of petals is of some taxonomic use. Species of section *Hexapetala* have 6 petals, whereas most other species usually have 8 or infrequently 6. *Gustavia romeroi* has 12 or 18 petals, a condition probably derived from an ancestor with flowers with 6 petals.

The style of species of *Gustavia* is always so short that it appears to be lacking. Placentation is an important diagnostic generic feature of *Gustavia.* The ovules are confined to the upper 1/2 of the locule, and the axile placenta is expanded (Fig 11C).

Grias Figs 9, 11F-L)

The actinomorphic flowers of *Grias* superficially resemble those of *Gustavia.* However, *Grias* flowers differ from those of *Gustavia* by having 4

D, Enlarged view of an anther showing the apical dehiscence characteristic of *Gustavia.* ×5.0; E, Cross section of the ovary showing the 6 locules characteristic of *Gustavia* section *Hexapetala,* species of other sections usually have 4 or 8 locules. ×1.6; F-J, *Grias cauliflora (Nee & Mori 3663);* K, *Grias neuberthii (Gentry 9756);* L, *Grias peruviana (Wurdack 2289).* F, Longitudinal section of the flower with two of the four petals removed. ×0.96; G, Longitudinal section of 1/2 of the ovary showing the pendulous ovule attached toward the apex of the septum. ×1.9; H, Cross section of the ovary showing the 4-locules and few ovules characteristic of *Grias.* ×2.48; I, Close-up of the anther showing how the anther sacs are separated by the filament. ×6.25; J, Bud development of *Grias cauliflora* showing first a young bud with the calyx forming an apical pore, then an older bud with the corolla emerging, and finally a flower after the petals and androecium have fallen. ×0.96; K, Bud of *G. neuberthii* showing the two bracteoles directly under the hypanthium and the presence of 4 well developed calyx lobes. ×0.64; L, Bud development of *Grias peruviana* showing first a young bud completely enclosed by the calyx, then an older bud with the calyptrate calyx beginning to open, and finally a bud after the top of the calyx has fallen. ×0.4; M-O, *Cariniana domestica (Prance 8834);* P-R, *C. pauciramosa (Prance 17516);* M, Lateral view of the flower with 2 petals removed. ×3.8; N, Longitudinal section of the flower. ×3.8; O, Cross section of the ovary. ×6.25; P, Lateral view of the flower with all petals removed. ×4.7; Q, Longitudinal section of the flower with all petals removed. ×4.7; R, Close-up of a stamen. ×15.0; S-U, *Allantoma lineata (Prance 17549);* S, Lateral view of the flower with all the petals removed. ×1.28; T, Longitudinal section of the flower with the petals intact. ×1.28; U, Cross section of the ovary. ×3.12.

instead of usually 6 or 8 petals, less than 215 stamens instead of 500 to 1200, anthers less than 1 mm instead of greater than 2 mm long, anthers dehiscing by longitudinal slits instead of pores, 2-4 ovules/locule instead of 7-93, ovules pendent from a non-expanded placenta instead of more or less horizontal from an expanded placenta. Moreover, the staminal ring and filaments of *Grias* are always more fleshy and the filaments more angular than those of *Gustavia.*

Calyx features provide excellent diagnostic characters in *Grias.* One species, *G. neuberthii,* has a 4-lobed calyx, the lobes of which are distinct in bud (Fig 11K). The remaining species have rim-like calyces which: 1) completely enclose the bud and open either by irregular splitting or by circumscissile dehiscence *(G. haughtii, G. colombiana, G. peruviana)* or 2) enclose the bud except for a small apical pore *(G. cauliflora).* The only other genus of Lecythidaceae to possess all these calyx types is *Barringtonia* of the Old World subfamily Planchonioideae (Payens, 1967).

The petals offer no valuable diagnostic features in *Grias;* they are always 4 in number and fleshy. They do differ somewhat in size and thickness; *G. neuberthii* has the largest, thickest petals and *G. cauliflora* the smallest, thinnest ones.

The reduced number of ovules (2-4) per locule, which are pendent from the apex of the non-expanded septa, distinguishes this genus from all other genera of New World Lecythidaceae.

Allantoma (Figs 9, 11S-U)

Allantoma lineata, the only species of the genus, has actinomorphic flowers. The staminal ring forms a tube which bears the stamens at different levels on its inner surface. The stamens are characteristically curved downwards (Fig 11T).

There are five shallowly triangular calyx lobes and five narrowly oblong petals. This is the only genus of neotropical Lecythidaceae to have 5-merous flowers and oblong buds instead of globose ones. The ovules are oriented horizontally or slightly angled upwards on the lower 1/2 of the septum. The ovary is commonly 4-locular, but flowers with 5-locular ovaries are frequent in the same individual with 4-locular ones.

Cariniana (Figs 9, 11M-R)

Cariniana has a slightly zygomorphic androecium in which the staminal ring is only slightly prolonged on one side and which does not have a well defined hood (Figs 11N, P, Q). We have included *Cariniana* in both major divisions of our key (i e actinomorphic vs zygomorphic) because, especially when dried, the flowers are often thought to be actinomorphic. The stamens arise from only the upper margin of the staminal ring in some species (e g *C. pauciramosa*) or from both the upper margin and inner surface in other species (e g *C. pyriformis, C. micrantha*).

The flowers of the genus have 6 sepals, 6 petals, and 3-locular ovaries. *Cariniana* and *Couratari* are the only genera of New World Lecythidaceae with consistently 3-locular ovaries.

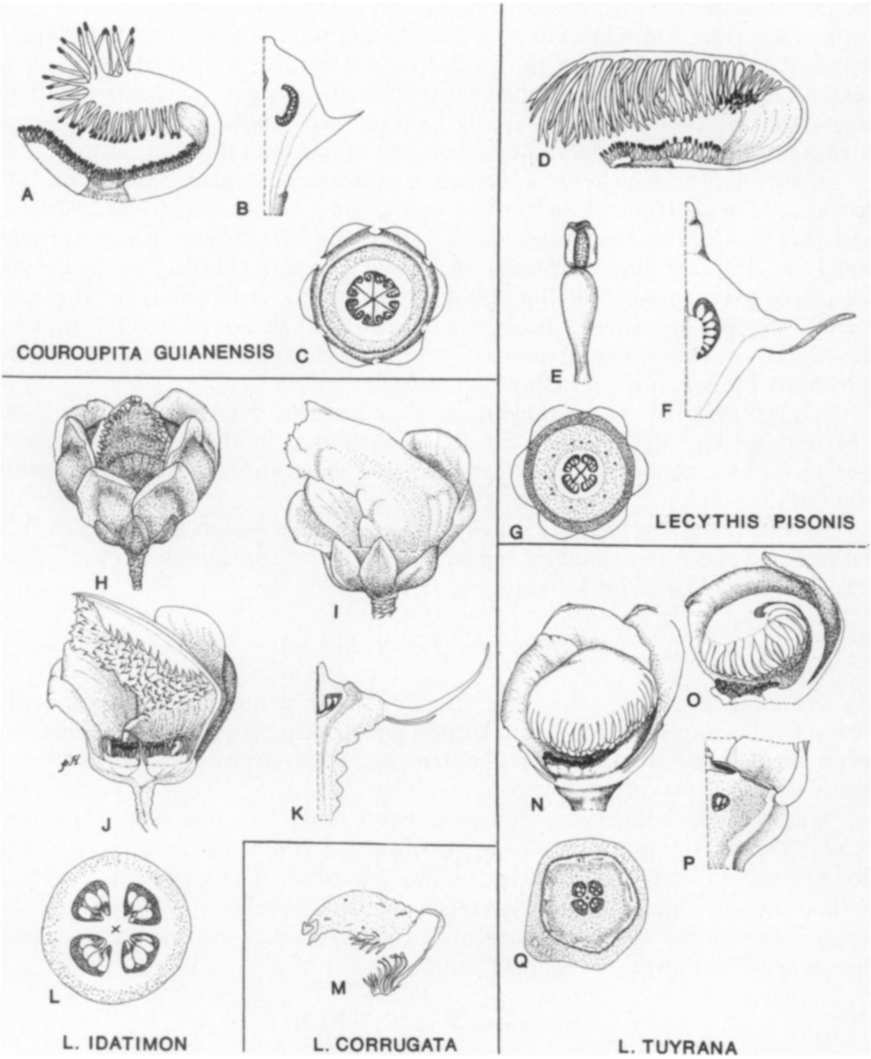

FIG 12. Floral characteristics of *Couroupita* and *Lecythis*. A-C, *Couroupita guianensis (Mori sn)*: A, Longitudinal section of androecium. ×0.64; B, Longitudinal section of 1/2 of ovary. ×1.28; C, Cross section of ovary. ×1.28. D-G, *Lecythis pisonis (Nee 8955)*; D, Longitudinal section of androecium. ×0.96; E, Fertile stamen from staminal ring. ×6.25; F, Longitudinal section of 1/2 of ovary. ×2.48; G, Cross section of ovary. ×1.28. H-L, *Lecythis idatimon (LBB 14653)*; H, Front view of an intact flower. ×0.96; I, Lateral view of flower with two petals removed. ×0.96; J, Longitudinal section of flower. ×0.96; K, Longitudinal section of 1/2 of ovary. ×2.48; L, Cross section of ovary. ×6.25; M, *Lecythis corrugata (LBB 14436)*, longitudinal section of androecium. ×0.96; N-Q, *Lecythis tuyrana*, N-O *(Mori & Kallunki 2067)*, P-Q *(Mori & Kallunki 5772)*; N, Lateral view of flower with 3 petals removed. ×0.64; O, Longitudinal section of androecium with 2 petals attached. ×0.64; P, Longitudinal section of 1/2 of flower. ×1.28; Q, Cross section of ovary. ×1.28.

Couroupita (Figs 9, 12A-C)

Couroupita has markedly zygomorphic flowers. The androecium has a strap-like prolongation, which arises from one side of the staminal ring and arches over the summit of the ovary (Figs 9, 12A). All of the following genera have essentially the same type of androecium. In *Couroupita,* the prolongation usually consists of the ligule, a stamen-free area adjacent to the staminal ring, and the hood, a stamen-bearing region at its apex. However, *C. darienensis* bears stamens on both the ligule and the hood. In *Couroupita,* both the stamens of the staminal ring and of the hood bear anthers. Thompson's (1921) study of zygomorphy in *C. guianensis* revealed that the cells of the ligule and hood are much larger than those of the staminal ring. This cell gigantism is also found in the pollen as the pollen of the hood anthers is much larger than that of the staminal ring anthers.

The hoods of *C. darienensis* and *C. subsessilis* are notched at the apex. In addition, the latter species has an unusual inward fold at the apex of the hood (Fig 10C).

An important diagnostic feature of the flowers of *Couroupita* is the 6-locular ovary with bilamellar placentae running the length of each locule (Fig 12B, C). Some species of *Lecythis* also have bilamellar placentae, but in these species the placentae are restricted to the lower part of the septum, and the ovaries are 4-locular.

Lecythis (Figs 9, 12D-Q)

The androecium of *Lecythis* consists of a staminal ring, ligule, and hood. The hood may be:

1. flat, with the distal appendages sterile and the proximal ones fertile (e g *L. pisonis* (Figs 9, 12D), *L. usitata, L. poiteaui*);
2. flat but dorsiventrally expanded, with the hood appendages completely sterile and mostly fused together (only in *L. corrugata,* Figs 9, 12M); and
3. expanded at the apex, with the appendages completely sterile and swept backwards but not forming a full coil (e g *L. chartacea, L. ollaria, L. tuyrana* (Figs 9, 12N-O).

These hood modifications will be recognized at some subgeneric level in our forthcoming treatment of *Lecythis.*

Diagnostic features of *Lecythis* include a 4-locular ovary, a truncate ovary summit, and a distinction between the ovary summit and the style. In addition, the ovules are inserted at the base of the locule or on the lower part of the septum.

Corythophora (Fig 9)

The androecium of *Corythophora* has a dorsiventrally expanded hood (Fig 9). In the two described species, *C. alta* and *C. rimosa,* the hood appen-

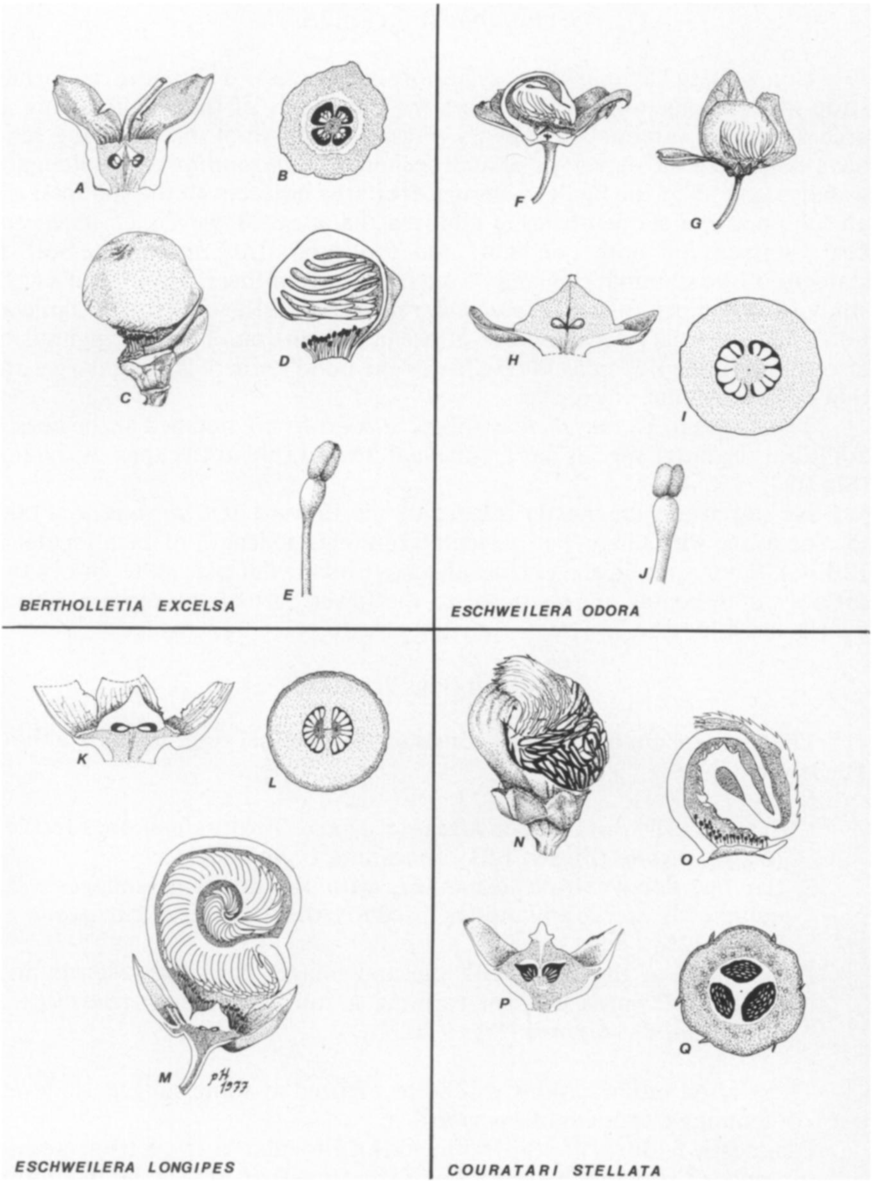

FIG 13. Floral characteristics of *Bertholletia, Eschweilera* and *Couratari*. A-E, *Bertholletia excelsa (Prance 20205);* A, Longitudinal section of ovary, note long, curved style. ×0.34; B, Cross section of ovary. ×0.34; C, Androecium intact on summit of ovary, petals and one calyx lobe removed. ×0.34; D, Longitudinal section of androecium. ×0.34; E, Stamen from staminal ring. ×5.12; F-J, *Eschweilera odora (LLB 14651):* F, Longitudinal section of flower. ×0.5; G, Lateral view of flower with 3 petals removed. ×0.5; H, Longitudinal section of ovary. ×2.1; I, Cross sec-

dages bear anthers. However, in two other species, one described as *Eschweilera labriculata* Eyma and the other undescribed, the hood appendages have no anthers. The latter two species have hoods which resemble that of *Lecythis corrugata.* Nevertheless, they differ from *L. corrugata* by having 1) a smooth instead of rugose hypanthium, and 2) a 2-locular ovary or, if the ovary is 4-locular its summit is umbonate instead of truncate.

Bertholletia (Figs 9, 13A-E)

The flowers of the single species, *B. excelsa,* have androecial hoods which are curved under at the apex but do not form a complete coil (Figs 9, 13D) and which bear sterile hood appendages.

Calyx structure alone distinguishes the flowers of *Bertholletia.* The bud is enclosed by the calyx except for a narrow slit at the apex. At anthesis the calyx splits into two large lobes. All other zygomorphic flowered genera have 6-lobed calyces. Two minute teeth at the apex of each lobe suggest that the 2-lobed calyx of *Bertholletia* is derived from a 4-lobed one.

The ovary summit is truncate and surmounted by a long, obliquely oriented style. Long styles, bent toward the anterior end of the flower, are also encountered in *Lecythis.*

Eschweilera (Figs 9, 13F-M)

All species of *Eschweilera* are characterized by hoods which form at least one complete coil. At the apex of the coil are blunt tipped appendages which apparently serve as nectaries (Figs 9, 13F, M). Another characteristic of *Eschweilera* is the almost universal presence of 2-locular ovaries. The few species with 4-locular ovaries have a coiled hood typical of *Eschweilera.*

Couratari (Figs 9, 13N-Q)

The most important diagnostic character of the flowers of *Couratari* is the highly convoluted hood. Not only does the hood form a complete coil but an additional flap extends outward from the apex of the coil and covers the top of the hood (Figs 9, 13 O). Furthermore, in contrast to the laterally flattened ovules of other genera, those of *Couratari* are flattened dorsiventrally.

In summary, the flowers of New World Lecythidaceae exhibit the following evolutionary trends:

1. Loss of petals and the concomitant development of a petaloid corona of staminal origin. This has occurred only in *Asteranthos brasiliensis.*

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tion of ovary. × 1.68; J, Stamen from staminal ring. × 10.33; K-M, *Eschweilera longipes (Mori & Bolten 8480),* drawn from bud; K, Longitudinal section of ovary. × 1.0; L, Cross section of ovary. × 1.68; M, Longitudinal section of androecium intact on summit of ovary. × 1.0; N-Q, *Couratari stellata (Prance 22918);* N, Androecium intact on summit of ovary. × 0.76; O, Longitudinal section of androecium. × 0.76; P, Longitudinal section of ovary. × 1.0; Q, Cross section of ovary, note dorsiventrally flattened ovules. × 1.34.

However, a similar, but somewhat more complicated, structure is found in *Crateranthus* and *Napoleonaea,* also of the subfamily Napoleonaeoideae but native to Africa. Petal loss, without the development of a petaloid corona of staminal origin appears in *Foetidia,* an Old World genus of the subfamily Foetidioideae.

2. Increasing zygomorphy. The androecia of *Asteranthos, Gustavia, Grias,* and *Allantoma* are actinomorphic, and those of *Couroupita, Lecythis, Corythophora, Bertholletia, Eschweilera,* and *Couratari* are zygomorphic. The androecia of species of *Cariniana* are intermediate, i e the staminal ring is only slightly prolonged on one side. Increasing zygomorphy also involves changes in the complexity of the hood. The most primitive kind of hood is flat (e g *Couroupita* spp, *L. pisonis* (Figs 9, 12D), *L. idatimon, L. usitata*), whereas the more advanced ones are coiled (e g *Eschweilera* spp Figs 9, 13M). The most advanced coiled hood has a flap which projects outwardly from the apex of the coil and which rests on the top of the hood (*Couratari* spp, Figs 9, 13N, O).

3. Sterilization of hood stamens. In primitively zygomorphic species, such as *L. alba* and *Couroupita* spp (Figs 9, 12A), the hood is flat, and all of the hood appendages are antheriferous. The hood appendages of *L. pisonis* (Figs 9, 12D), *L. poiteaui* and *L. usitata* represent the next step in staminal sterilization. In these species, the appendages near the apex of the hood are sterile, and those near the base bear anthers. It is only in species with flat, i e non-coiled hoods, that antheriferous appendages are found on the hood. All species of Lecythidaceae with partially or fully coiled hoods have all their hood appendages sterile.

4. Modification of the hood appendages. Sterilization of the hood appendages is often accompanied by fusion and/or differentiation of the appendages into blunt-tipped structures which apparently serve as nectaries. Blunt-tipped appendages are best developed in *Eschweilera* at the apex of the coil of the hood (Figs 9, 13F, M).

5. Reduction in stamen number. As the androecium of the New World Lecythidaceae increases in zygomorphy there is a concomitant reduction in stamen number. The actinomorphic genus, *Gustavia* has 500-1200 stamens, whereas the most advanced genus, *Couratari,* may have as few as 10 stamens. Reduction in stamen number is not perfectly correlated with increase in zygomorphy. For example, *L. poiteaui,* a zygomorphic-flowered species, pollinated by bats, has 1000 stamens. Nevertheless, there is a trend for increasing zygomorphy to be accompanied by staminal reduction.

6. Production of nectar. Nectar production is also correlated with increasing zygomorphy. *Gustavia* and *Grias,* and probably *Allantoma,* utilize pollen as the pollinator reward and produce no apparent nectar. Zygomorphic species with open flowers (e g *L. pisonis* (Figs 9, 12D), *L. alba, L. usitata, Couroupita* spp (Figs 9, 12A) also use pollen as the pollinator reward. The anthers of the hood appendages are often colored differently from those of the staminal ring. For example, the hood anthers are black in *L. usitata* and yellow in *L. alba,* whereas the staminal ring anthers are yellow in the former and white in the latter species. Nectar is most abundantly produced in those species

that possess closed flowers with highly coiled hoods and relatively fewer stamens.

5. Fruits, Seeds and Seedlings

The fruits, seeds, and seedlings of neotropical Lecythidaceae provide an array of characters which are valuable in generic as well as specific classification (Prance and Mori, 1978). Features such as fruit dehiscence and dispersal, embryo structure, and the nature of the funicle-aril are extremely important in understanding the taxonomy of the family.

Previous workers (Miers, 1874; Ducke, 1925; Knuth, 1939b) had difficulty deciding if a species had dehiscent fruit and in interpreting the structure of the funicle-aril. For example, Ducke (1925) established *Holopyxidium* as distinct from *Eschweilera* because he thought the fruit to be indehiscent rather than dehiscent. However, by 1930 Ducke had observed in the field that the fruit of *Holopyxidium* was also dehiscent, and therefore, he synonymized his genus with *Eschweilera.* Miers (1874) and Knuth (1939b) mistakenly referred to the seed attachment of the Lecythidaceae as a funicle, but in most species it is actually a funicle surrounded by a fleshy aril. In addition, erroneous reports that *Eschweilera* had no funicles (Miers, 1874; Knuth, 1939b) led to the establishment of *Neohuberia* (Ledoux, 1963) which was thought to be distinguished from *Eschweilera* by the presence of a funicle. We are now convinced that presence of a funicle-aril is the rule rather than the exception in *Eschweilera.*

The following review summarizes our knowledge and clears up some of the earlier misconceptions about the fruits and seeds of Lecythidaceae. Many of our observations were made in the field, and, therefore, we have been able to record structure and dispersal mechanisms not readily apparent from herbarium material.

Structure of the Fruit

The fruits of neotropical Lecythidaceae are either indehiscent *(Gustavia, Grias, Couroupita)* or dehiscent *(Allantoma, Asteranthos?, Cariniana, Corythophora, Bertholletia, Couratari, Eschweilera, Lecythis).* Although the fruit of the monotypic genus *Bertholletia* (*B. excelsa* H.B.K.) is dehiscent, the diameter of the opercular opening is smaller than that of the seeds, and the operculum falls inward. Consequently, the seeds are retained within the fruit when it falls from the tree at maturity. This is clearly a case of functional indehiscence developing from an ancestor with dehiscent fruits which, as suggested by floral morphology and leaf anatomy, was related to extant species of *Lecythis.*

There has been some confusion as to whether the fruits of *Gustavia* are dehiscent or indehiscent. Woodson (1958) suggested that *G. brachycarpa* Woodson is dehiscent, and Corner (1976) reported that the genus has dehiscent capsules. Our numerous field observations confirm that *Gustavia* is indehiscent. Those species which appear to be dehiscent simply have thin opercular regions which are easily fragmented by insects or that readily rot away.

As far as we know, there are no species of *Gustavia* with freely falling opercula.

The fruit of *Lecythis* illustrates most features of the fruits of neotropical Lecythidaceae (Fig 14). Its large, woody fruit is separated into three zones by two rings of scars. The proximal ring, that closest to the pedicel, marks the position of the sepals and has been called the "Calcary zone" (Miers, 1874), "calycinal zone" (Pittier, 1912, 1927), and the "calycine zone" (Dwyer, 1965). The distal ring, that closest to the summit of the fruit, delineates the line of opercular dehiscence. To avoid confusion with other zones of the fruit we propose to call the two rings the *calycine ring* and the *line of opercular dehiscence* respectively (Fig 14). These rings divide the fruit into three zones. The first, situated below the calycine ring, consists of the rounded fruit base with its pedicel scar in the center, and is called the *infracalycine zone* (Dwyer, 1965), equivalent to the "basal band" of Pittier (1912, 1927). The second zone, located between the two rings, is the *supracalycine zone* (Dwyer, 1965), previously called the "interzonary band" (Miers, 1874) and the "interzonal band" (Pittier, 1912, 1927); it develops from the area under the staminal ring of the flower (Fig 14A). The third zone is the deciduous operculum which develops from the summit of the ovary; it is sometimes marked by an umbo (Figs 17 O, 18H). To summarize, proceeding from the proximal end of the fruit, one observes: 1) the pedicel scar, 2) the infracalycine zone, 3) the calycine ring, 4) the supracalycine zone, 5) the line of opercular dehiscence, and 6) the operculum.

The relative sizes of the two zones are variable and are therefore of little use as taxonomic characters although previous workers have used them (Miers, 1874; Knuth, 1939b). Dugand (1947), for *Lecythis minor* Jacq., and Mori (1968), for *L. ampla* Miers, have demonstrated this variability, and during our field work we have observed the same in other species, e g *Couroupita guianensis* Aubl. and *Allantoma lineata* Miers. Fruit size is another character which must be used with caution. For example, the large fruits of *L. ampla* take nearly a year to mature (Mori, 1970), and those of *Bertholletia excelsa* take 14 months. During such a long developmental period they encounter environmental factors which may accelerate or retard growth. Consequently, year to year variation in fruit size is great. Furthermore, when the fruits are dried young they dehisce and are impossible to differentiate from mature pyxidia. Many synonymous names have resulted from misinterpretation of the pyxidia of a single species at different stages of development as those of several species. For example, at least seven of the described species of *Allantoma* were based on different stages of development and decay of the fruits of the one species, *A. lineata.*

The woody pericarp of Lecythidaceae may have evolved in response to animal predation. The thick, tough walls of the pyxidium protect the developing seeds from most but not all predators. Moreover, in the fruits of *Lecythis chartacea* Berg and *Eschweilera jarana* (Huber ex Ducke) Ducke we have noted the presence of viscid mucilage which oozes out of ducts in the sepals and pericarp. We feel that this mucilage is important in reducing insect fruit predation. Similar fruit defense mechanisms are found in *Hymenaea*

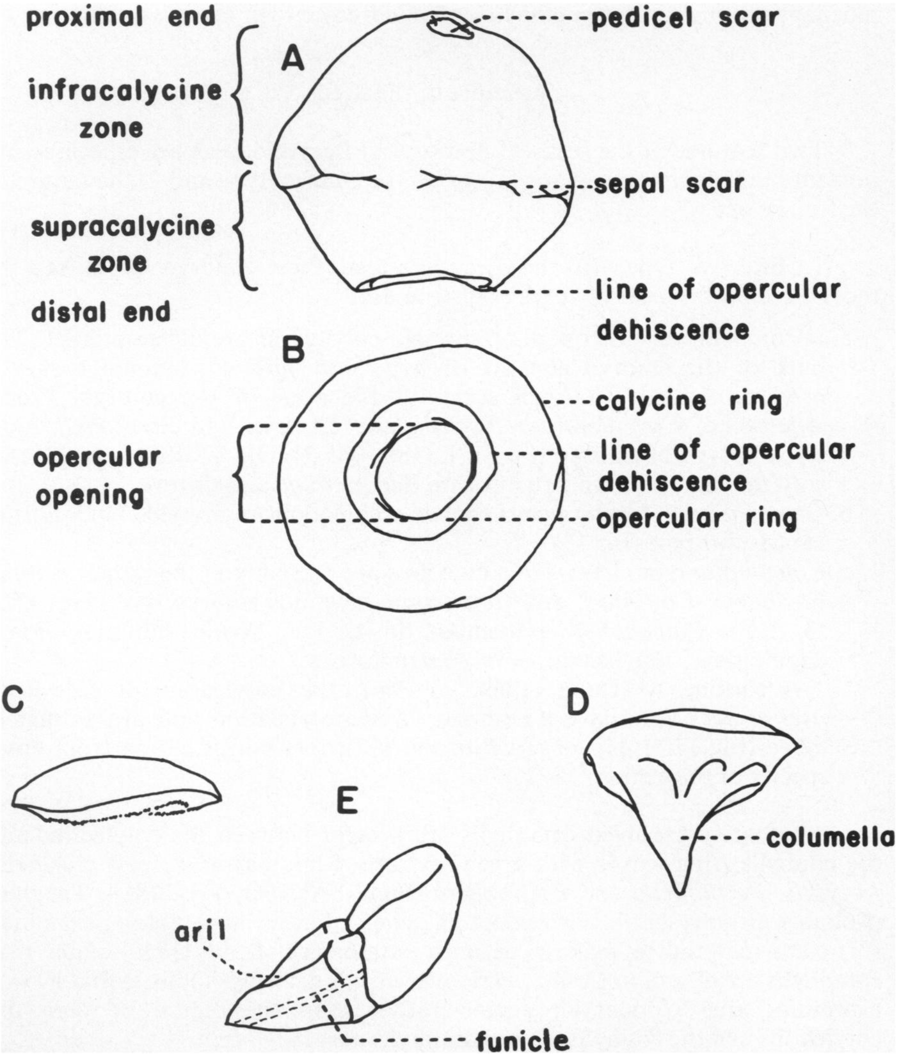

FIG 14. General fruit characteristics of neotropical Lecythidaceae as illustrated by *Lecythis*, a genus with dehiscent fruits: A, Lateral view of the fruit of *L. ampla* (operculum removed, *Mori 316)*; B, Distal view of the fruit of *L. ampla* (operculum removed, *Mori 316)*; C, Operculum of the fruit of *L. ampla (Mori 316)*; D, Operculum of the fruit of *L. pisonis (Mori 399)*, note the persistent columella; E, Seed of *L. minor (Mori 423)*.

courbaril L. (Janzen, 1975) and *Stemmadenia donnell-smithii* Woodson (McDiarmid et al, 1977). The mucilage may be distasteful or somewhat toxic or, more likely, it may gum up the mouthparts of any insect attempting to prey upon the fruit. Further field studies are needed to determine the extent of mucilage producing ducts in the Lecythidaceae and their adaptive value.

Structure of the Seeds

Two features of the seeds of neotropical Lecythidaceae are especially important in the taxonomy of the group: 1) the embryo type and 2) the nature of the funicle-aril.

1. Embryo type. In the Lecythidaceae three embryo types can be recognized on the basis of cotyledon structure.

a. *Bertholletia* or macropodial type. No cotyledons are differentiated. The bulk of the embryo consists of hypocotyl with cotyledonal tissue, if present, reduced to small scales at the apex of the embryo. *Grias, Allantoma, Corythophora, Eschweilera, Lecythis* and *Bertholletia* possess this type of embryo (Figs 17L, 18C, M, R). Old World Lecythidaceae with the same embryo structure are *Barringtonia* and *Careya.*

b. *Gustavia* type. Fleshy plano-convex cotyledons are present. Only *Gustavia* has this type (Fig 15).

c. *Couroupita* type. Leaf-like cotyledons are present and the radicle is long. *Cariniana, Couratari,* and *Couroupita* have this embryo type (Figs 17D, H, 19F). *Planchonia,* a member of the Old World subfamily Planchonioideae, also has this embryo structure.

According to Duke (1969, Fig 66), the cotyledons of *Cariniana pyriformis* Miers have a complex circinate venation and are palmately lobed (Fig 17D). His observations need further confirmation from other species of the genus.

Alternately arranged cataphylls are present between the cotyledons and the eophylls (first leaves with green, expanded lamina) in at least *Gustavia, Lecythis, Bertholletia* and *Eschweilera* (Figs 15A, 16G, 17L, 18C). They are probably also present in the remaining genera, but we have not yet examined sufficient material to make a definitive statement. Duke (1969) states that cataphylls are absent in *Couratari.* However, his drawings indicate that he was examining the hypocotylar region rather than the region between the cotyledons and the eophylls where cataphylls normally occur.

In all species with foliaceous cotyledons that we have observed, the cotyledons are withdrawn from the seed coat upon germination (phanerocotylar cotyledons; Duke, 1969). However, Duke (1969) reports the presence of cryptocotylar as well as phanerocotylar cotyledons in *Couratari.* We have never observed cryptocotylar cotyledons in *Couratari* and believe that his Figure 61 illustrates phanerocotylar rather than cryptocotylar cotyledons. In Duke's Figure 61 the opposite arrangement of the "leaves" and the absence of cataphylls below these "leaves" indicates that they are cotyledons rather than eophylls (Duke, 1969). Until more data indicate otherwise the cotyledons of all neotropical Lecythidaceae with foliaceous cotyledons must be considered phanerocotylar.

In genera with macropodial embryos, the germinating embryo may penetrate the seed coat at opposite ends of the seed (e g *Lecythis minor* Jacq., Fig 17L; *L. tuyrana* Pittier, Fig 19C; *Bertholletia excelsa,* Fig 18C; *Eschweilera pittieri* R. Knuth, Fig 18R) or less frequently at opposite sides of the seed (*Eschweilera* section *Jugastrum,* Figs 18M, 19D). In some cases the seed coat splits along one side and is carried upward with the growing stem until it drops off (*Lecythis tuyrana,* Fig 19C).

The three embryo types of the neotropical Lecythidaceae are paralleled in the Myrtaceae. Keys to the genera of New World Myrtaceae (e g McVaugh, 1956; Amshoff, 1958) often present a first dichotomy between embryo types, i e the foliaceous cotyledons of subtribe Myrciinae versus the plano-convex or undifferentiated cotyledons of subtribe Eugeniinae. The embryos of the third subtribe, the Myrtinae, are incurved with elongate radicles and minute cotyledons, a type not found in neotropical Lecythidaceae. The occurrence of all three embryo types of the New World Lecythidaceae in the Myrtaceae may indicate common ancestry rather than convergent evolution.

2. Structure of the funicle-aril. The seeds of neotropical Lecythidaceae are attached to the ovary wall in the following ways:

a. With no apparent organ of attachment, i e sessile. *Gustavia superba* (Kunth) Berg and *G. speciosa* (Kunth) DC. as well as most *Eschweilera* species west of the Andes do not have developed funicles and arils.

b. By a well developed funicle and no aril. *Gustavia augusta* L. has a yellow tortuous funicle but no apparent aril (Fig 15E).

c. By a funicle surrounded by a fleshy aril. *Lecythis usitata* Miers exemplifies this type (Fig 17K). This type is also found in most species of *Eschweilera* east of the Andes.

   The position of the funicle-aril is of taxonomic importance. In all species that we consider to belong to *Lecythis,* the funicle-aril is basal (Fig 17K), while in *Eschweilera* it is usually lateral (Figs 18 O; 19E).

d. By an aril completely surrounding the seed. We have observed this arrangement in one species of *Eschweilera* sect *Jugastrum (Prance & Mori et al 24357,* Fig 18I-L). In addition to the unusual aril this species has lateral germination (Figs 18M, 19D).

e. By an aril flattened to form a wing. *Cariniana* has a unilateral wing (Fig 17C), and *Couratari* a wing which surrounds the seed (Fig 18F).

Seeds with fleshy arils, sarcotestas, and wings are also present in the Meliaceae (Pennington and Styles, 1975). The diverse seed structure of these ecologically important families suggest that generic evolution in tropical trees has been promoted by different dispersal agents. Further support for the importance of dispersal agents in the adaptive radiation of tropical plants is given by Ducke (1948). He has cited many good examples of adaptations for dispersal by water, wind, or animals in closely related taxa of Amazonian plants.

Seed Dispersal

New World Lecythidaceae are adapted for dispersal by a wide variety of animals, by water or, in *Cariniana* and *Couratari,* by the wind.

The orange mesocarps of *Gustavia superba* and *G. grandibracteata* Croat & Mori are eaten by animals. Once the exocarp is broken the orange color of the mesocarp serves to attract mammals which in turn scatter the seeds while eating the mesocarp. Humans also consume the mesocarps of *G. superba* and *G. speciosa* in Panama and Colombia respectively. Fish may play a role in dispersal of the riverine species, *G. augusta,* for seeds have been found in fish intestines by Prance (unpublished field data) and Honda (1974).

The seeds of *Bertholletia excelsa* are dispersed by scatter-hoarding rodents. At maturity the fruits drop to the ground, retaining the seeds because the opercular opening is too small to permit their release. Agoutis gnaw through the woody pericarp to remove the seeds. Those seeds which are not immediately eaten are cached, and some of the cached seeds are forgotten and left to germinate (Huber, 1909; Prance, unpublished field data).

We have confirmed Greenhall's (1965) observation that the seeds of *Lecythis usitata* are dispersed by bats. After dehiscence of the operculum the seeds hang from the base of the fruit by cord-like funicles that are surrounded by a large, fleshy, sweet tasting aril and are available to dispersal agents (Figs 17K; 19A-B). Bats remove the funicle-aril with the seeds attached and, after eating the former, drop the intact seeds at their roosts or while in flight. Monkeys may play a negative role in seed dispersal of *L. usitata.* While collecting in the Rio Cuieiras region (Amazonas, Brazil), Prance heard a distant banging noise in the forest. When asked what it was the local guide explained that the sound was made by monkeys opening fruits of the Sapucaia Nut Tree (= *L. usitata*). This was confirmed by following the sound to a large tree of *L. usitata (Prance et al 17970)* where monkeys were observed opening fruit. The ground was strewn with seeds, arils, and pyxidia, the latter showing bruise marks resulting from the banging process. Many of the seeds were partially eaten thereby indicating that monkeys are seed predators of *L. usitata.*

The relative importance of monkeys as seed predators and/or dispersal agents is not yet known. Marc van Roosmalen (pers. comm.) informs us that the fleshy funicle-aril of *L. poiteaui* Berg is eaten by monkeys, especially *Chiropotes satanas* (Hoffmannsegg) and *Ateles paniscus* (L.). He adds that the funicle-arils are so thoroughly harvested by these monkeys that he was unable to "collect untouched ones despite all possible efforts." Van Roosmalen (pers. comm.) has also discovered that monkeys of the genera *Pithecia* and *Chiropotes* are able to open fruit of Lecythidaceae before dehiscence with their well developed canine teeth. His observations suggest that these monkeys are specialized Lecythidaceae fruit eaters. However, their role as dispersal agents and/or predators is unknown for it depends on the stage of seed development when the fruit is opened and on what part of the fruit is eaten. We await the results of van Roosmalen's two-year study of monkey-plant interactions in Surinam to answer these questions.

The fruit of several species of *Eschweilera* are opened by parrots and macaws. In a tree of a species of *Eschweilera (Prance et al 23804),* many parrots were observed pecking out the seeds. However, more than half of the seeds were dropped to the ground relatively undamaged. This species produced abundant fruit during the 2 years it was observed (1974, 1975). In another species of *Eschweilera (Prance et al 25502),* a pair of macaws were observed feeding on the seeds and scattering many intact seeds on the ground. In a tree of another species of *Eschweilera (Mori & de Granville 8828),* macaws were observed opening the nearly mature fruits. Many seeds and partially damaged fruits covered the ground under the tree. All of the seeds on the ground were without arils and some seeds were damaged. To one of us (Mori) the arils tasted good but the mesocarp and seeds were very bitter, leaving an after-taste for several hours. From these three examples it is apparent that parrots and macaws serve as dispersal agents and/or predators of Lecythidaceae. Further observations are needed to determine the role that large birds play in the seed dispersal of Lecythidaceae.

Water dispersal occurs in several riverine species of Lecythidaceae. *Asteranthos brasiliensis* Desf. is restricted to the Rio Negro region of Colombia, Venezuela, and Brazil where it is abundant in blackwater flooded forests on sandy soil. The persistent calyx (Fig 16A) serves as a flotation device for the water dispersed fruits (Ducke, 1948). Another Amazonian riverine species, *Allantoma lineata* (Martius ex Berg) Miers, has water dispersed seeds which are released during the river's annual crest. After fruit dehiscence the seeds drop directly into the water where they float because of their high oil content (Ducke, 1948). Flotation experiments demonstrate that seeds of *A. lineata* float for at least 3 months (Prance, unpublished data). It is probable that other common riverine species of Lecythidaceae are hydrochorous.

The seeds of species of *Cariniana* and *Couratari* are dispersed by wind. The aril, which is normally thick and fleshy in other genera and serves to attract animals, is here flattened to form a wing (Figs. 17C, 18F). Trees of both genera are mostly either emergent or riverine and, therefore, expose their fruits to maximum wind velocities.

Generic Review

Asteranthos brasiliensis

The fruits of this monotypic genus are characterized by a persistent calyx (Fig 16A-D) that serves as a flotation device (Ducke, 1948; see discussion of seed dispersal above). The mature fruit contains a single ovate seed.

The seed is unlike any other species of Lecythidaceae in that the embryo is surrounded by copious, ruminate endosperm (Fig 16C, D). The embryo, although described by Knuth (1939c) as tubular, has two membranous cotyledons at the apex and a curved lower portion which gives it an overall "J" shape (Fig 16C).

The seed structure of *A. brasiliensis* supports Knuth's (1939c) treatment of *A. brasiliensis* as a monotypic family (Asteranthaceae) rather than as a member of Lecythidaceae subfamily Napoleonaeoideae (Niedenzu, 1892; Thompson, 1927; Pichon, 1945).

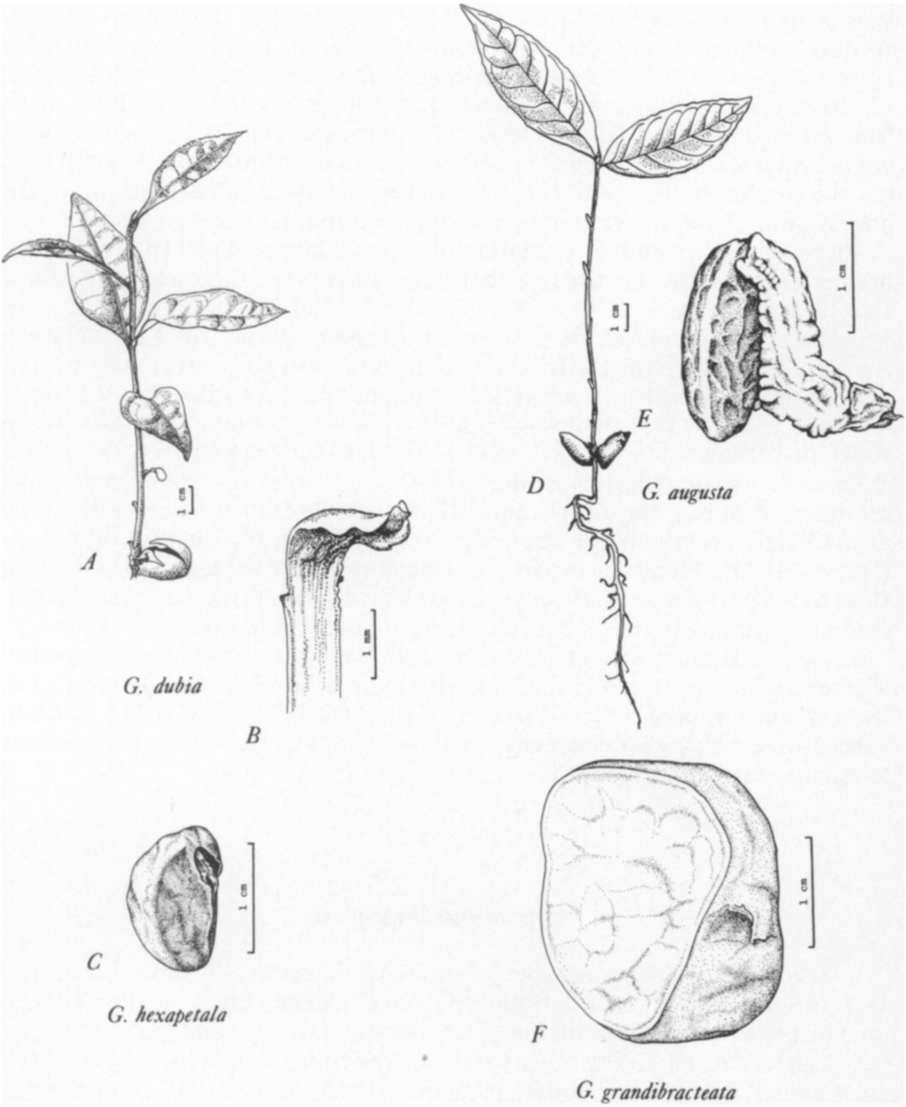

FIG 15. Seeds and seedlings of selected species of *Gustavia:* A, Seedling of *G. dubia (Dressler sn),* note cataphylls between cotyledons and first leaves; B, Enlarged cataphyll from A, note minute stipules; C, Seed of *G. hexapetala (Nee & Mori 4190),* note remnant funicle and slight bulge above the funicle which represents the caruncle; D, Seedling of *G. augusta (Nee & Mori 4209),* note cataphylls along stem; E, Seed of *G. augusta (Nee & Mori 4209),* note expanded funicle; F, Seed of *G. grandibracteata (Mori 836),* note scar where seed was attached and apparent lack of a funicle.

Gustavia

The fruits of this genus have indehiscent pericarps, and the seeds are released when the pericarp is eaten by animals or when it rots away. We have also observed that seeds of *Gustavia augusta* sometimes germinate while still within the pericarp. Although Woodson (1958) and Corner (1976) report that *Gustavia* has dehiscent fruits, our field observations confirm that the fruits are indehiscent. In some species, e g *G. brachycarpa* and *G. longifuniculata,* the opercular areas may be weaker than the remainder of the pericarp. Consequently, in these species the opercular area is often removed by animals but in no case does it fall spontaneously.

Costate pericarps, which are present in several species, are especially well developed in species of section *Hexapetala* (figs 16F, 43). Although useful in specific classification, costae must be used with some caution for both costate and ecostate fruits may appear in the same population (e g *G. dubia* on El Llano-Carti road, Panama). Mesocarp color is a useful, but little recorded, character of *Gustavia* fruits. The mesocarp is yellow-orange in some species (e g *G. superba* and *G. grandibracteata)* and white in others (e g *G. fosteri* and *G. dubia*). Mesocarp color may be an adaptation to attract animals that eat the mesocarp and in turn disperse the seeds.

The fleshy, plano-convex cotyledons of *Gustavia* (Fig 15) are unique in the family. The funicles are well developed and contorted in some species (e g *G. augusta,* Fig 15E), inconspicuous and straight in others (e g *G. hexapetala,* Fig 15C), and apparently lacking in still others (e g *G. grandibracteata,* Fig 15F). In no species have we seen an aril that envelops the funicle. However, we have observed that mature seeds of *G. hexapetala (Nee & Mori 4190)* are sometimes surrounded by a whitish film that may be an aril which attracts animals for seed dispersal. The seeds of some species have a slight bulge near the hilum that is slightly different in color from the remainder of the seed coat (e g *G. dubia*). In our descriptions of the seeds of *Gustavia* this structure is referred to as a caruncle.

Our observations of the seedlings of *G. augusta* and *G. dubia* demonstrate that the cotyledons remain within the seed coat upon seed germination (haustorial) and that they are positioned above the ground (epigeal) Fig 15A, D). The lower part of the stem of the seedlings bears 4-10 cataphylls, each provided with a pair of minute stipules at its base (Fig 15B). The first true-leaves (eophylls) also possess small, white, caducous stipules.

Grias

The fruits of this genus have indehiscent pericarps which become pulpy at maturity and contain a single seed (Fig 16N). The fact that the pulp is edible suggests that animals play a role in seed dispersal.

The seeds lack cotyledons, i e the embryo is undifferentiated or macropodial.

Observations on the fruits of *G. cauliflora* (Guppy, 1917) show that the seeds of this species germinate quite readily when they fall into fresh water but

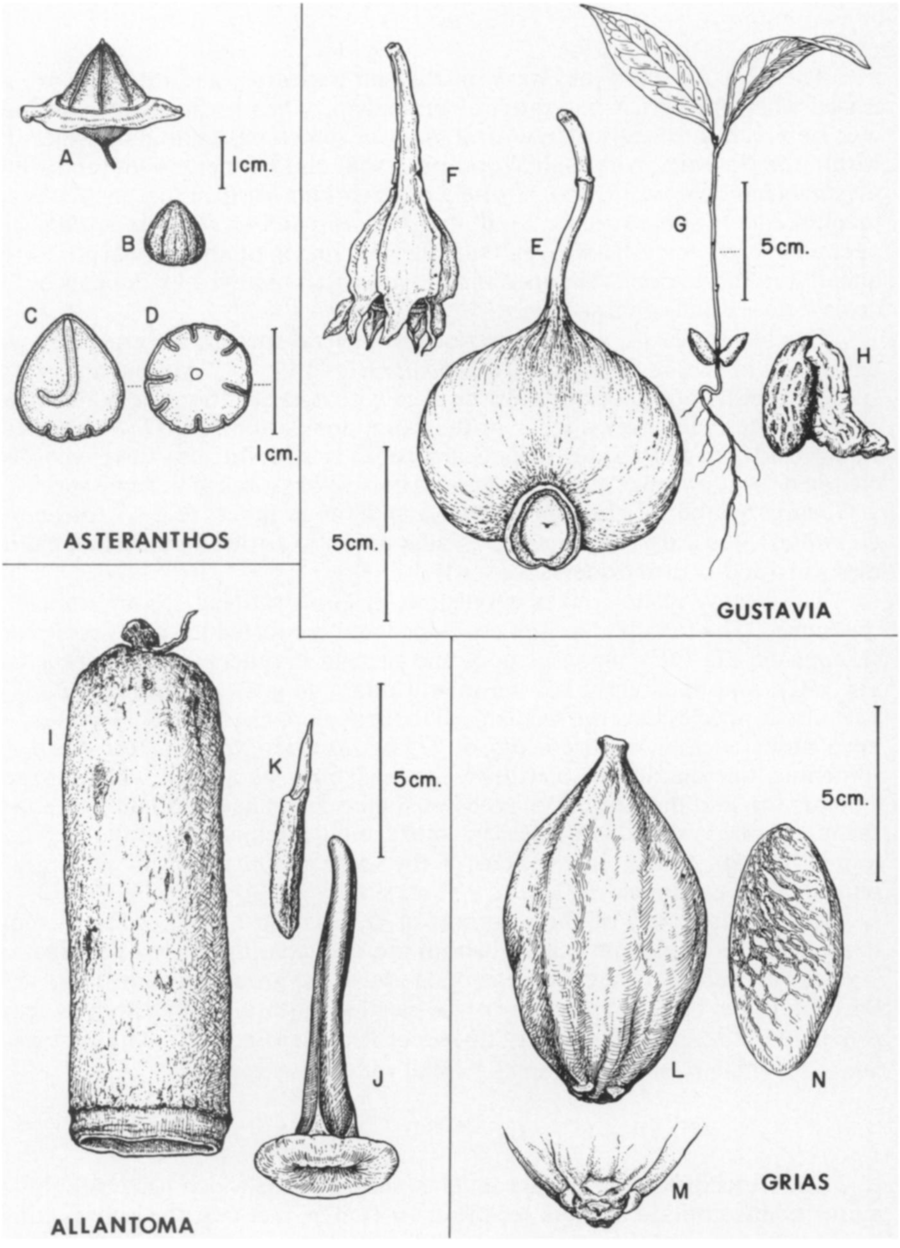

FIG. 16. Fruit, seed, and seedling characteristics of *Asteranthos, Gustavia, Allantoma,* and *Grias:* A-D, *Asteranthos brasiliensis (Prance et al 15481):* A, Entire fruit, note the persistent calyx; B, Lateral view of the seed; C, Longitudinal section of the seed showing the tubular embryo embedded in copious endosperm; D, Cross section of the seed showing the tubular embryo and the ruminate endosperm; E-H, *Gustavia* spp: E, Fruit of *G. superba (Mori 837);* F, Fruit of *G.*

that the embryos are killed by salt water. The pericarps are frequently encountered in the drift on Jamaican beaches (Guppy, 1917) and have been observed in the drift on San Jose Island, Panama (Johnston, 1949, plate 12, fig 4 as unidentified "seed"). The disjunct population of *G. cauliflora* on Jamaica (Fig 59) might be explained by chance long distance dispersal over salt water. Because this species grows in riverine habits, a large enough number of fruits are carried to the Caribbean and it is probable that one or more seeds may have reached Jamaica from Central America without being killed by salt water.

We have not been able to recognize interspecific differences in the fruits of *Grias*.

Allantoma lineata

The fruits of this monotypic genus are cylindric and have 4-5 locules and freely falling opercula. (Fig 16I-J).

The embryo is undifferentiated.

The seeds are notched at the base and have a rugulose seed coat that is finely pitted (Fig 16K). The high oil content of the seeds permits them to float and aids in water dispersal (Ducke, 1948).

Cariniana

The fruits of this genus are obconic, obovate, or cylindrical, have 3 locules, and freely falling opercula (Fig 17A-B).

The seeds have unilateral wings that facilitate dispersal by wind. The wing is the flattened aril through which passes the vein-like funicle (Fig 17C).

The embryo possesses two foliaceous cotyledons (Fig 17D).

Couroupita

The fruits of this genus are round and indehiscent, have 6 locules and a 6-segmented pulp which turns bluish-green upon exposure to the air (Fig 17E-H). At maturity they fall intact and often split on impact with the ground. We have observed natives of the Amazon basin feeding the pulp to chickens and suggest that feral animals disperse the seeds.

Professor H.-W. Koepcke (pers. comm.) observed a tree of *Couroupita guianensis* in Amazonian Peru with many fruits on the ground around its trunk. The tree was observed over a three week period during which no animals touched the fruit although there were many rodents around. When he was about to cease daily observation a herd of wild pigs came past the tree and broke open, destroyed and ate all the fruits under the tree. Professor Koepcke

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brachycarpa (Pittier 5269), note the winged (= costate) exocarp; G, Seedling of *G. augusta (Nee & Mori 4194);* H, Seed of *G. augusta (Nee & Mori 4209),* note the fleshy funicle; I-K, *Allantoma lineata (Prance et al 11618):* I, Base of fruit; J, Operculum; K, Seed with attached funicle-aril, note notched base of seed; L-M, *Grias neuberthii (Boeke 2211);* L, Entire fruit; M, Apex of fruit showing remnant calyx lobes and style; N, Seed.

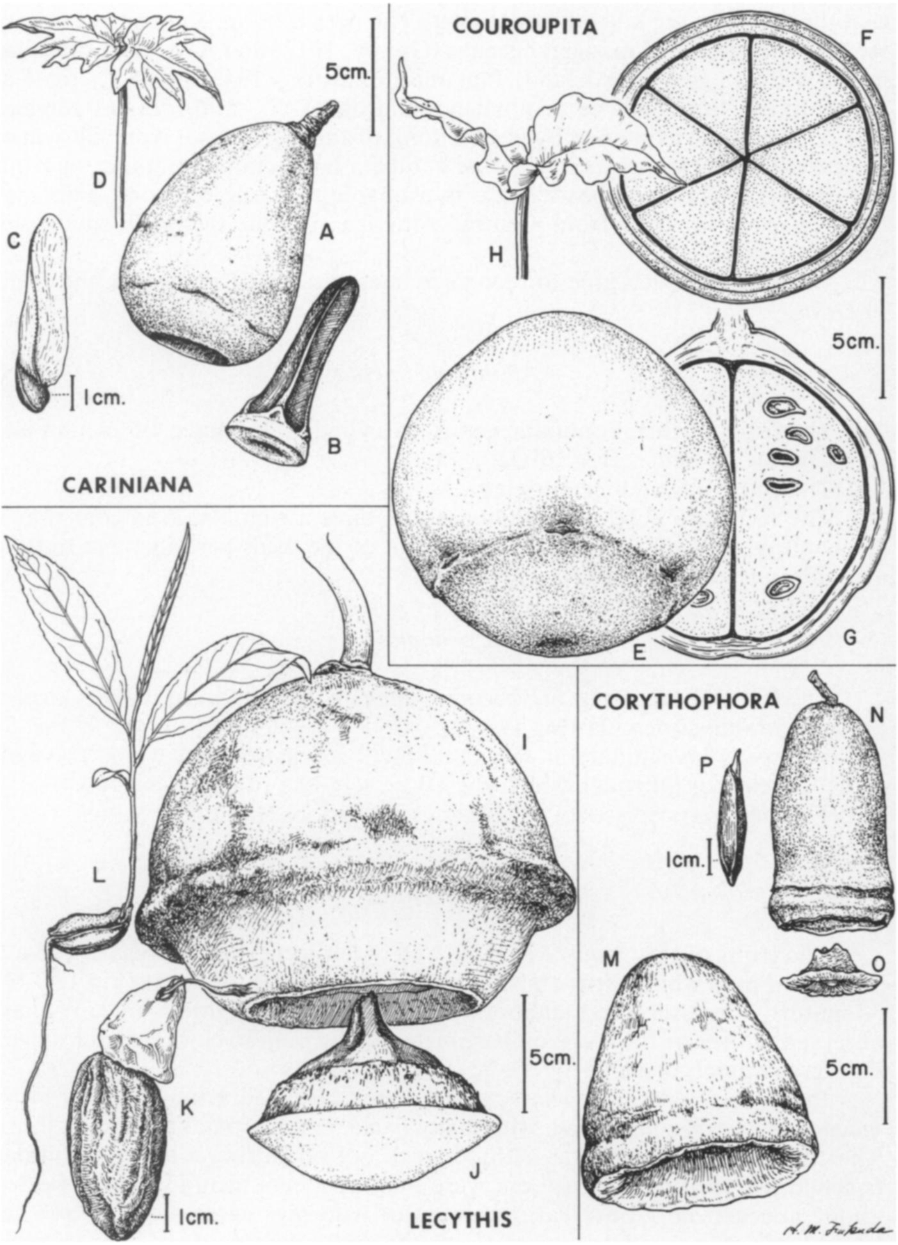

FIG 17. Fruit, seed and seedling characteristics of *Cariniana, Couroupita, Lecythis,* and *Corythophora:* A-C, *Cariniana micrantha (Krukoff 5095);* D, *C. pyriformis,* redrawn from Duke (1969): A, Base of fruit; B, Operculum; C, Winged seed, the wing is a flattened aril with the funicle passing through it; D, Apex of seedling showing the foliaceous cotyledons. E-H, *Couroupita guianensis* (E-G, *Fróes 1705;* H, *Mori & Kallunki 3263);* E, Entire fruit; F, Cross section of fruit

believes that the seeds are thus dispersed by the swine who make only occasional visits to the *Couroupita* trees during their long foraging treks through the forest.

The seeds are lenticular and have a hairy covering which arises from the seed coat. The embryo possesses two foliaceous cotyledons (Fig 17H).

Corythophora

The fruits of this genus are campanulate or cylindric, have 4 locules, and freely falling opercula (Fig 17M-P).

The seeds are attached by a basal, erect funicle that is surrounded by a fleshy aril. The embryo is undifferentiated.

Bertholletia excelsa

The fruits of this monotypic genus are round, have 4 locules and an inwardly falling operculum which is smaller in diameter than the seeds (Fig 18A-C).

The strongly 3-angled seeds with their thick, indurate, rugose seed coats are unique in the family (Fig 18B). We have observed no funicle or aril in *Bertholletia.* The embryo of this genus is undifferentiated.

Several workers have suggested that there are two species of *Bertholletia,* one in which the operculum falls into the fruit and another in which it falls out of the fruit (Miers, 1874; Young, 1911; see discussion of uses in this monograph). We have found no support for this claim and therefore recognize only *B. excelsa.*

The fruit and seed structures of this genus are apparently adaptations for seed dispersal by scatter-hoarding rodents (see above discussion on seed dispersal).

Couratari

The fruits of this genus are cylindrical, have 3 locules and freely falling opercula (Fig 18D-G).

The seeds are unique in the family in that they are surrounded by a wing which represents a flattened membranous aril (Fig 18F). The wing is penetrated by the funicle which surrounds the seed. The winged seeds of *Couratari,* like *Cariniana,* are adapted for wind dispersal. In both genera the wings of the seeds are derived from arils but the position of the wing is different, being unilateral in *Cariniana* and surrounding the seed in *Couratari.*

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showing the 6 pulpy segments; G, Longitudinal section of fruit showing seeds embedded in pulp; H, Apex of seedling showing foliaceous cotyledons; I-K, *Lecythis usitata* (I-J, *Prance et al 20210;* K, *Prance et al 24363);* L, *L. minor (Prance 23171);* I, Base of fruit with attached pedicel; J, Operculum; K, Seed, note funicle surrounded by fleshy aril; L, Seedling; M, *Corythophora rimosa (Prance et al 23518);* N-P, *C. alta (Prance & Ramos 23312):* M, Base of fruit; N, Base of fruit; O, Operculum; P, Seed.

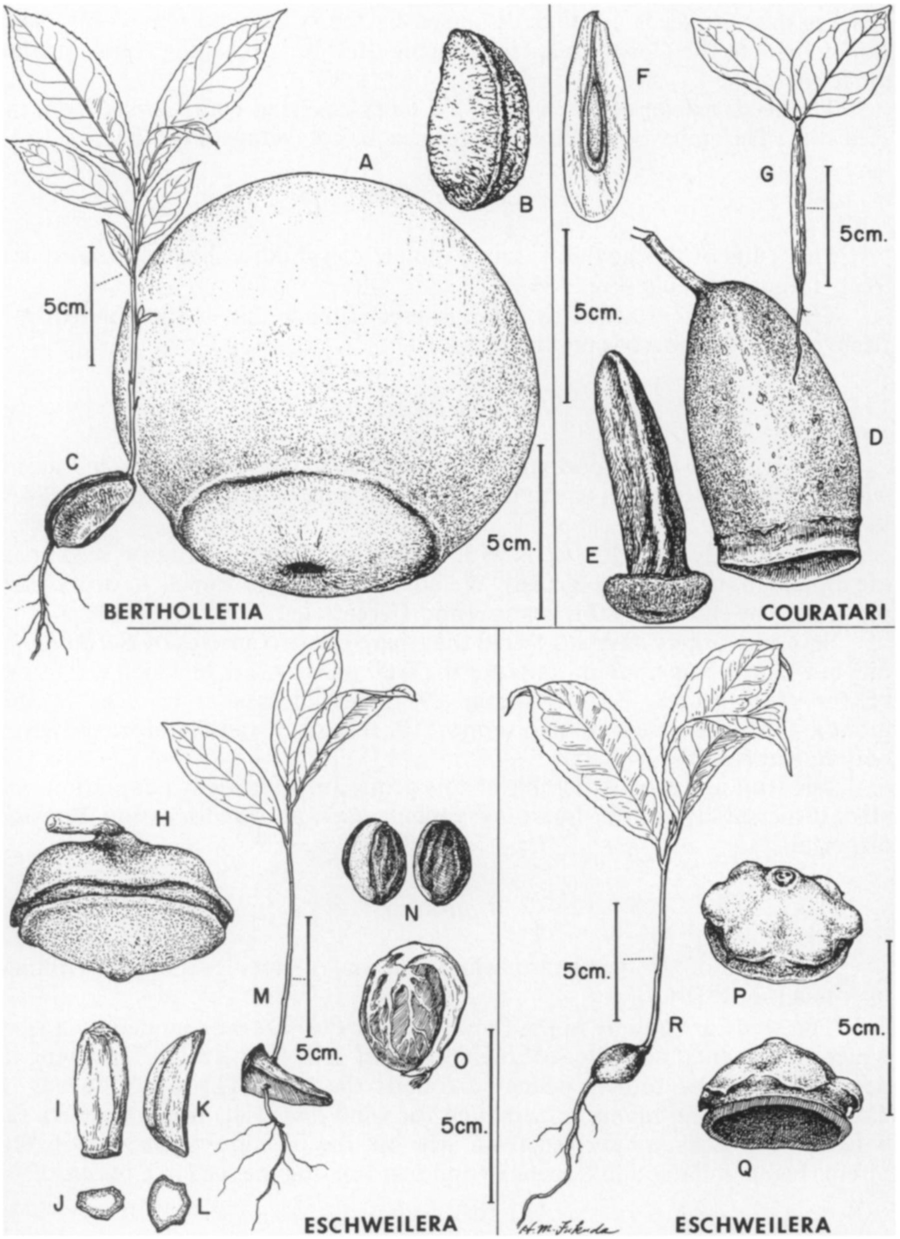

FIG 18. Fruit, seed, and seedling characteristics of *Bertholletia, Couratari,* and *Eschweilera:* A-C, *Bertholletia excelsa* (A-B, *Prance et al 16599;* C, *Prance blastogeny coll. no. 4):* A, Entire fruit; B, Seed; C, Seedling; D-F, *Couratari guianensis (Maguire & Cowan 39318);* G, *C. stellata (Mori et al 9160):* D, Base of fruit; E, Operculum; F, Seed; G, Seedling showing flattened stem and foliaceous cotyledons; H-O, *Eschweilera* spp: H-M, *Eschweilera* sp section *Jugastrum* (H-L, *Prance et*

The embryo possesses two foliaceous cotyledons and the stem of the seedling is often flattened (Fig 18G).

Eschweilera

The fruits of this genus have 2 locules and freely falling opercula (Fig 18H-R).

The seeds have a lateral funicle-aril (Fig 18 O), or an aril which completely surrounds the seed (Fig 18I-L), or no funicle or aril. The embryo is undifferentiated, and in most cases the germinating seed penetrates the seed coat at opposite ends (Fig 18R). However, in those species that have wedged-shaped seeds surrounded by an aril the germination is lateral, i e the seedling penetrates the seed coat at opposite sides (Figs 18M, 19D). Species with seeds possessing the latter array of characters have been segregated from *Eschweilera* as the genus *Jugastrum* (Miers, 1874; Knuth, 1939b). Nevertheless, we feel that the similarity of flowers of *Eschweilera* and *Jugastrum* argues against their separation. Consequently, we have retained *Jugastrum* within *Eschweilera* and will recognize the above differences at the subgeneric level in our forthcoming treatment of the genus.

Lecythis

The fruits of *Lecythis* have 4 locules and freely falling opercula (Fig 17I-L). In addition, some species of *Lecythis* (e g *L. pisonis, L. usitata, L. ampla*) have the largest fruits known to occur in the family.

The seeds are attached to the placenta by a straight funicle which is surrounded by an enlarged, white, fleshy aril. The funicle-aril of *Lecythis* is basal (Fig 17K) rather than lateral as in most species of *Eschweilera.* The embryo is undifferentiated, and at germination the seedling penetrates the seed coat at opposite ends (Fig 17L). After germination the seed coat may persist on the seedling until it rots away or it splits longitudinally and falls off (Fig 19C).

Fruit size and shape, although useful as interspecific taxonomic characters, must be used with some caution because of intraspecific variation (Dugand, 1947; Mori, 1970; Prance and Mori, 1978).

In summary, evolution of the fruits, seeds, and seedlings of the genera of New World Lecythidaceae has resulted in the following differences:

1. Indehiscent vs dehiscent fruits. Fruits of *Gustavia, Grias,* and *Couroupita* are indehiscent, whereas those of the remaining genera are dehiscent. Indehiscent fruits usually fall intact from the tree, and dehiscent ones remain on the tree until after the seeds have been dispersed. The correlation of indehiscent fruits with unspecialized flowers suggests that in-

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al 24357; M, *Prance et al 23397):* N, *E. odora (Mori et al 8727);* O, *Eschweilera* sp *(Mori et al 9098);* H, Entire fruit; I, Lateral view of seed; J, Cross section of I; K, Lateral view of seed; L, Cross section of K; M, Seedling showing lateral germination; N, Two different lateral views of the seed of *E. odora;* O, Lateral view of the seed of *Eschweilera* sp; P-R, *Eschweilera pittieri (Mori & Kallunki 2830):* P, Basal view of the fruit; Q, Lateral view of the fruit; R, Seedling.

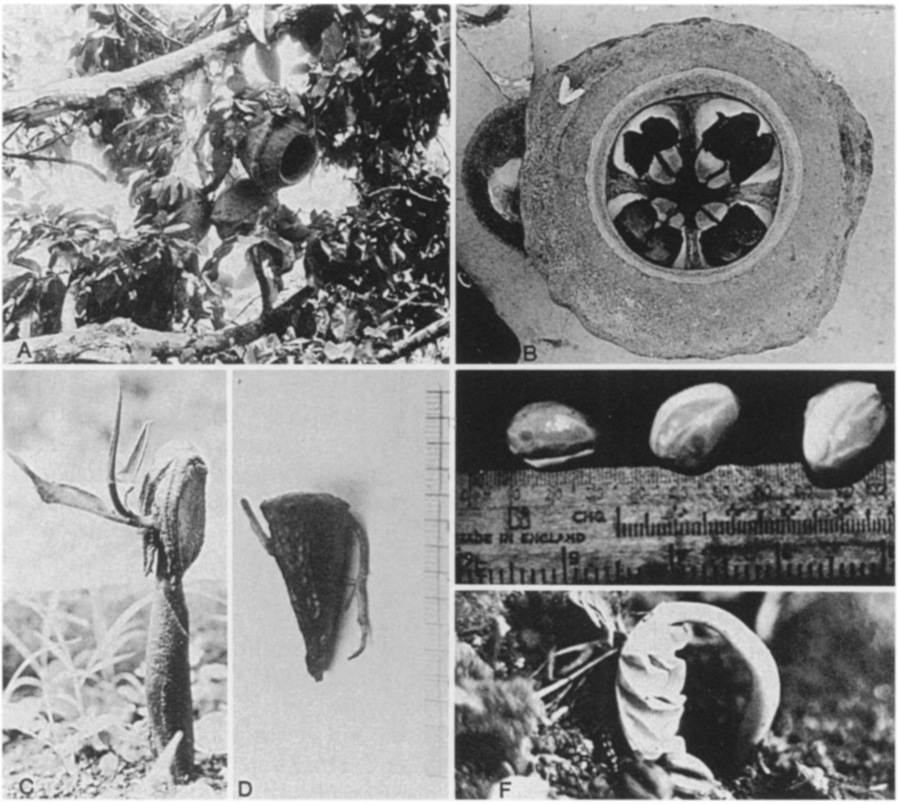


FIG 19. Fruit, seed, and seedling characteristics of *Lecythis, Eschweilera,* and *Couroupita:* A, *Lecythis usitata,* the operculum of the uppermost fruit has fallen *(Prance et al 24363);* B, *L. usitata,* fruit without the operculum, showing the seeds attached by the funicle-aril *(Prance et al 24363);* C, *L. tuyrana* seedling showing the macropodial embryo *(Mori & Kallunki 1705);* D, *Eschweilera* section *Jugastrum* showing lateral germination *(Prance & Ramos 23397);* E, *Eschweilera* sp showing the lateral funicle-aril *(Mori et al 8727);* F, *Couroupita guianensis* showing the foliaceous, phanerocotylar cotyledons *(Mori & Kallunki 3263).*

dehiscent fruits should be considered primitive in the New World Lecythidaceae. A special example of "functional indehiscence" is found in *Bertholletia excelsa.* In this species the operculum dehisces, but the seeds are retained within the pericarp until after the fruit falls to the ground because the size of the opercular opening is smaller than the diameter of an individual seed. Our studies of floral structure and leaf anatomy indicate that *B. excelsa* is most closely related to species of *Lecythis,* and, therefore, the "functionally indehiscent" fruits of *Bertholletia* probably evolved from ancestors with dehiscent *Lecythis*-like fruits.

2. Fleshy vs woody pericarps. Some species of *Gustavia* and *Grias* have relatively soft pericarps which are eaten by animals. The woody pericarps of the remaining genera apparently do not serve to attract animals but instead protect the developing seeds from animal predation.

3. Thick vs thin pericarps. The indehiscent fruits of species of *Couroupita* have relatively thin pericarps which tend to split open when the fruit falls, thereby revealing the pulpy mesocarp to animals which may disperse the seeds. Significant differences in pericarp thickness are found within a genus. For example, *Cariniana pyriformis* and *C. micrantha* (Fig 17A) have very thick pericarps in relation to overall fruit size whereas the pericarps of other species (cf *C. estrellensis*) are thinner. Thick pericarps probably give more protection to the developing seeds from animal predation.

4. Presence vs absence of mucilage. Mucilage-producing ducts are present in the pericarps of some species of Lecythidaceae (e g *Lecythis chartacea*). The mucilage may help protect the developing seeds from insect damage by being somewhat toxic or by gumming up the insects' mouthparts when they try to chew through the pericarp.

5. One vs several to many seeds per fruit. *Asteranthos brasiliensis* and all species of *Grias* have only one seed per fruit whereas the remaining genera have several to many seeds.

6. Presence vs absence of a funicle or a funicle-aril. *Asteranthos brasiliensis,* all species of *Grias,* and some species of *Gustavia* and *Eschweilera* lack apparent funicles and arils. Some taxa such as *Gustavia augusta* have a well developed tortuous funicle but no aril (Fig 15E). In contrast, all species of *Lecythis* and most of *Eschweilera* have a funicle which is surrounded by a fleshy aril (Figs 17K, 18 O). The presence of a fleshy aril usually indicates that animals eat the aril and in turn disperse the seed. However, two genera, *Cariniana* and *Couratari* have membranous, wing-like arils which are adaptations for wind dispersal.

7. Position of the funicle-aril. The funicle-aril may be basal as in all species of *Lecythis* (Fig 17K), lateral as in some species of *Eschweilera* (Figs 18 O, 19E), or completely surround the seed as in other species of *Eschweilera* (Fig 18I-L). Consequently, the position of the funicle-aril is often a useful taxonomic character.

8. Embryo type. The embryos of *Grias, Allantoma, Bertholletia, Corythophora, Lecythis* and *Eschweilera* are undifferentiated, i e lack cotyledons. In the genera with differentiated embryos the cotyledons are fleshy and planoconvex in shape in species of *Gustavia,* foliaceous in species of *Cariniana, Couroupita,* and *Couratari,* or small, membranous, translucent, and at the apex of a tubular, curved hypocotyl in *Asteranthos.*

9. Germination. Upon germination, seedlings which arise from undifferentiated embryos may penetrate opposite ends (e g *Bertholletia,* Fig 18C; *Lecythis,* Fig 17L; *Eschweilera,* Fig 18R) or opposite sides (e g *Eschweilera,* Figs 18M, 19D) of the seed coat. Sometimes the seed coat remains until it rots away or falls from the embryo (Fig 19C).

In seedlings that arise from differentiated embryos, the cotyledons may remain within the seed coat (e g *Gustavia,* Fig 15A) or be withdrawn from the seed coat (e g *Couroupita,* Fig 17H; *Cariniana,* Fig 17D; *Couratari,* Fig 18G) upon germination.

10. Flattened vs terete seedling stem. Seedlings of species of *Couratari* differ from species of other genera in that the hypocotyl is flattened instead of terete (Fig 18G).

Many of the fruit, seed, and seedling features of New World

Lecythidaceae can be attributed as adaptation to specific dispersal agents. For example, the "functionally indehiscent" fruits of *Bertholletia excelsa* are adapted for rodent dispersal, the fleshy aril of *Lecythis usitata* is an adaptation for bat dispersal, the flattened, wing-like arils of *Cariniana* and *Couratari* are adapted for wind dispersal, and the oily seeds of *Allantoma* are adapted for water dispersal. Continued field observations may demonstrate that other features such as number of seeds, position of the funicle-aril, embryo type, and germination type may have some adaptive significance.

V. POLLEN

by J. Muller

The genera described in this part of the monograph all possess the *Lecythis* main pollen type (Figs 20, 21) as defined by Muller (1972). This is characterized by tricolpate pollen in contrast to the *Planchonia* main type which is syntricolpate. The colpi in the *Lecythis* main type are generally provided with more or less distinct endoapertures (Fig 20:4). The pollen grains of *Asteranthos* and *Grias* have indistinct endoapertures, mostly developed as equatorial constrictions only. Such grains may be termed colporoidate. In some species of *Gustavia* the endoapertures are well developed as thinned areas in the nexine and these grains are colporate. Shape is generally subprolate, occasionally spherical, size varies between 24 and 44 μm.

Exine structure of the genera described here is rather similar and consists of an inner nexine, generally of uniform thickness, a layer of columellae which are rather indistinct in *Asteranthos, Allantoma* and *Cariniana,* but more pronounced in *Grias* where the columellae may be arranged in a reticulate pattern in conformity with the surface sculpture of the tectum. The latter varies between perforate, reticulate, fossulate and perforate-verrucate. In some species of *Grias* the reticulate pattern is coarser on the poles. *Asteranthos* is characterized by reticulate-fossulate grains (Fig 21:1), perforate-reticulate grains occur in *Allantoma* (Fig 21:2) *Cariniana* (Fig 21:3-6), and *Grias* (Fig 20:1-2), while perforate-verrucate grains are found only in *Gustavia* (Fig 20:6).

The evolutionary significance and further interpretation of the pollen morphology of Lecythidaceae will be given in the second part of this monograph, after the pollen of all neotropical genera has been studied. In the meanwhile descriptions of all genera treated in this part are given below.

1. *Asteranthos* (Fig 21:1)

Material investigated: *Asteranthos brasiliensis, Ducke 57a.*

Tricolpate, suprolate-prolate, 33-37 μm.
Colpi fairly long, no distinct endoapertures present, although a slight equatorial constriction may occur.
Colpus membranes with scattered small verrucae.
Exine thick, columellae short, fine, spaced in a duplicolumellate pattern underneath muri, tectum evenly reticulate-fossulate, muri fairly wide.

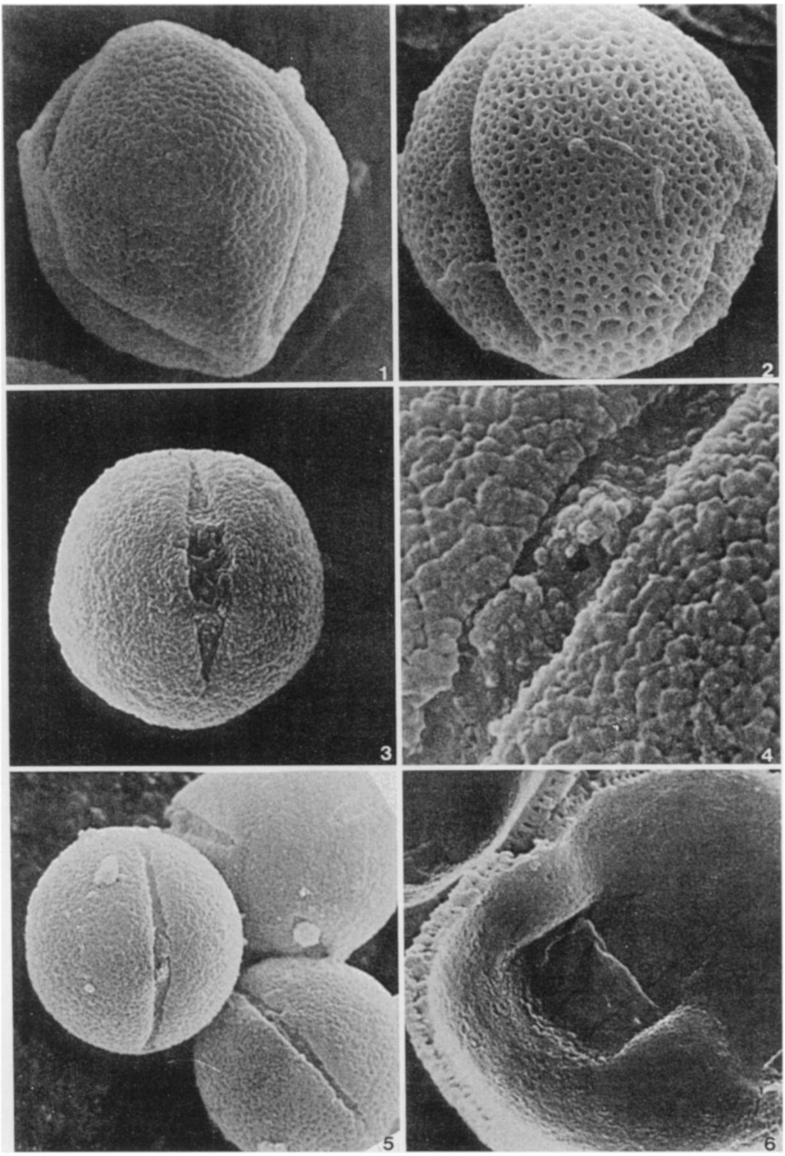


FIG 20. Pollen of *Grias* and *Gustavia:* 1, *Grias cauliflora* (Perkins 1354). Equatorial view ×2770; 2, *Grias peruviana* (Gentry 12018). Equatorial view ×2270; 3, *Gustavia romeroi* (Haught 2042). Equatorial view ×2100; 4, *Gustavia romeroi* (Haught 2042). Interior view of endoaperture ×4200; 5, *Gustavia pubescens* (Gentry 12298). Equatorial views and polar view ×1930. 6, *Gustavia pubescens* (Gentry 12298). Detail of 5, ×9660.

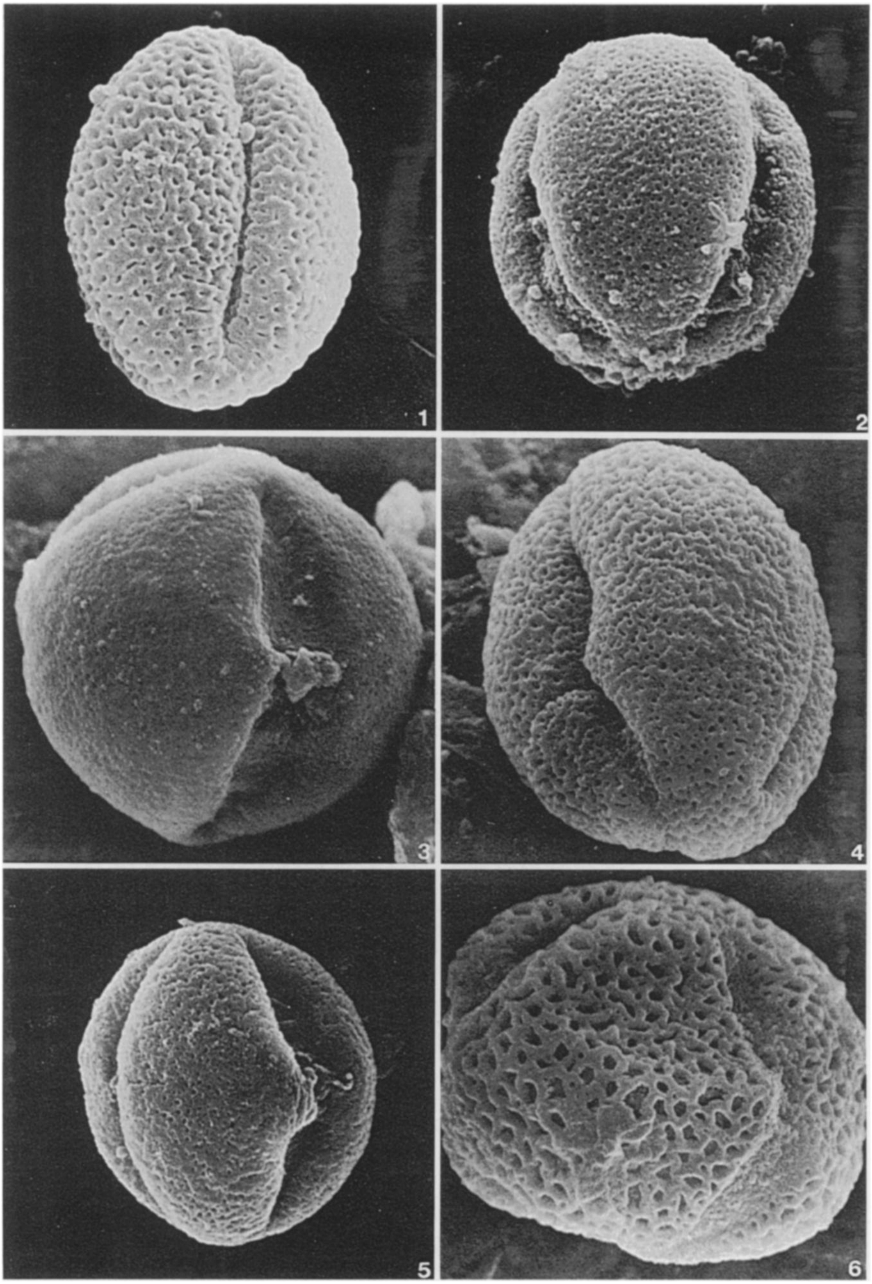


FIG 21. Pollen of *Asteranthos, Allantoma* and *Cariniana:* 1, *Asteranthos brasiliensis* (Ducke 57). Equatorial view ×2200; 2, *Allantoma lineata* (Prance 23694). Equatorial view ×2300; 3, *Cariniana pyriformis* (Duke 11594). Equatorial view ×2900; 4, *Cariniana decandra* (Krukoff 8717). Equatorial view ×2250; 5, *Cariniana micrantha* (Prance et al 8499). Equatorial view ×2300; 6, *Cariniana multiflora* (Krukoff 8164). Equatorial view ×2400.

2. *Gustavia* (Fig 20:1, 3-6)

Material investigated: *Gustavia augusta, Lanjouw 1215, Prance 11246; G. grandibracteata, Nee & Mori 3697; G. hexapetala, Black 48-3020, Krukoff 4691, Kubitzki 75-35, Prance 15585, 15771, Steyermark 94490; G. longifuniculata, Nee & Mori 4305; G. macarenensis* subsp *pauci-sperma, Bernardi 1030; G. monocaulis, Leisner 1312; G. nana* subsp *rhodantha, Mori & Gentry 4524; G. pubescens, Gentry 12298; G. pulchra, Berry 2050; G. romeroi, Haught 2042; G. superba, Lewis 5448.*

Tricolporate, occasionally tetracolporate *(G. hexapetala)*, spherical-subprolate, 21-33 μm.
Colpi rather short or long, endoapertures generally distinct, varying from equatorial constrictions to large oval or subrectangular *(G. hexapetala, G. romeroi)* or butterfly-shaped thinnings in the nexine *(G. augusta)*, sometimes with thickened polar borders *(G. superba, G. hexapetala)*.
Colpus membranes finely verrucate.
Exine thin to fairly thick, columellae generally indistinct or fine, tectum perforate or perforate with a very finely scabrate to verrucate or irregularly areolate-rugulate sculpture. Although no distinct subtypes can be recognized, the species investigated can be arranged in a rather continuous series according to the degree of coarseness of the verrucate sculpture as follows:

A. Species in which the sculptural details are very fine (below the resolution of the light microscope).
G. augusta, G. monocaulis, G. pubescens, G. romeroi, G. superba.

B. Species in which the verrucate sculpture is medium fine and visible with the light microscope.
G. augusta, G. grandibracteata, G. hexapetala, G. macarenensis, G. nana.

C. Species with a rather coarsely verrucate-rugulate sculpture.
G. pulchra.

The finely perforate pollen grains of *G. longifuniculata* apparently lack the verrucate sculpture.

3. *Grias* (Fig 20:1)

Material investigated: *Grias cauliflora, Perkins 1354, G. haughtii, Fernández & Jaramillo 7100; G. neuberthii, Cuatrecasas 11232; G. peruviana, Gentry 12018, Kuhlmann RB21501, Schunke 3404.*

Tricolpate or tricolporoidate, suprolate, 23-43 μm.
Colpi long, endoapertures mostly developed as indistinct equatorial constrictions.
Colpus membranes finely verrucate.
Exine very thin to medium thin, columellae indistinct or distinct, tectum very finely perforate to reticulate, lumen size uniform or larger on poles.
The species investigated can be divided into three subtypes as follows:

Grias cauliflora subtype *(G. cauliflora).*
Grains small (23-29 μm), tricolpate, colpi very long, exine very thin, columellae indistinct, tectum very finely perforate.

Grias peruviana subtype *(G. haughtii, G. peruviana).*

Grains large (35-43 μm), tricolpate, colpi rather long, equatorially constricted, exine thin, columellae rather distinct, simpli- or duplicolumellate under muri, tectum evenly, rather finely reticulate.

Grias neuberthii subtype *(G. neuberthii, G. peruviana, Gentry 12018).*

Grains large (31-43 μm), tricolporate, colpi rather long, equatorially constricted, exine rather thin, columellae distinct, coarser on poles, widely spaced, tectum finely reticulate on equatorial belt, coarsely reticulate on poles.

4. *Allantoma* (Fig 21:2)

Material investigated: *Allantoma lineata, Ducke 1414, Prance 21160, 23694.*

Tricolporate, spherical-subprolate, 35-40 μm.
Colpi long, endoapertures variably developed as indistinct equatorial constrictions or distinct subrectangular thinnings in the nexine.
In Prance 21160 irregular pericolpate apertures are present.
Colpus membranes densely covered with small verrucae.
Exine medium thick, columellae fine to very fine, rather long, tectum evenly perforate-reticulate.

5. *Cariniana* (Fig 21:2)

Material investigated: *Cariniana decandra, Krukoff 8717; C. domestica, Prance 7967; C. estrellensis, Irwin 8885; C. legalis, Duarte 6209; C. micrantha, Prance et al 8499; C. multiflora, Krukoff 8164; C. pyriformis, Duke 11594(6); C. rubra, Irwin 21284.*

Tricolporate, spherical-subprolate, 23-44 μm.
Colpi long to very long, endoapertures generally developed as more or less distinct equatorial constrictions, rarely as equatorially elongated slits in the nexine.
Colpus membranes smooth or covered with small verrucae.
Exine thin or thick, columellae indistinct or distinct, tectum finely perforate-reticulate.
The species investigated can be divided into three subtypes as follows:

Cariniana rubra subtype *(C. domestica, C. rubra).*

Grains small (23-28 μm), subprolate-spherical, endoapertures distinct, often equatorially elongated, exine thick on mesocolpia, thinning towards colpi, columellae distinct, long, densely spaced, tectum very finely perforated.

Cariniana micrantha subtype *(C. decandra, C. estrellensis, C. legalis, C. micrantha, C. pyriformis).*

Grains small to large (25-44 μm), subprolate, endoaperatures indistinct, developed as equatorial constrictions, exine uniformly thin, columellae very fine, either short, densely spaced, tectum very finely to finely perforate.

Cariniana multiflora subtype *(C. multiflora).*

Grains small (23-25 μm), subprolate-spherical, endoapertures very indistinct, exine thin, columellae very short, tectum evenly, coarsely reticulate with scattered verrucae in lumina.

VI. ECOLOGY

Most ecological or floristic studies of lowland tropical American forests on mesic sites demonstrate the importance of the Lecythidaceae. The family is often abundant in both numbers of species and individuals present. For example, Prance et al (1976) found 18 species, represented by 67 individuals over 15 cm DBH, in a one hectare study plot near Manaus, Brazil. These figures represented 10.1% of the species and 22% of the individuals over 15 cm DBH present in the plot. Only the Leguminosae sensu lato, with 25 species, was more diverse, and no other family had more individuals. Other studies have also demonstrated the prevalence of Lecythidaceae in lowland tropical forests. Pires et al (1953) recorded 273 individuals of Lecythidaceae over 10 cm DBH in a 3.5 hectare plot near the village of Tres de Outubro, Pará, Brazil. In their study area only Leguminosae sensu lato (30 species) and Sapotaceae (25 species) were more diverse and no family had more individuals. In another study of primeval *terra firme* forest near Mocambo, Pará, Brazil, Cain et al (1956) calculated the importance value (= sum of relative densities, frequencies, and dominances) of Lecythidaceae to be 37.77, second only to Burseraceae (47.92). However, not all lowland tropical forests are as rich in Lecythidaceae as the above areas. Schulz (1960) has demonstrated that Lecythidaceae in the rain forests of northern Surinam may be abundant in some areas and absent in others, i e individuals over 25 cm DBH of canopy and emergent species of Lecythidaceae represented 0 to 22.4% of all individuals depending on the study area. In a study of *terra firme* forest near Manaus Klinge (1973) found only 6.6% of the individuals over 10 cm DBH in or above the canopy to be Lecythidaceae. In summary, absolute densities of Lecythidaceae of 19-88 (over 10 cm DBH; Davis and Richards 1934), 78 (over 10 cm DBH; Pires et al, 1953), 69 (over 15 cm DBH; Pires unpublished data), 0-28 (over 25 cm DBH; Schulz, 1960), and 67 (over 15 cm DBH; Prance et al 1976) trees/hectare have been reported (Tables V-VII).

Pires (unpublished data) carried out a detailed study of 10.5 hectares in a forest reserve near Belém, Brazil. The rectangular study area of 420 × 250 m contains 5.7 hectares of *terra firme* forest called the Mocambo Reserve. It is surrounded by 4.8 hectares of tidal *várzea* forest which is inundated twice daily by the Catú stream which backs up at high tide. In addition Pires studied 5 hectares of periodically flooded forest in the nearby Aurá Reserve (see Pires and Prance, 1977). The 15.5 hectare study area contained 1,072 trees of Lecythidaceae of 15 or more cm DBH, or 69.16 trees per hectare. However, the density of Lecythidaceae of the *terra firme* forest (Mocambo Reserve) was 117.72 trees/ha whereas those of the periodically inundated forests (Catú and Aurá Reserves) were only 33.5 and 39 trees/ha respectively (Table VI). In a study of the vegetation of Moraballi Creek, Guyana, Davis and Richards (1933, 1934) recognized 5 forest types. Individuals of Lecythidaceae over 10 cm DBH were most abundant in their Greenheart forest (88/ha), less abundant in the Mixed (57.8/ha) and Morabukea (47/ha) forests and relatively uncommon in their Mora (30.9/ha) and Wallaba (18.8/ha) forests. The Mora and Wallaba forests are at the two extremes of a soil moisture-organic content continuum, the former grows on periodically waterlogged soils high in organic content whereas the latter is found on white sand which is relatively poor in

Table V

Species of Lecythidaceae of 15 cm diameter or more found on a hectare of forest on *terra firme,* Km 30, Manaus-Itacoatiara road (data from Prance et al, 1976)

Species	**No. of trees**
Corythophora alta Knuth	2
Corythophora rimosa Rodrigues	5
Couratari guianensis Aubl.	1
Couratari atrovinosa Prance	2
Eschweilera amara Ndz. (= *Lecythis idatimon* Aubl.)	4
Eschweilera fracta Knuth	2
Eschweilera odora (Poepp.) Miers	26
Eschweilera polyantha A.C. Smith	3
Eschweilera sp 1	1
Eschweilera sp 2	4
Eschweilera sp 3	1
Eschweilera sp 4	1
Eschweilera sp 5	2
Eschweilera sp 6	4
Holopyxidium latifolium (A. C. Smith) Knuth (= *Eschweilera jarana* (Huber) Ducke var *latifolia* Ducke)	4
Holopyxidium jaranum (Hub.) Ducke (= *Eschweilera jarana* (Huber) Ducke	2
Holopyxidium sp 1 (= *Lecythis* sp.)	2
Holopyxidium sp 2 (= *Lecythis* sp.)	1
	67

Table VI

Frequency of trees of Lecythidaceae 15 cm diameter or more in Belém study areas in the Mocambo, Catú, and Aurá reserves

Species	**Mocambo terra firme (5.7 ha)**	**Catú tidal várzea (4.8 ha)**	**Aurá várzea (5 ha)**	**Total**
Allantoma lineata (Martius ex Berg)Miers	7	34	59	100
Couratari guianensis Aublet	9	4	2	15
Couratari oblongifolia Ducke & R. Knuth	0	0	2	2
Eschweilera apiculata (Miers) A. C. Smith	27	1	0	28
Eschweilera alba R. Knuth	2	0	3	5
Eschweilera amara (Aubl.) Ndz. (= *Lecythis idatimon* Aubl.)	291	45	45	381
Eschweilera collina Eyma	0	0	2	2
Eschweilera blanchetiana (Berg) Miers	0	1	0	1
Eschweilera odora (Poeppig) Miers	361	67	69	452
Eschweilera ovata (Camb.) Mart.	0	1	1	2
Eschweilera blanchetiana (Berg) Miers	8	0	0	8
Gustavia augusta L.	8	6	11	25
Lecythis paraensis Huber	3	2	0	5
Lecythis usitata Miers	0	0	1	1
	671	161	195	1,027
No. of Lecythidaceae/ha	117.72	33.5	39	69.16

Table VII
Occurrence of Lecythidaceae in 5 types of forest in Guyana (data from Davis and Richards, 1934)

	Species	10-20 cm	20 cm	Total
Mora Forest 1.488 ha	*Eschweilera sagotiana* Miers	9	1	10
	E. decolorans Sandw. and *E. pallida* Miers	11	3	14
	E. longipes (Poit.) Miers	11	7	18
	Lecythis davisii Sandw.	3	1	4
				46
	46 trees of 462 over 10 cm diameter = 9.96% 5 species of 56 total = 8.9% Density of Lecythidaceae = 30.9/ha			
Morabukea Forest 1.488 ha	*Eschweilera sagotiana*	18	16	34
	E. wachenheimei (R. Ben.) Sandw.	5	6	11
	E. decolorans Sandw. and *E. pallida*	4	21	25
				70
	70 trees of 460 over 10 cm diameter = 15.2% 4 species of 99 total = 4.04% Density of Lecythidaceae = 47/ha			
Mixed Forest 1.488 ha	*Eschweilera sagotiana* Miers	5	34	39
	E. wachenheimei (R. Ben.) Sandw.	2	—	2
	E. decolorans and *E. pallida*	19	23	42
	Lecythis davisii Sandw.	—	1	1
	Couratari pulchra Miers (= *C. guianensis*)	—	2	2
				86
	86 trees out of 644 over 10 cm diameter = 13.35% 6 species of 91 total = 6.59% Density of Lecythidaceae = 57.8/ha			
Greenheart Forest 1.488 ha	*Eschweilera sagotiana* Miers	34	25	59
	E. wachenheimei (R. Ben.) Sandw.	26	7	33
	E. decolorans Sandw. and *E. pallida* Miers	16	21	37
	Lecythis davisii Sandw.	2	—	2
				131
	131 trees out of 773 over 10 cm diameter = 16.9% 5 species of 93 total = 5.37% Density of Lecythidaceae = 88/ha			
Wallaba Forest 1.488 ha	*Eschweilera corrugata* (Poit.) Miers	14	14	28
	28 trees out of 919 over 10 cm diameter = 3.04% 1 species of 75 total = 1.33% Density of Lecythidaceae = 18.8/ha			

organic matter and moisture. The Morabukea, Mixed, and Greenheart forests are on intermediate soils. A comparison of densities of Lecythidaceae in each forest type reveals that the family is most abundant on mesic sites with rich soils. Although 5 species are found in the Mora forest, they are represented by relatively few individuals. Only one species, *Lecythis corrugata,* was recorded in the Wallaba forest, and it was present in low numbers.

Species of Lecythidaceae have been most successful in mesic habitats, less successful in wet habitats, and least successful in dry habitats. Throughout Amazonia two distinct forest habitats are easily recognized, *terra firme* or forest on well drained sites and *várzea* or forest on periodically inundated sites. Many species of Lecythidaceae have adapted to *terra firme* and fewer to *várzea,* but some species have adapted to both habitats. Figures 22-28 show the distribution of species of Lecythidaceae in the Mocambo, Catú, and Aurá reserves (Pires, unpublished data). From these maps it is clear that some species prefer *terra firme* (*Lecythis idatimon* (Fig 24), *Eschweilera paniculata* (Fig 26), *E. apiculata* (Fig 28), and *E. odora* (Fig 25)) whereas others prefer *várzea (Gustavia augusta* (Fig 23) and *Allantoma lineata* (Fig 22)). Nevertheless, the habitat separation is not absolute for species predominantly of *terra firme* such as *E. odora* and *L. idatimon* (Figs 24, 25) which are frequently found in *várzea* or for species predominantly of *várzea* such as *Gustavia augusta* and *Allantoma lineata* which are sometimes found on *terra firme* (Figs 22, 23). In the Guianas we have occasionally observed *Gustavia augusta* on terra firme along ephermeral creeks or on soils underlain by hardpan which causes waterlogging in the wet season but allows dessication in the dry season, conditions similar to the riverine habitat where *G. augusta* is commonly found.

Drier habitats such as forests on white sands (e g *campina* forest), the *cerrado* of the planalto of Brazil, the *caatinga* of northeastern Brazil, and savannas are poor in species of Lecythidaceae. *Cariniana rubra* and *Eschweilera trochiformis* are *cerrado* species and *Lecythis corrugata* is common in the white sand forests of the Guianas, but we know of no other species of Lecythidaceae characteristic of these drier habitats. A possible explanation for the lack of Lecythidaceae in the drier habitats, which are also characterized by poor soils, is the apparent inability of most species of Lecythidaceae to form mycorrhizal associations. Only one of 11 species of Lecythidaceae occurring in a one hecare plot near Manaus (studied by Prance et al, 1976) had mycorrhizae (St. John, pers. comm.). In contrast, all nine species of Leguminosae examined from the same hectare had mycorrhizae. Mycorrhizal associations may be essential for extracting nutrients from the poor soils of the above dry habitats.

Lecythidaceae are not well represented in secondary forest on areas that have been previously cut and burned. However, in one area which had been cleared but not burned Lecythidaceae were abundant because of their ability to sprout from cut stumps. Prance (1975) studied a 2500 m^2 area of secondary forest near Manaus which had developed after the original forest had been cut but not burned. This area had many species of primary forest trees from many families, including 97 individuals in 5 species of Lecythidaceae (Table VIII). The high frequency of Lecythidaceae in the plot indicated that the original forest was also rich in Lecythidaceae. Studies of other areas which have been

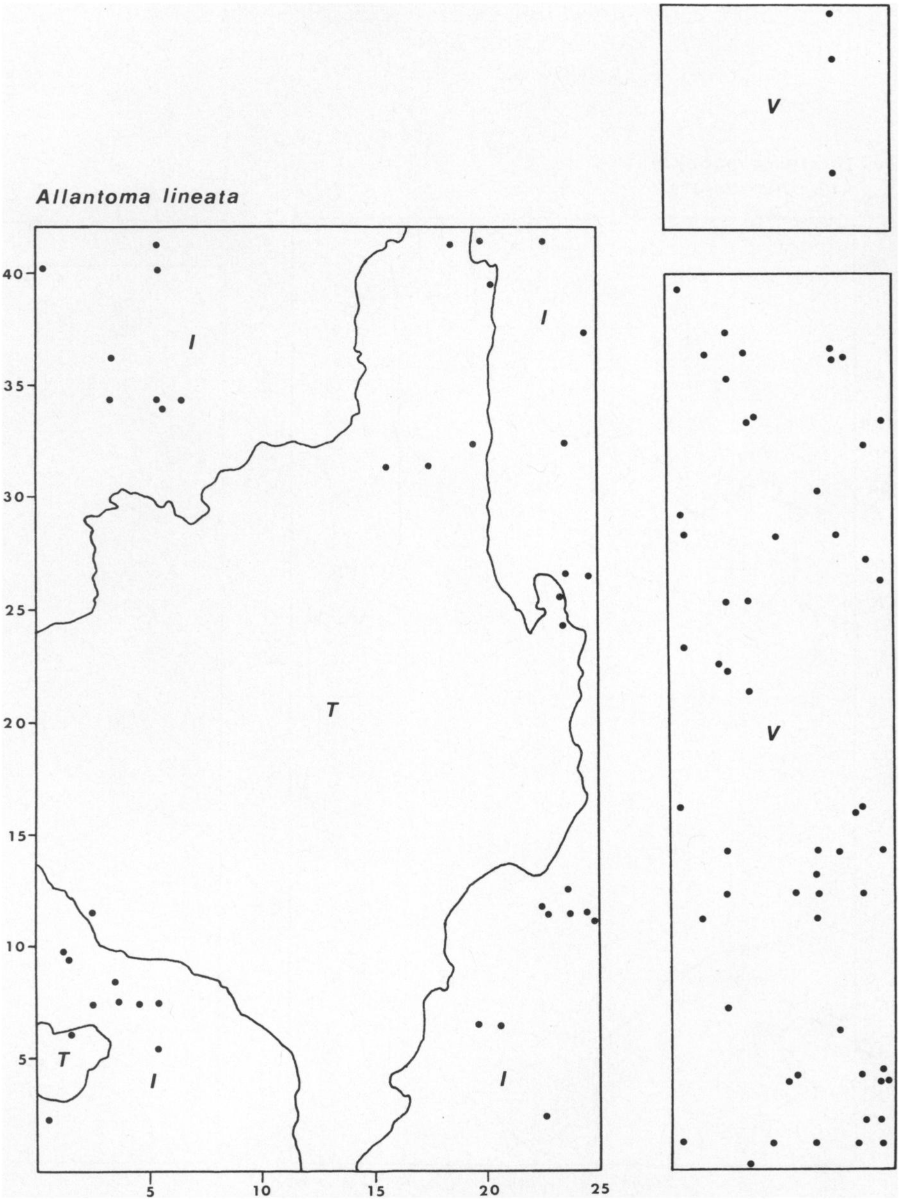


FIG 22. Distribution of *Allantoma lineata* in study areas within the Catú and Aurá Reserves Belém, Pará, Brazil (see Pires and Prance, 1977 for more details on the study areas). Each closed circle represents a tree with a circumference greater than or equal to 30 cm. The numbers on the sides of the large rectangle are in 10's of meters, ie the rectangle is 420 × 250 meters. The other two areas are drawn to the same scale. T = *terra firme,* I = *igapó,* V = *várzea. Terra firme* is never inundated, *igapó* is swamp forest that seldom dries out, and *várzea* is periodically inundated but may dry out for extended periods. Note the marked preference of *A. lineata* for the wetter forest types.

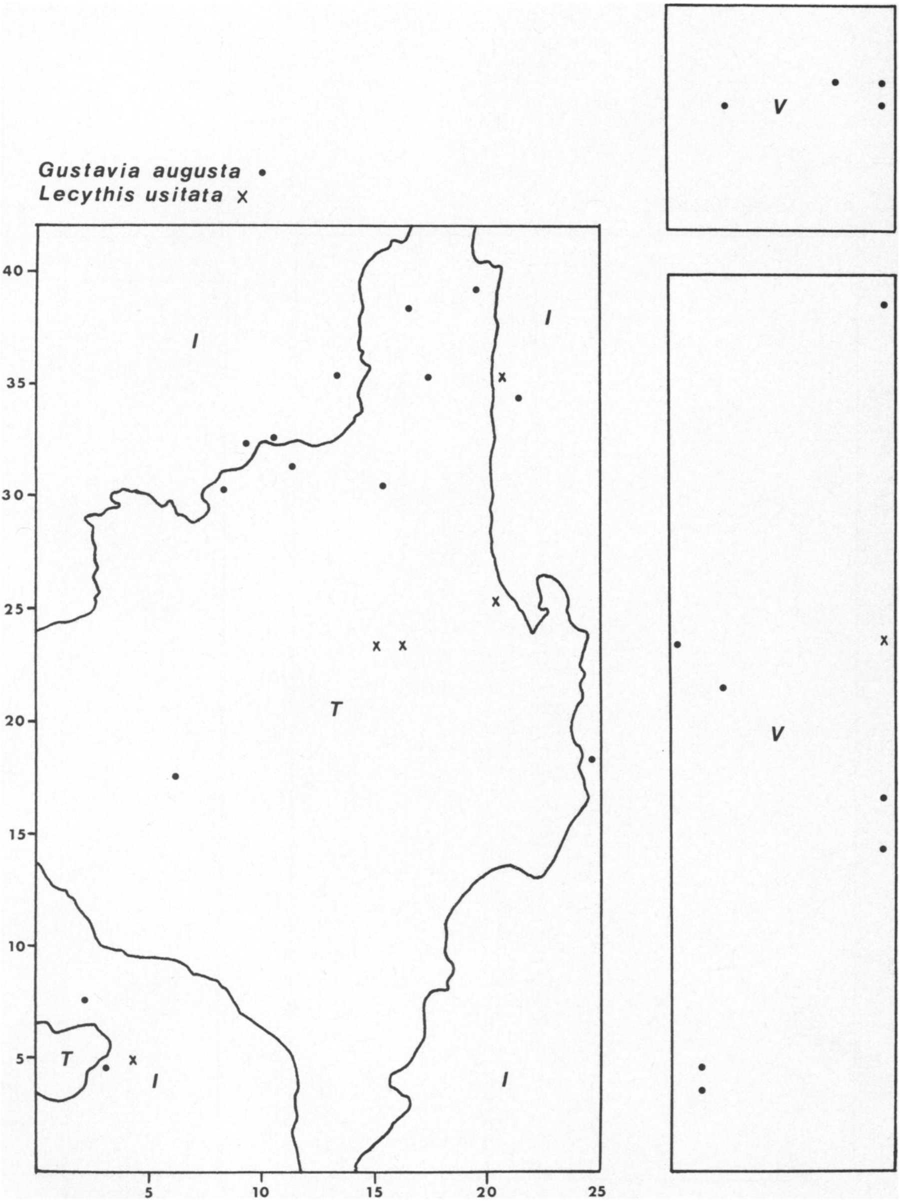


FIG 23. Distribution of *Gustavia augusta* and *Lecythis usitata* in study areas within the Catú and Aurá Reserves Belém, Pará, Brazil (see Pires and Prance, 1977 for more details on the study areas). Each symbol represents a tree with a circumference greater than or equal to 30 cm. The numbers on the sides of the large rectangle are in 10's of meters, ie the rectangle is 420 × 250 meters. The other two areas are drawn to the same scale. T = *terra firme,* I = *igapó,* V = *várzea. Terra firme* is never inundated, *igapó* is swamp forest that seldom dries out, and *várzea* is periodically inundated but may dry out for extended periods.

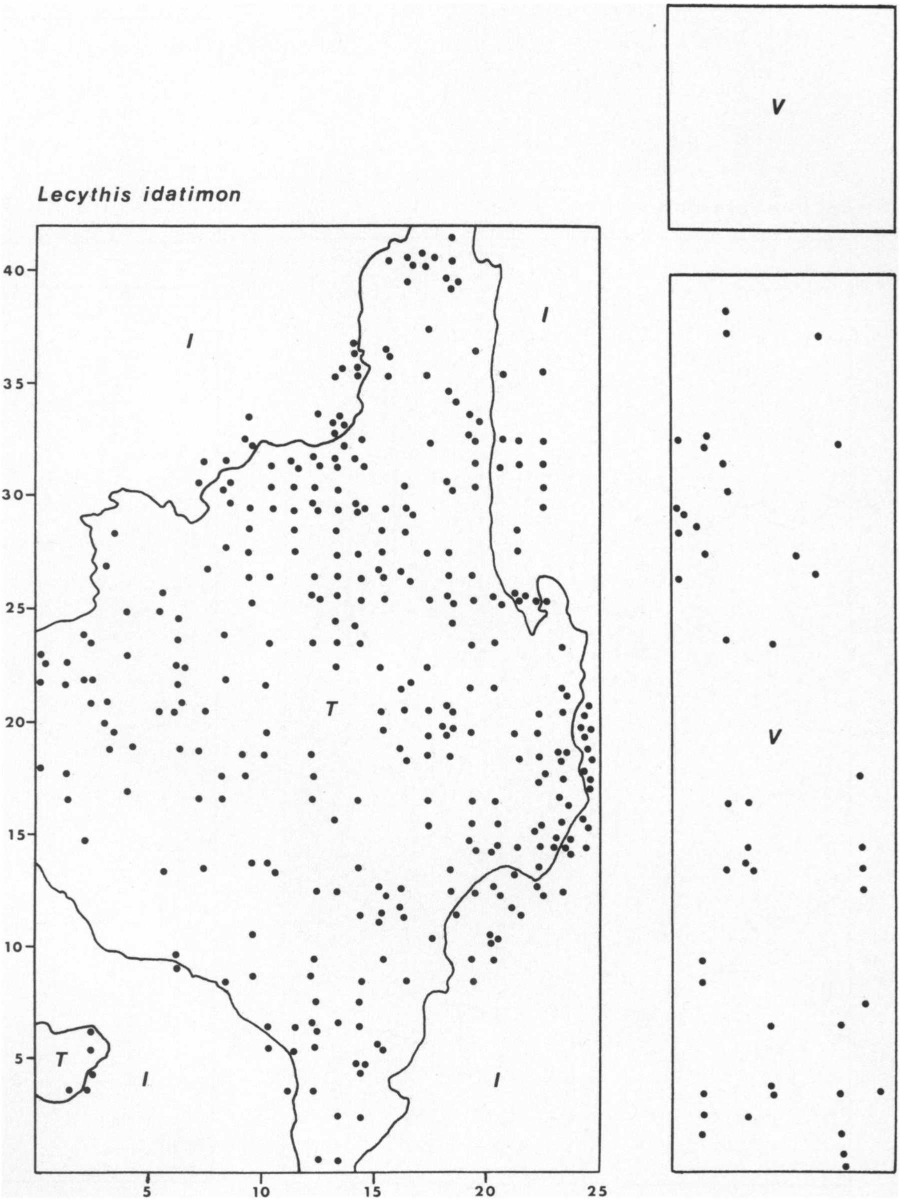


FIG 24. Distribution of *Lecythis idatimon* in study areas within the Catú and Aurá Reserves Belém, Pará, Brazil (see Pires and Prance, 1977 for more details on the study areas). Each closed circle represents a tree with a circumference greater than or equal to 30 cm. The numbers on the sides of the large rectangle are in 10's of meters, ie the rectangle is 420 x 250 meters. The other two areas are drawn to the same scale. T = *terra firme,* I = *igapó,* V = *várzea. Terra firme* is never inundated, *igapó* is swamp forest that seldom dries out, and *várzea* is periodically inundated but may dry out for extended periods. Note the preference of *L. idatimon* for *terra firme* and *várzea.*

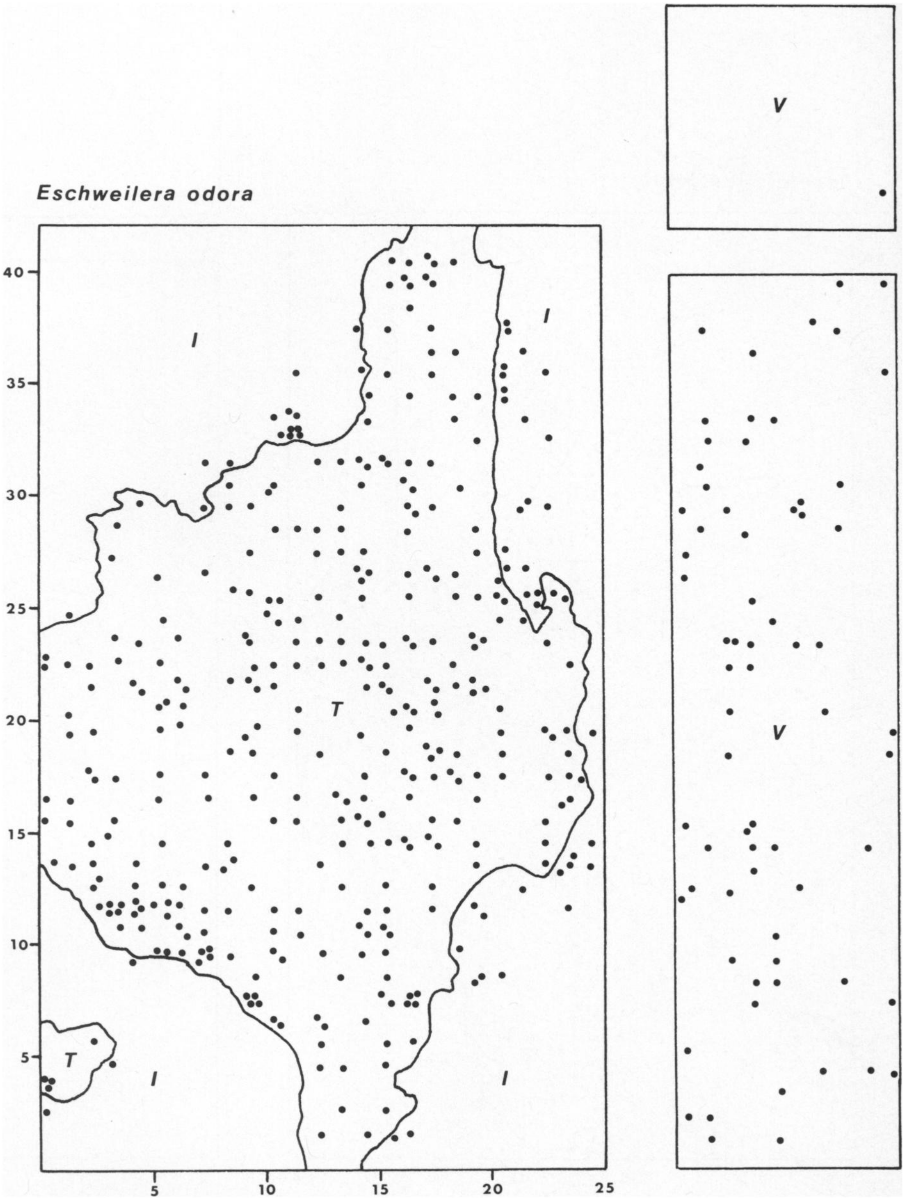


FIG 25. Distribution of *Eschweilera odora* in study areas within the Catú and Aurá Reserves Belém, Pará, Brazil (see Pires and Prance, 1977 for more details on the study areas). Each closed circle represents a tree with a circumference greater than or equal to 30 cm. The numbers on the sides of the large rectangle are in 10's of meters, ie the rectangle is 420 × 250 meters. The other two areas are drawn to the same scale. T = *terra firme,* I = *igapó,* V = *várzea. Terra firme* is never inundated, *igapó* is swamp forest that seldom dries out, and *várzea* is periodically inundated but may dry out for extended periods. Note the preference of *E. odora* for *terra firme* and *várzea.*

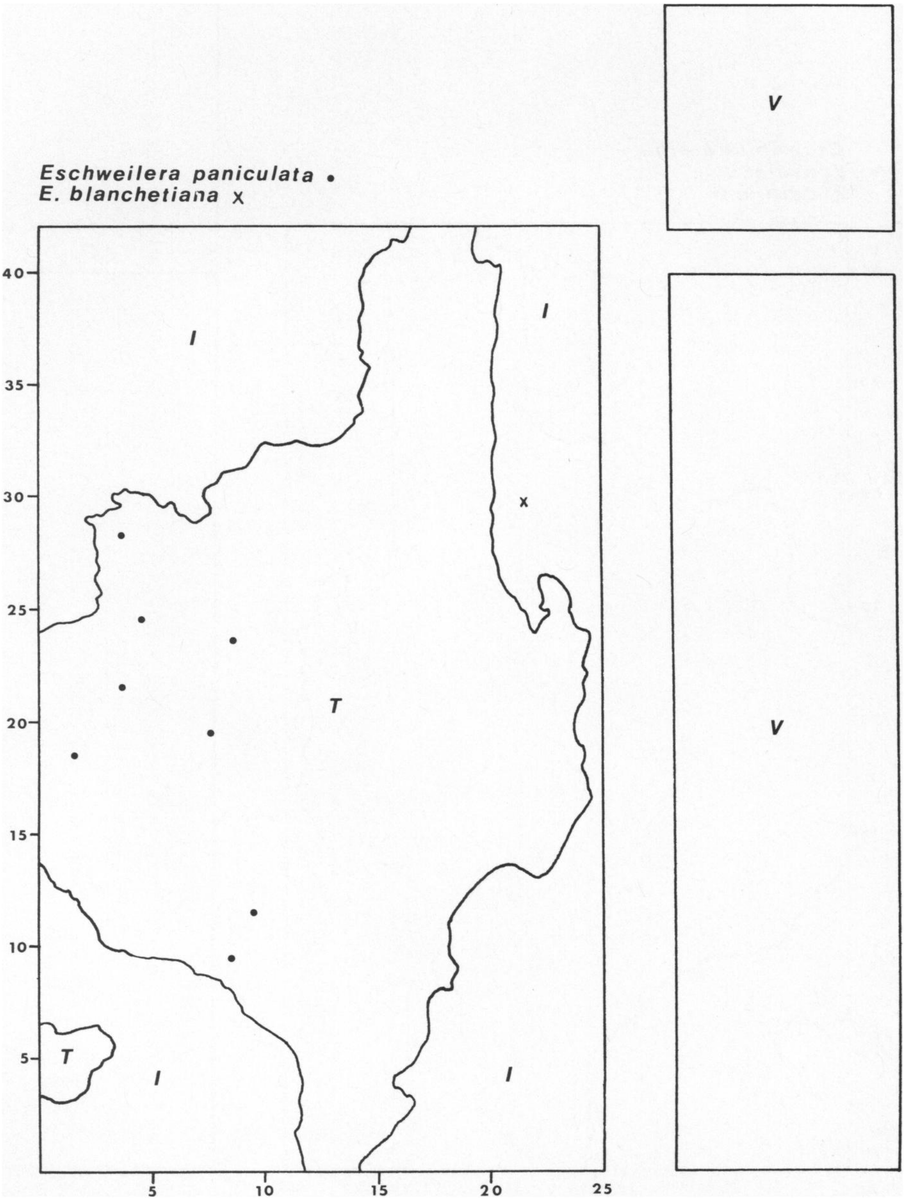


FIG. 26. Distributions of *Eschweilera paniculata* and *E. blanchetiana* in study areas within the Catú and Aurá Reserves Belém, Pará, Brazil (see Pires and Prance, 1977 for more details on the study areas). Each symbol represents a tree with a circumference greater than or equal to 30 cm. The numbers on the sides of the large rectangle are in 10's of meters, ie the rectangle is 420 x 250 meters. The other two areas are drawn to the same scale. T = *terra firme,* I = *igapó,* V = *várzea. Terra firme* is never inundated, *igapó* is swamp forest that seldom dries out, and *várzea* is periodically inundated but may dry out for extended periods. Note the localized distribution of *E. paniculata* and its marked preference for *terra firme.*

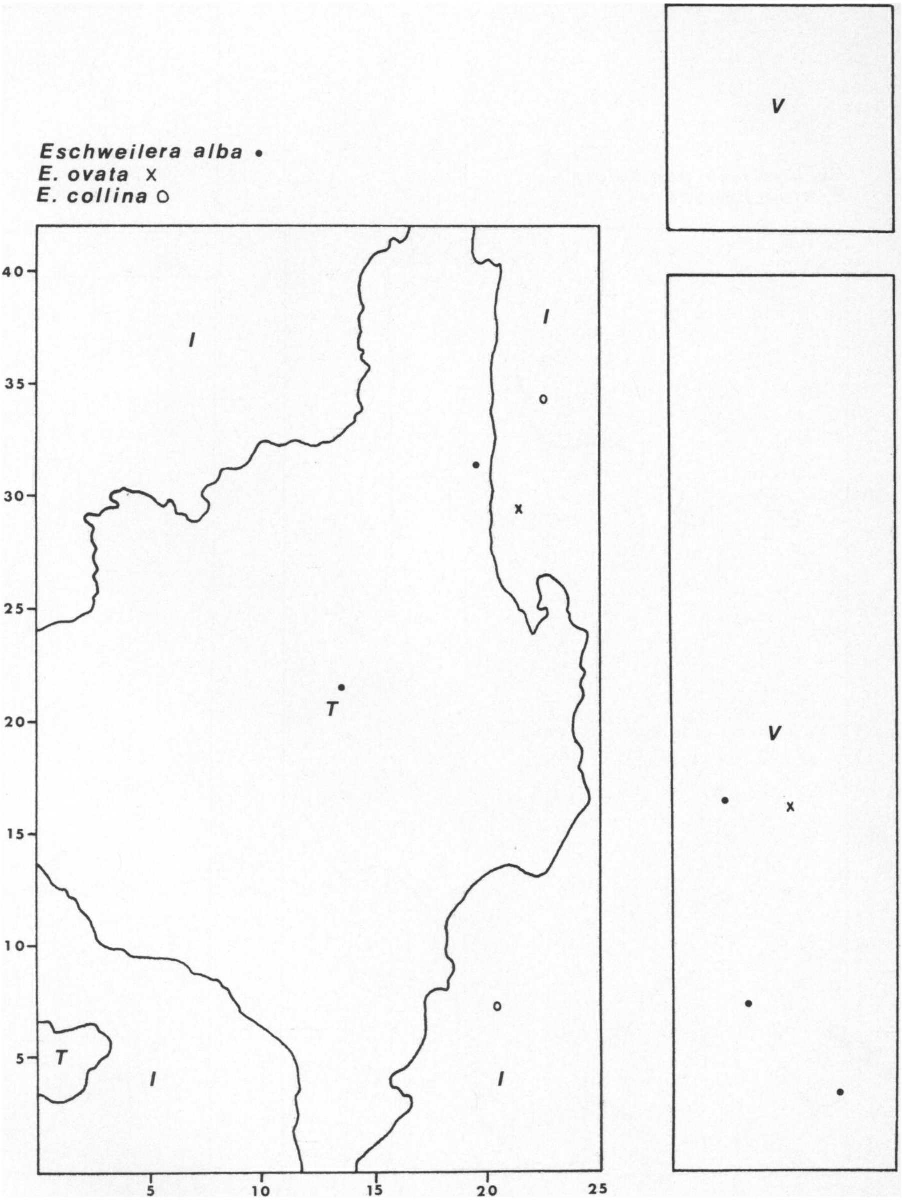


FIG 27. Distributions of *Eschweilera alba, E. ovata,* and *E. collina* in study areas within the Catú and Aurá Reserves Belém, Pará, Brazil (see Pires and Prance, 1977 for more details on the study areas). Each symbol represents a tree with a circumference greater than or equal to 30 cm. The numbers on the sides of the rectangle are in 10's of meters, ie the rectangle is 420 x 250 meters. The other two areas are drawn to the same scale. T = *terra firme,* I = *igapó,* V = *várzea. Terra firme* is never inundated, *igapó* is swamp forest that seldom dries out, and *várzea* is periodically inundated but may dry out for extended periods. Note that of these three species only *E. alba* is found on *terra firme* but that it is also found in *várzea.*

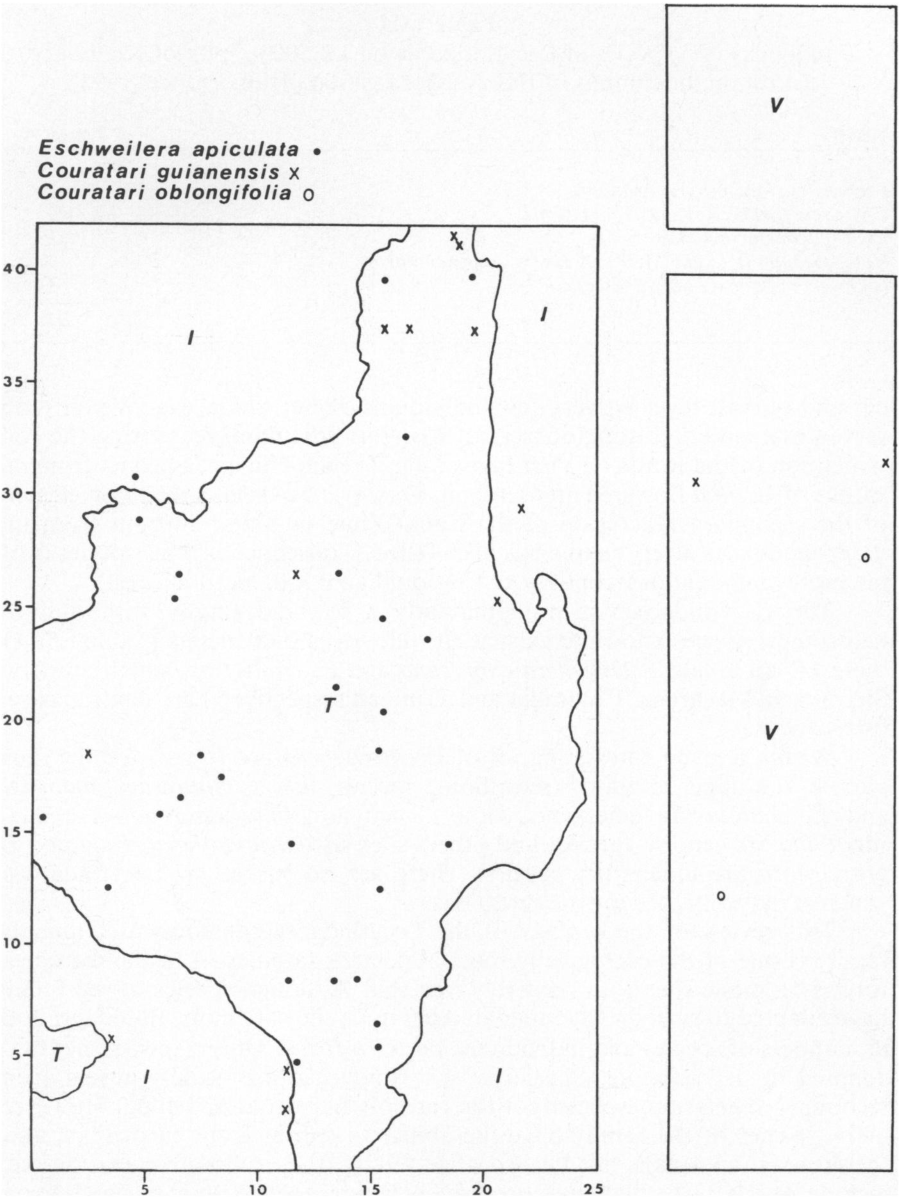


FIG. 28. Distributions of *Eschweilera apiculata, Couratari guianensis,* and *C. oblongifolia* in study areas within the Catú and Aurá Reserves Belém, Pará, Brazil (see Pires and Prance, 1977 for more details on the study areas). Each symbol represents a tree with a circumference greater than or equal to 30 cm. The numbers on the sides of the large rectangle are in 10's of meters, i e the rectangle is 420 × 250 meters. The other two areas are drawn to the same scale. T = *terra firme,* I = *igapó,* V = *várzea. Terra firme* is never inundated, *igapó* is swamp forest that seldom dries out, and *várzea* is periodically inundated but may dry out for extended periods. Note the marked preference of *Eschweilera apiculata* for *terra firme.*

Table VIII

Frequency of 5 species of Lecythidaceae on a 2,500 m² plot of secondary forest on the campus of INPA, Manaus (data from Prance, 1975)

Species	Frequency
Eschweilera longipes (Poit.) Miers	12
Chytroma foetida R. Knuth (= *Lecythis)*	9
Eschweilera fracta R. Knuth	11
Holopyxidium jaranum (Hub.) Ducke (= *Eschweilera)*	2
Eschweilera odora (Poepp.) Miers	63
	97

cut and burned revealed very few individuals of Lecythidaceae. We have observed extensive sprouting of trees of *Lecythis alba* damaged during the constructiuon of the Route de l'Est highway in French Guiana. Sprouts from cut trunks of *L. alba* flowered and set fruit. *Gustavia superba,* a common element of the secondary vegetation of the Canal Zone, is able to sprout from underground parts after the tree has been felled. Consequently, this species is often more abundant in secondary vegetation than it is in mature forest.

The Lecythidaceae is predominantly a lowland family with only 14 neotropical species known to exist at altitudes over 1000 meters (Table IX). Of these 14, all except *Eschweilera cabrerana* and *E. trinitensis,* which are from Sierra de la Macarena, Colombia and Trinidad respectively, are Andean cloud forest species.

Within a given forest, species of Lecythidaceae are found, for the most part, in the upper strata of trees. Some species such as *Couratari guianensis* and *C. stellata* are emergents, others such as *Eschweilera odora* and *E. sagotiana* are canopy species, and others such as *Gustavia hexapetala* and *E. grandiflora* are understory species. There are no species of Lecythidaceae, which at maturity, occupy the shrub layer.

This review of the ecology of the Lecythidaceae demonstrates that the family is one of the ecologically most important families of lowland tropical forests on mesic sites with relatively rich soil. Although species of the family have adapted to periodically inundated habitats, they are more abundant, both in numbers of species and individuals, on *terra firme*. Only a few species have adapted to dry habitats. Species of Lecythidaceae are usually absent from secondary vegetation especially if the forest is burned after felling. However, many species of the family have the ability to sprout from cut trunks, and, therefore, if an area is not burned after felling, the resultant vegetation may include a relatively high number of Lecythidaceae. Within a given forest almost all mature individuals of Lecythidaceae are restricted to the upper three strata.

VII. PHENOLOGY

Throughout most of the neotropics monthly rainfall fluctuates, resulting in at least several drier months each year. For example, in central Panama

Table IX

Species of Lecythidaceae known to occur at altitudes of over 1000 m

Eschweilera antioquensis Dugand & Daniel
E. cabrerana Philipson
E. cauliflora Cuatr.
E. ciroana R. Knuth
E. montana Cuatr.
E. papillata Uribe
E. perumbonata Pittier
E. sessilis A. C. Smith
E. tenax Moritz ex Berg (incl. *E. fendleriana* Miers, *E. monosperma* Pitt.)
E. trinitensis Smith & Beard
E. violacea Cuatr.
Lecythis karuaiensis Steyerm.
Gustavia macarensis Philipson
  subsp *paucisperma* Mori
Gustavia speciosa (Knuth) Berg
  subsp *occidentalis* (Cuatr.) Mori

there is an annual four- to five-month dry season with little or no rain between December and April (Mori and Kallunki, 1976). In Surinam, there are four seasons, a long dry season from August through November, a short wet season from December to January, a short dry season from February to March, and a long wet season from April through July (Schulz, 1960). These are the basic seasons, with yearly and geographic modifications, throughout the Guianan region. For instance, to the west and into Guyana the short dry season becomes more pronounced, and to the east, especially in eastern French Guiana, rainfall increases and the seasons are less distinct (Schulz, 1960). Even in Surinam the short wet season may be absent in some years and the short dry season absent in other years, producing dry and wet years respectively (Schulz, 1960). Rainfall in the Amazon Basin also fluctuates, more or less predictably, throughout the year. The dry season, which is more or less pronounced depending on locality, usually extends from September to March in the northern hemisphere and from April through September in the southern hemisphere (Meggers, 1971).

In seasonally dry forests, peak flowering of trees occurs during the dry season (Fournier and Salas, 1966; Janzen, 1967; Croat, 1969; Frankie et al, 1974; Frankie, 1975; Mori and Kallunki, 1976). Not only do more species bloom during this time of the year, but those that do have larger, more spectacular flowers (Mori and Kallunki, 1976). These species are pollinated, for the most part, by medium to large bees which are more abundant during the dry than the wet season (Frankie, 1975).

Our studies of flowering periods in the Lecythidaceae indicate that the greatest number of species and individuals flower during the dry season. Peak flowering occurs in the Guianas in the long dry season and in central Amazonia during the dry season. After the onset of heavy rains fewer species flower. In contrast, flowering of Lecythidaceae in Panama occurs mostly during the wet season (May to November). However, most species of Panamanian Lecythidaceae grow in mountainous areas which have less pronounced or no real dry seasons.

The induction of flowering in tropical plants has been attributed to photoperiod (McClelland, 1924; Allard, 1935; Bünning, 1948; Njoku, 1958; Hopkins, 1963; Murashige, 1966; Lawton and Akpan, 1968), to reduction in soil moisture (Mori and Kallunki, 1976), to reduction of water stress (Went, 1957; Alvim, 1960, 1964); or to a sharp drop in temperature associated with tropical storms (Kerling, 1941; Holttum, 1953; Went, 1957; Richards, 1970). Opler et al (1976) demonstrate that rainfall is important in the timing of flowering of some tropical plants.

We do not know what factors trigger flowering in most species of Lecythidaceae which flower in the dry season. Nevertheless, flowering of *Gustavia superba* is apparently triggered by low soil moisture, for this species blooms only after several weeks without rain (Mori and Kallunki, 1976).

Smythe (1970) has pointed out that many tropical species with large animal-dispersed seeds mature fruit in the early wet season. Seeds dispersed at this time are able to take advantage of the first rains and are able to utilize the nutrients being released from the litter which accumulated during the dry season (Smythe, 1970). Most animal-dispersed Lecythidaceae, for example, *Gustavia superba* in central Panama (Mori and Kallunki, 1976), mature fruits at the beginning of the wet season.

The relationship of reproductive and vegetative stages of development in the species of Lecythidaceae that we have studied indicate the following phenological strategies: 1) leaf drop, leaf flush, flowering; 2) leaf drop, flowering, leaf flush; and 3) leaf drop independent of flowering with leaf production more or less continuous throughout the year.

The first strategy is utilized by a closely related group of large-fruited *Lecythis* species which includes *L. pisonis, L. usitata,* and *L. ampla.* Near Puerto Viejo, Costa Rica, flowering of *L. ampla* immediately follows leaf flush at the onset of increased rainfall. Frankie et al (1974) report that leaf drop occurs in April, leaf flushing from May to June, flowering from May to July, and mature fruit from March to April in this area. Here, between 8 and 10 months lapse from flowering to mature fruits. The same species in Darién Province, Panama loses its leaves and flowers a short time after new leaves appear. Here, on the lower slopes of Cerro Pirre, Mori observed several trees of this species without leaves and one tree with young leaves and flowers at the beginning of the wet season during the first two weeks of April 1975.

The preceding observations show that *L. ampla* drops its leaves for a short time at the end of the dry season and produces flowers shortly after new leaf production at the beginning of the wet season. Its fruits reach maturity about 8 to 10 months later.

Observations were made at Summit Gardens, Canal Zone of cultivated trees of *L. pisonis,* a species native to Brazil. This species, too, loses all leaves and produces flowers shortly after the new leaves are flushed. Leaf fall and flowering occur during the dry season, and the fruits mature 10 months later in the wet season.

Phenological events of five trees of *L. usitata* have been observed for 5 to 10 years each between 1965 and 1974 at the Reserva Florestal Ducke by the personnel of the reserve, the silvicultural section and the herbarium of the Instituto Nacional de Pesquisas da Amazônia (INPA). As in *L. ampla* and *L.*

pisonis, L. usitata drops its leaves in the dry season and shortly thereafter produces new leaves and flowers (Fig 29). In some years, leaf fall and subsequent leaf flush were not followed by flowering. For example, tree 279 did not flower at all in five years of observation, whereas trees 96 and 296 flowered in 5 of 10 and 3 of 5 years, respectively. Individual trees flowered from 1 to 4 months, and the fruits matured 7 to 10 months later.

Phenological events of five trees of *Cariniana micrantha* were observed between 1965 and 1976 at the Reserva Florestal Ducke by the personnel of INPA. This species also flowered after leaf fall and subsequent leaf production. Leaf fall, leaf flush, and flower production occurred predominantly in the dry season, and mature fruits were also observed most frequently during the dry season (Fig 30). Because the seeds of *C. micrantha* are winged and dispersed by wind their release at the beginning of the dry season probably insures maximum dispersal. Of the 50 tree years of observation of this species, flowers and/or fruits were observed in 36 years. Eleven of the 14 tree years in which flowers or fruits were not observed occurred in the period from 1970 to 1973, perhaps because of some climatic factor we have not recognized.

The nocturnally flowering, bat-pollinated *Lecythis poiteaui* has the same phenological strategy as the preceding four species. This species loses its leaves shortly before flowering, flushes new leaves, and then flowers before the new leaves have lignified. Four trees of *L. poiteaui,* observed for a total of 20 tree years (between 1963 and 1971) by the Surinam Forest Service in their Kamp 8 Arboretum, started to bloom at the end of the long dry season (Oct-Nov), continued through the short wet season (Dec-Jan), and finished flowering halfway into the short dry season (Feb). No trees flowered during the long wet season. Individual trees bloomed from one to four months in a year.

The second phenological strategy in the Lecythidaceae, i e leaf fall, flowering, and then leaf flush is found in *Couratari oligantha, C. atrovinosa* and *C. guianensis. Couratari guianensis* loses all of its leaves in a short time, flowers, and then flushes new leaves. This strategy makes the tree more conspicuous at anthesis and, therefore, probably more attractive to pollinators. Two trees of *C. guianensis* observed between 1963 and 1971 by the Surinam Forest Service at their Kamp 8 Arboretum bloomed from April to October (long wet into long dry seasons). Two trees of *Couratari stellata,* a species sympatric with *C. guianensis,* retained their leaves during anthesis. Flowering of *C. stellata* was observed by the Surinam Forest Service, in the same arboretum, for a two-year period, to occur between October and January (long dry into short wet seasons). These differences in phenology and flowering strategy may have evolved to reduce competition for pollinators between these two sympatric species of *Couratari.*

The third phenological strategy in the Lecythidaceae, i e leaf fall independent of flowering and more or less continuous production of leaves, characterizes many species of Lecythidaceae. Mori and Kallunki (1976) found that *Gustavia superba* loses leaves all year long but has a marked peak of leaf loss at the end of the dry season into the first month of the wet season (Fig 31). Increased leaf fall at the end of the dry season is probably an adaptation to increased water stress, and increased leaf loss in the first month of the wet season may be necessary to maintain a proper leaf number to plant ratio as new leaves

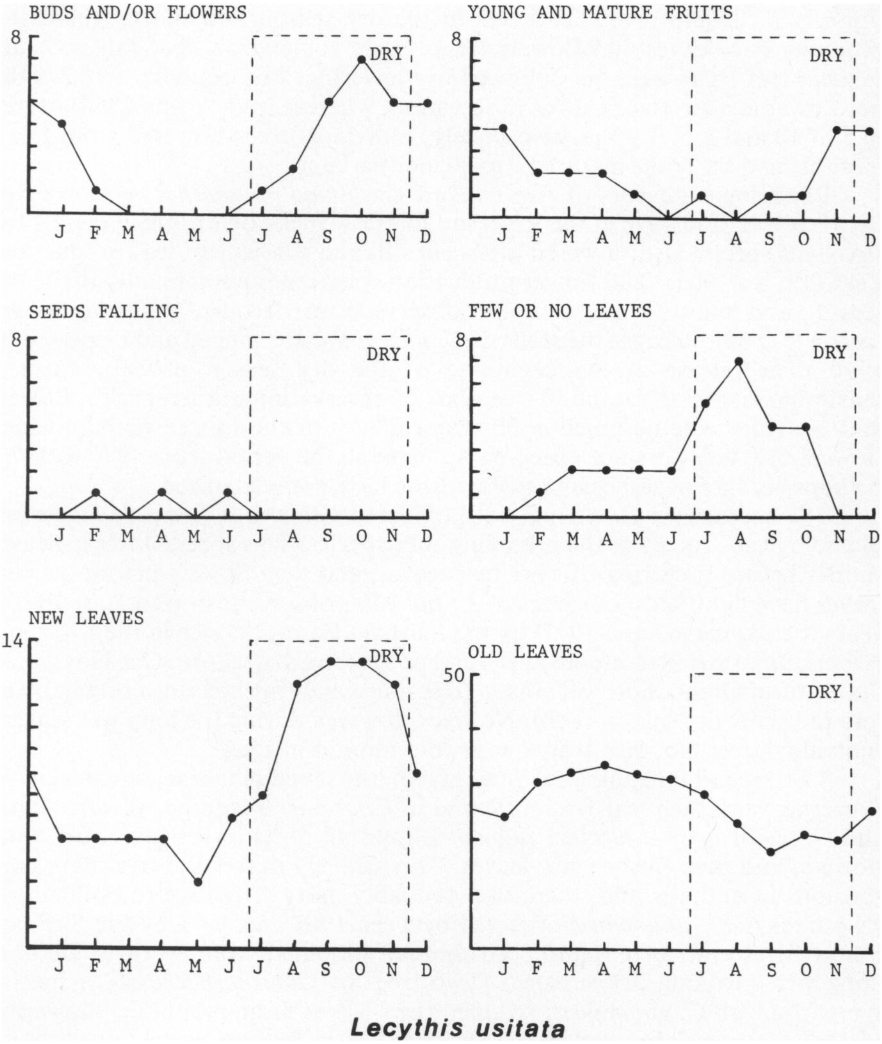


FIG 29. Phenological events of *Lecythis usitata*. The closed circles represent the number of trees observed each month displaying a given phenological event. The observations were made on five trees over a 10 year period in the Reserva Florestal Ducke, Amazonas, Brazil. The dry season is represented by the rectangular area. The data were provided through the courtesy of the Instituto Nacional de Pesquisas da Amazônia (INPA).

are being produced. Alvim (1964) suggests that competition between newly expanding leaves and old leaves for photosynthate and/or hormones may cause leaf drop. Leaf production in *G. superba* is bimodal, with a peak of activity at the beginning of the dry season and another at the beginning of the wet season (Fig 31). Mori and Kallunki (1976) suggest that the first flush is an adaptation to a period of the year when phytophagous insects are least abundant and, therefore, the new leaves have the greatest chance to become established, and

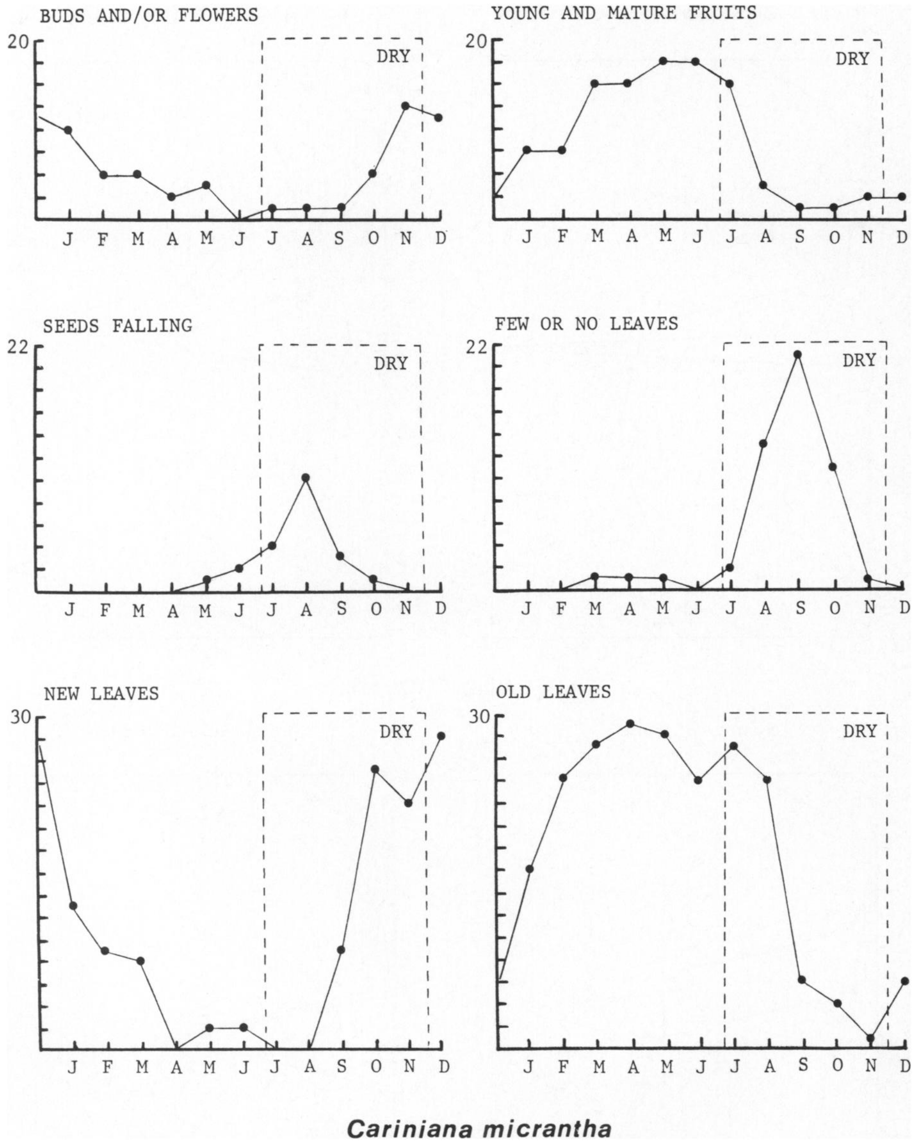
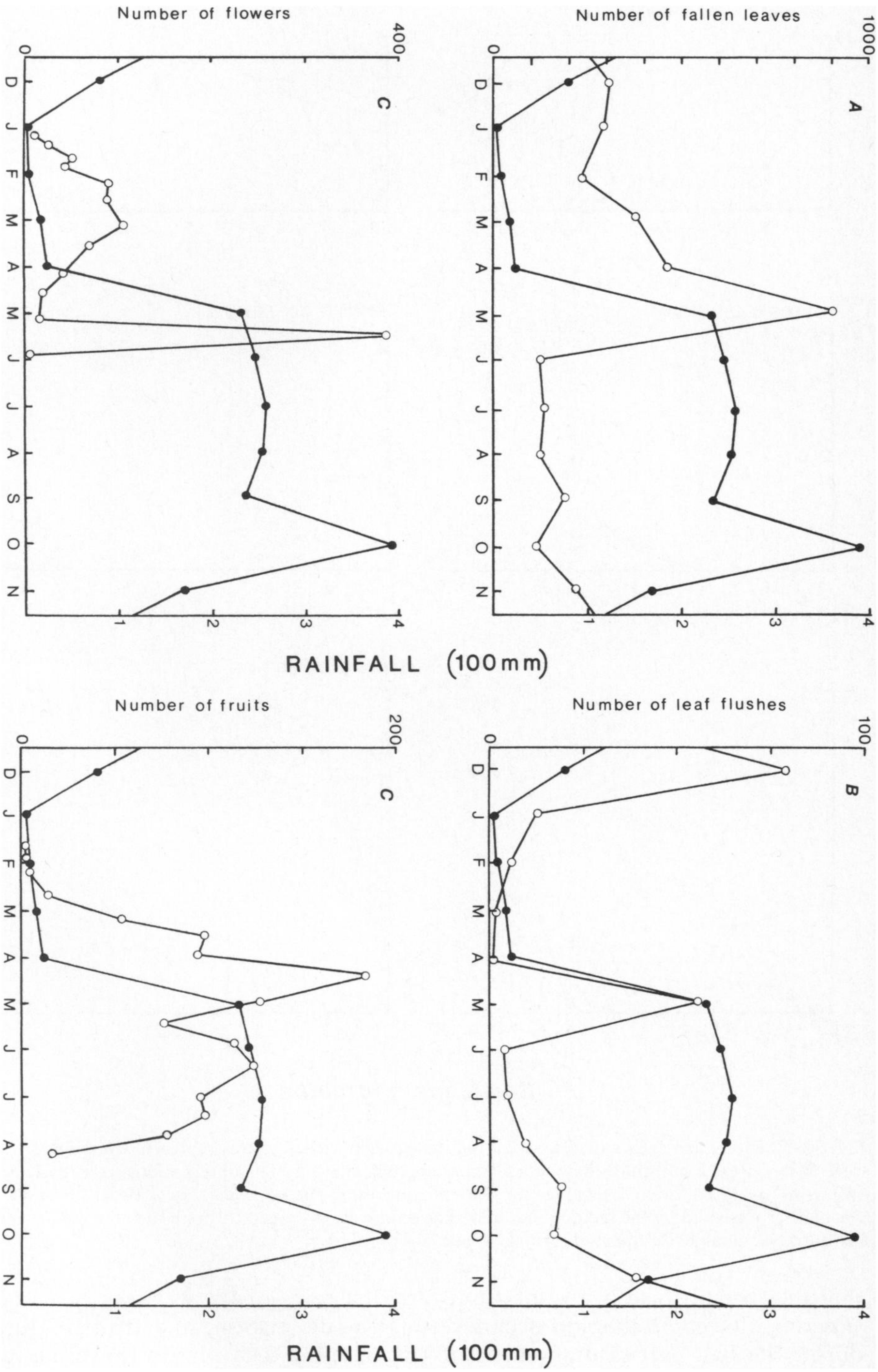


FIG 30. Phenological events of *Cariniana micrantha.* The closed circles represent the number of trees observed each month displaying a given phenological event. The observations were made on five years over a 12 year period in the Reserva Florestal Ducke, Amazonas, Brazil. The dry season is represented by the rectangular area. The data were provided through the courtesy of the Instituto Nacional de Pesquisas da Amazônia (INPA).

that the second flush is a response to the first rains of the wet season. In *G. superba,* flower production occurs during the dry season, and fruits mature during the first part of the wet season (Figs 31, 32). Dry season flowering insures that the flowers will be present when the proper bees are available for


Number of flowers
0
400
C
D
J
F
M
A
M
J
J
A
S
O
N
1
2
3
4
Number of fallen leaves
0
1000
A
D
J
F
M
A
M
J
J
A
S
O
N
1
2
3
4
RAINFALL (100mm)
Number of fruits
0
200
C
D
J
F
M
A
M
J
J
A
S
O
N
1
2
3
4
Number of leaf flushes
0
100
B
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RAINFALL (100mm)

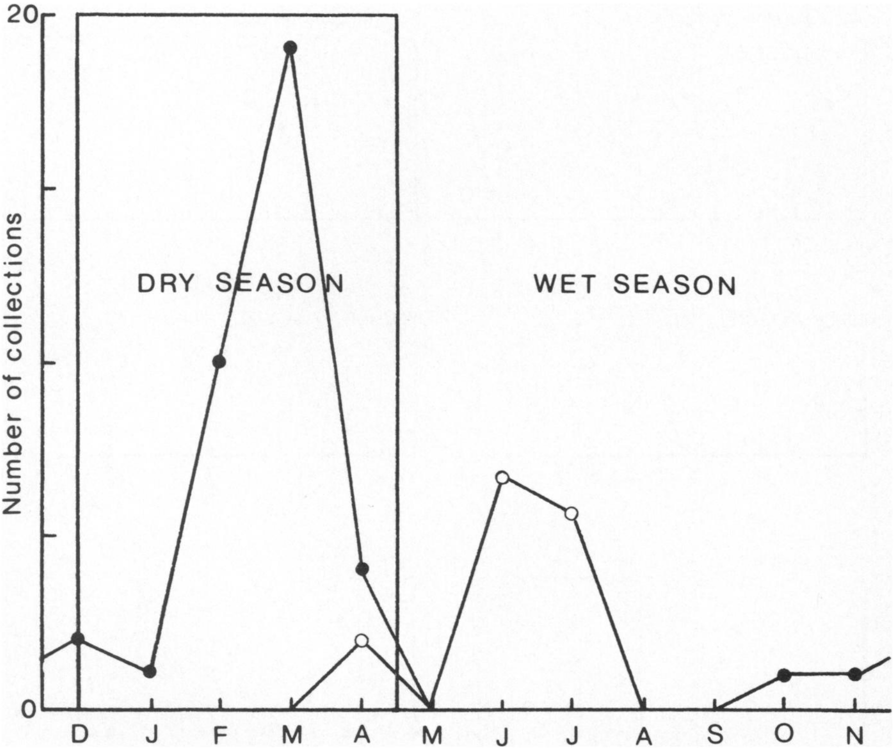

FIG 32. Graph depicting the number of fertile collections of *Gustavia superba* known for each month of the year from Panama. Closed circles represent flowering collections and open circles represent fruiting collections.

pollination. Fruit maturation during the first part of the wet season enables the seeds to utilize the increased supply of rainfall and the nutrients which become available from the decomposition of litter which accumulates during the dry season (Smythe, 1970; Mori and Kallunki, 1976).

Corythophora alta and *C. rimosa* are two sympatric species which flower and fruit at different times of the year (Figs 33, 34). *Corythophora alta* flowers from October to April (late dry season into wet season) and matures fruit between June and September (late wet season into middle dry season). In contrast, *C. rimosa* flowers from February to October (wet season into middle dry season) with a peak in November and matures fruit from August to February

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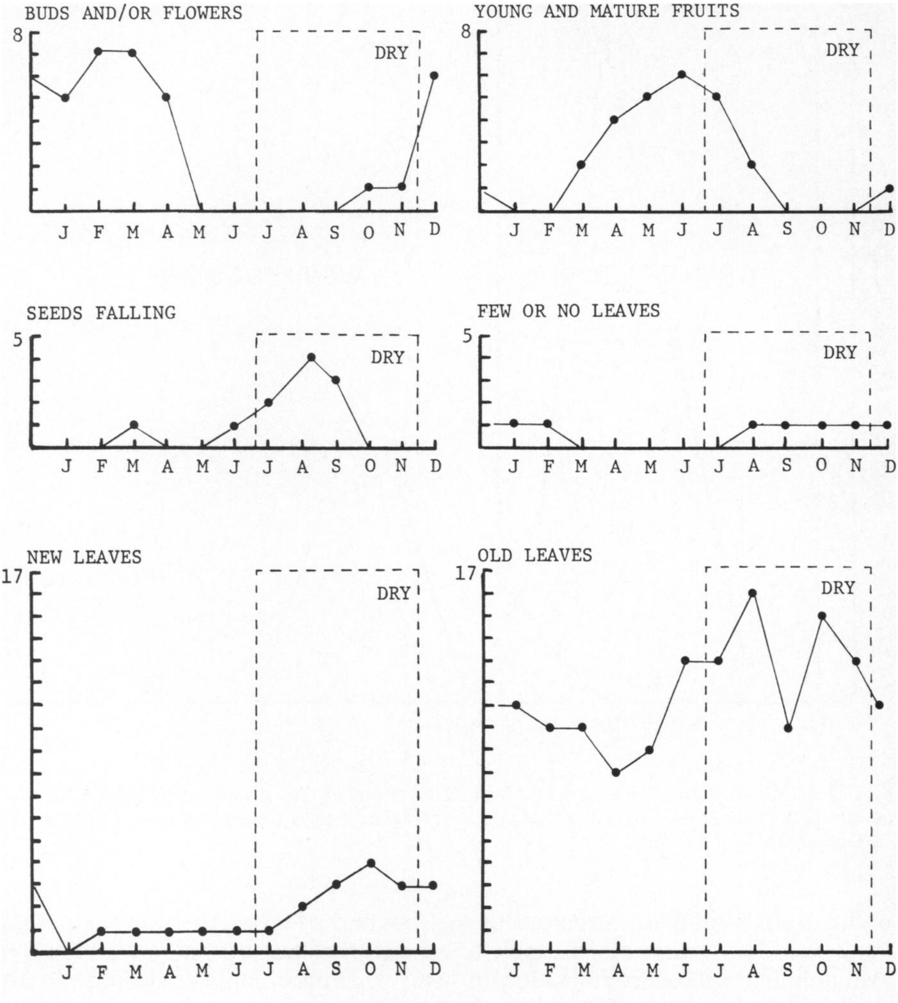
FIG 31. Graphs depicting phenological events of *Gustavia superba*. A. Leaf fall. The open circles represent the number of leaves that fell each month into an area 77 m^2. B. Leaf production. The open circles represent the number of leaf flushes observed on the first of the following month. C. Flower production. The open circles represent the number of flowers observed on a given date. D. Fruit production. The open circles represent the number of fruits observed on a given date. In all graphs the rainfall for each month during the course of the study is represented by a closed circle and the tick marks on the abscissa represent the middle of the month.



Corythophora alta

FIG 33. Phenological events of *Corythophora alta*. The closed circles represent the number of trees observed each month displaying a given phenological event. The observations were made on four trees over a seven year period in the Reserva Florestal Ducke, Amazonas, Brazil. The dry season is represented by the rectangular area. The data were provided through the courtesy of the Instituto Nacional de Pesquisas da Amazônia (INPA).

(dry season into early wet season). The staggered flowering and fruiting times of these closely related species may be an adaptation to reduce competition for pollinators and dispersal agents.

In summary, the Lecythidaceae have at least three phenological strategies which are based on the relationship between vegetative and reproductive stages

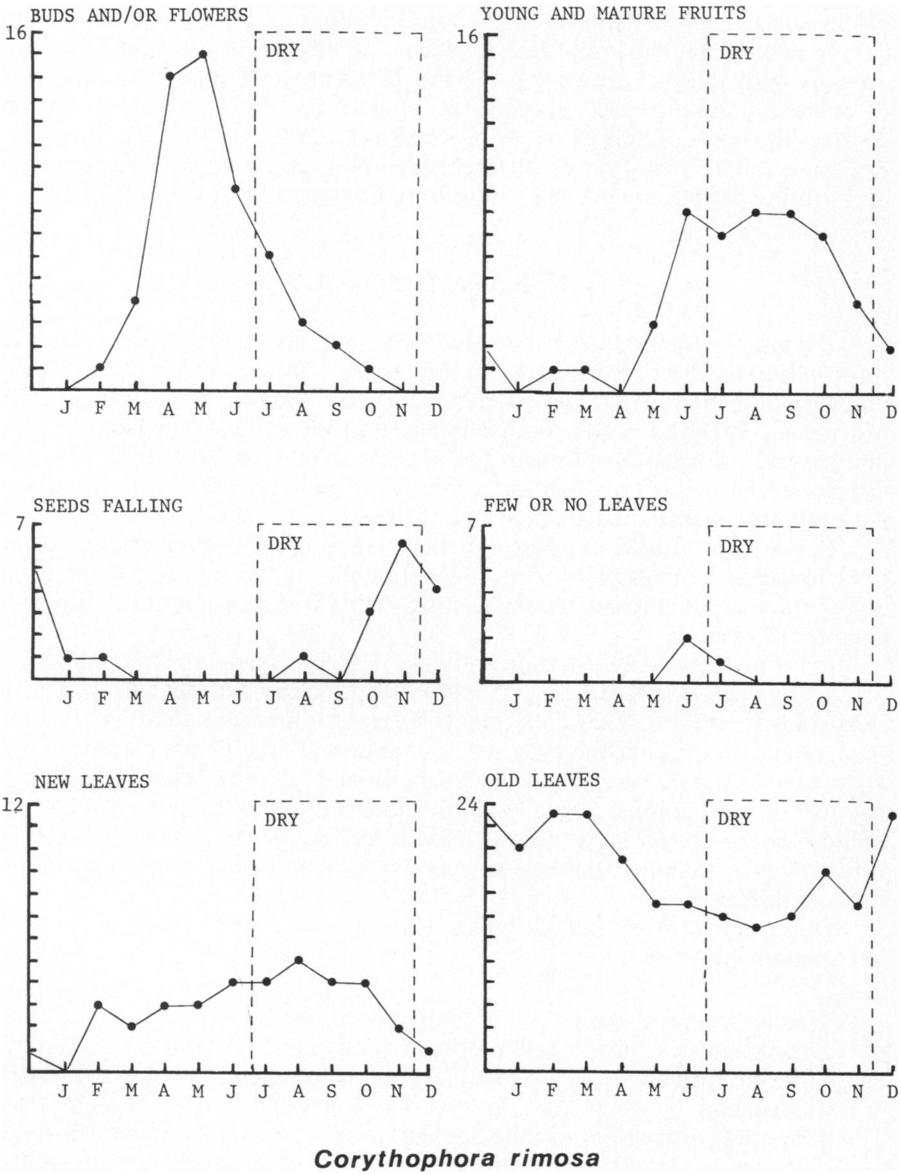


FIG 34. Phenological events of *Corythophora rimosa*. The closed circles represent the number of trees observed each month displaying a given phenological event. The observations were made on five trees over a 7 year period in the Reserva Florestal Ducke, Amazonas, Brazil. The dry season is represented by the rectangular area. The data were provided through the courtesy of the Instituto Nacional de Pesquisas da Amazônia (INPA).

of development. Most species of the family bloom in the dry season. Several closely related sympatric species, of which *Corythophora alta* and *C. rimosa* are only one example, are known to have different flowering times. The fruits of most animal-dispersed species reach maturity during the wet season, whereas the fruits of at least one wind-dispersed species are released during the dry season. The evolution of different phenological strategies and flowering and fruiting periods are probably important interspecific isolating factors.

VIII. FLORAL BIOLOGY

Despite the abundance of Lecythidaceae in many neotropical forests little information has been gathered about the family's floral biology. Only recently (Jackson and Salas, 1965; Dias, 1967; Mori and Kallunki, 1976; Prance, 1976; Mori et al, 1978) have data been published on the subject. This chapter summarizes the information given in the aforementioned papers. Lists of insect visitors to the flowers of Lecythidaceae and of the vouchers of the species of the Lecythidaceae studied are provided in Mori et al (1978).

Because an understanding of the structure of the androecium of Lecythidaceae is necessary for an understanding of the family's pollination, this chapter should be read in conjunction with our discussion of the flower in Chapter IV, Part 4.

Prior to our studies, Jackson and Salas (1965) investigated the pollination of *Lecythis elliptica* H.B.K. (=*L. minor* Jacq.) cultivated outside its natural range in Puerto Rico. They collected 43 species of insects in 10 orders from its flowers and found that the primary pollinator was the female carpenter bee, *Xylocopa brasilianorum* (L.). Their experiments also demonstrated that *L. elliptica* is allogamous. Dias in 1967 made an unpublished study of the pollination of *Bertholletia excelsa* Humb. & Bonpl. His insect collection, which Prance examined in Belém, reveals that the principal pollinators are Euglossine bees.

Our studies (Mori and Kallunki, 1976; Prance, 1976; Mori et al, 1978) have demonstrated that:

1. at least several species of the family are allogamous;
2. bees are the principle pollinators of neotropical Lecythidaceae;
3. those species with the most zygomorphic flowers have the fewest stamens;
4. species with actinomorphic or zygomorphic, open flowers utilize pollen as an attractant and those with zygomorphic closed flowers utilize nectar;
5. increasing zygomorphy and reduction in stamen number are concomitant with nectar production;
6. species with more specialized flowers (i e more zygomorphic, with closed hoods, fewer stamens, and nectar) are visited by more specialized bees than those species with less specialized flowers;
7. a combination of factors operate to reduce interspecific competition for pollinators.

The following is a summary of our knowledge of the pollination biology of neotropical Lecythidaceae. We begin with *Gustavia,* which has the least specialized flowers, and end with *Couratari,* which has the most specialized flowers.

Gustavia has large, actinomorphic flowers with numerous stamens that are fused at their bases to form a staminal ring. The species of *Gustavia* which we have observed produce few flowers daily over relatively long periods and do not produce nectar. The flowers of different species may have no scent detectable by humans, a scent detectable only at close range, or a strong, sweet odor. In some species odor may be produced only during a specific time of the day. The actinomorphic, open flowers of *Gustavia* do not restrict the entrance of insect visitors. Consequently, a large variety of pollen-gathering bees have been observed visiting the flowers. The commonest visitors are species of *Melipona* and *Trigona* bees. Examination of the pollen loads of 14 bees visiting *G. superba* and one visiting *G. hexapetala* showed that the pollen on the bees was 100% that of the plant species being visited. The bees generally enter the flowers by flying directly into the center of the ring of stamens. However, a few land on the filaments and crawl over or through them into the center of the flower. The arched arrangement of the stamens over the ovary directs the pollinators towards the stigma. After gathering pollen the bees often push their way out between the filaments and become completely covered by pollen. Bagging and crossing experiments with *G. superba* have shown that it is allogamous (Mori and Kallunki, 1976).

Pollination data for the other genera of Lecythidaceae with actinomorphic flowers *(Asteranthos, Grias, Allantoma,* and *Cariniana)* are lacking, although one of us (Prance) has observed many bees of several species visiting the flowers of *Cariniana legalis.*

Species of *Couroupita* have an asymmetrical androecium with anthers on both the staminal ring and the hood appendages. The hood is not appressed to the staminal ring and therefore the androecium is open to all kinds of insects. In addition, Thompson (1921) has demonstrated that the hood pollen of *C. guianensis,* although identical in structure to that of the staminal ring, is much larger. The larger pollen of the hood anthers may induce insects to collect pollen from there rather than from the staminal ring anthers. Comparative studies are needed of the hood and staminal ring pollen of all species of Lecythidaceae bearing the two types of stamens to determine if there are any structural and/or physiological differences between the pollen of the two.

Prance (1976) has previously described and illustrated the flowers of *C. subsessilis.* He also reported flower visits to this species by five species of wasp (*Polybia flavitincta* Fox, *P. rejecta* (F.), *P. sericea* (Oliver), *Synoeca virginea* (F.), and *Chartergus* sp.) and by honey bees (*Apis mellifera* L.) of the African variety. However, because wasps are not generally known to collect pollen and because *C. subsessilis* does not produce nectar, we are uncertain of the role wasps play in pollination. They may have been frequenting the flowers to prey upon other flower visitors.

More recently, we have collected *Trigona dallatoreana* Friese, *T. capitata* Smith, and *T. pallida* Latreille as they collected pollen from *C. subsessilis* (Mori et al, 1978). During an hour's observation the flowers of this species were repeatedly visited by many individuals of these species of bee. Examination of the pollen load of one individual of an undetermined species of *Trigona* revealed the pollen to be 100% that of *C. subsessilis*. Because of our position of observation we were unable to determine whether the bees were collecting pollen from the anthers of the staminal ring or of the hood. Nevertheless, the fact that the bees worked the flowers with their ventral surface against the hood suggests that they were collecting pollen from the hood rather than from the staminal ring.

The androecium is more variable in species of *Lecythis* than in species of other genera. The hood may be flat with all of the appendages bearing anthers as in *L. alba* (Fig 10E), flat with only the most proximal appendages bearing anthers as in *L. poiteaui* and *L. pisonis* (Figs 9, 12D), dorsiventrally expanded and antherless as in *L. corrugata* (Figs 9, 12M), or expanded at the apex with the antherless appendages swept inward as in *L. tuyrana* (Figs 9, 12N, O). Moreover, there may be a space between the hood and the staminal ring as in *L. alba* (Fig 10E) or the hood may be tightly appressed to the staminal ring as in *L. corrugata* (Fig 10F).

We have observed and collected visitors to flowers of *L. alba, L. poiteaui* and *L. corrugata* (Mori et al, 1978). The former is a species with a flat, open hood that bears anthers on all of its appendages, the second is a species with a flat open hood that bears anthers only on its proximal appendages, and the latter is a species with a dorsiventrally expanded, closed hood without anthers.

On three different occasions we have observed many small bees (only *Trigona heideri* was collected) landing on the inside of the hood and collecting pollen from the hood anthers of *L. alba.* However, the bees we observed are shorter than the gap between the hood and the staminal ring. Therefore, when these small bees collect pollen from the hood their backs are not dusted with pollen from the staminal ring. We suggest that the legitimate pollinator of *L. alba,* which we have not observed, is probably a bee large enough to touch the anthers of the staminal ring while it is collecting pollen from the hood anthers.

Our observations of *L. corrugata* are more complete. In this species there are no hood anthers. The last row of anthers on the ligular side of the staminal ring is yellow while the remaining anthers of the staminal ring are white. In addition, there is a small amount of nectar produced at the junction of the hood and ligule. In the two trees studied, one in Surinam and the other in French Guiana, *Bombus cayennensis* Spinola, *Xylocopa* sp, and *Megachile* sp were observed entering the flowers. Only *Xylocopa* sp was observed entering the flowers of the Surinam tree while all three species entered those of the French Guiana tree (Mori et al, 1978).

Xylocopa sp and *Bombus cayennensis* both landed on the anterior edge of the hood and entered the androecium by pushing the hood open with their feet. The pressure of the hood forced their backs against the fertile stamens of the staminal ring. Although bees of both species entered the flowers with equal ease, *Xylocopa* sp paid shorter visits (1-3 seconds) than *Bombus cayennensis* (6-10 seconds). Each individual visited most of the opened flowers in the crown during a given visit. Usually only one, but sometimes several individuals worked in the crown at the same time. We assume that *Xylocopa* sp and *Bombus cayennensis* were visiting the flowers to collect the small amount of nectar produced at the proximal end of the hood because bees of both species had no pollen in their corbiculae. However, these and other bees may also gather the small amount of pollen that is brushed off the anthers of the staminal ring onto the hood when the hood is closed or the pollen from the row of yellow anthers on the ligular side of the staminal ring.

Only once was an individual of *Megachile* sp observed entering a flower. In contrast to *Xylocopa* sp and *Bombus cayennensis,* it landed on the petals and entered the flower with its back against the hood. Consequently, the staminal ring anthers brushed against its ventral rather than its dorsal surface. Apparently *Megachile* sp visits flowers of *L. corrugata* to collect pollen rather than nectar and although it may effect pollination we feel that the infrequent visits of this bee limit its importance as a pollinator of *L. corrugata.*

The hood of *L. poiteaui* is flat, open, and bears stamens on the proximal appendages. In contrast to all other species of Lecythidaceae, the flowers are visited, and presumably pollinated, by bats (Mori et al, 1978). *Lecythis poiteaui* is adapted for bat pollination in the following ways: 1) it is a canopy tree; 2) the flowers are produced on simple racemes which project above the crown; 3) the flowers are nocturnal, they open at dusk and the petals and androecium fall around 3:00 a.m.; 4) the flowers are larger than those of any other species of *Lecythis;* 5) nectar, which is apparently the pollinator attractant, is produced by the hood; 6) the flowers produce a musty-fruity odor; 7) the staminal ring has more stamens (ca 1000) than any other species of *Lecythis* (150-500); and 8) the petals are green, reflexed, inrolled at the margins and are apparently without function in pollinator attraction.

The androecia of species of *Eschweilera* have coiled, closed, nectar producing hoods (Figs 9, 13F, G). Observations of trees of *E. longipes, E. odora,* and *E.* cf. *decolorans* have shown that the principal flower visitors are Euglossine bees of the genus *Eulaema* (Prance, 1976; Mori et al, 1978). The bees enter the flowers by landing on the anterior end of the androecium and pushing into the androecium by pressing their feet against the hood. The bee's backs are forced against the staminal ring anthers by the spring-like tension of the ligule-hood. The position of the bee in the flower indicates that it is collecting nectar which is produced at the apex of the coiled hood.

The androecia of species of *Couratari* are even more complicated than those of *Eschweilera.* Not only is the hood coiled inward but in addition there is an outwardly extended flap at the apex of the coil (Figs 9, 13N, O). Observations of *C. atrovinosa* by Prance (1976) have revealed that the principle pollinator of this species is *Eulaema meriana* (Oliver). The flowers of *C. atrovinosa* open at night fall, persist overnight, and are visited briefly in the morning (most activity between 0545-0600 hr) by *E. meriana.* Although Prance (1976) reports that the bees were visiting the flowers to collect pollen, we now believe that the principle pollinator attractant is nectar.

The preceding data indicate that those species of Lecythidaceae with the least specialized flowers (i e actinomorphic, with many stamens and no nectar, e g species of *Gustavia,* or zygomorphic, open flowers, with hood anthers, e g species of *Couroupita* and *Lecythis alba*) are pollinated by insects with generalized foraging strategies (e g species of *Trigona* and *Melipona*). In contrast, species with the most specialized flowers (i e zygomorphic, with coiled and closed hoods, fewer stamens, and nectar, e g species of *Eschweilera* and *Couratari*) are pollinated by bees with enough strength to force the hood open and with tongues long enough to reach the nectar at the apex of the coiled hood (e g Euglossine bees). Other species of Lecythidaceae with zygomorphic closed but uncoiled hoods may be mainly pollinated by robust bees without long tongues (e g species of *Xylocopa*).

Finally, we believe that certain mechanisms have evolved to insure that the pollinator(s) of a species of Lecythidaceae visit individuals of the same species consecutively, i e to insure floral constancy. Different species of Lecythidaceae appear to partition pollinator resources by: 1) occupying different habitats; 2) occupying different strata in the forest; 3) blooming at different times of the year; 4) having different flowering strategies (i e mass vs steady-state flowering); 5) having different floral structures adapted for different pollinators, and 6) offering either pollen or nectar as the pollinator attractant. Mori et al (1978) discuss these mechanisms in more detail.

XI. CHROMOSOME NUMBERS

Chromosome numbers support the separation of the Lecythidaceae into at least three of the four subfamilies recognized in this monograph. Different base numbers are found in the three subfamilies for which counts are known. The Planchonioideae has $x = 13$, the Napoleonaeoideae has $x = 16$, the Lecythidoideae has $x = 17$, (Figs 35, 36), and no counts are known for the Foetidioideae. Although chromosome data are useful in intrafamilial classification they do not indicate the relationship of the Lecythidaceae with other families (Kowal et al, 1977).

A recent report of chromosome numbers of Panamanian Lecythidaceae reviews all counts known for the family (Kowal et al, 1977). Since that time we have made six additional counts in the Lecythidoideae. Table X summarizes all known counts of Lecythidoideae. Sarker et al, 1978 confirmed the number $x = 13$ for Planchonioideae when they reported this number in *Careya arborea* Roxb.

A chromosome count of *Asteranthos brasiliensis* is needed to help understand the relationships of this monotypic genus. In this monograph, it is treated as a member of the west African subfamily Napoleonaeoideae. Nevertheless, certain features, such as its seeds with ruminate endosperm, argue against this alignment. A count of $n = 16$ or $n = 17$ or multiples of those numbers would support its placement with either the Napoleonaeoideae or Lecythidoideae respectively, whereas a different count would suggest its segregation as a monotypic family as has been done by Knuth (1939c) and Airy-Shaw (1973).

Tetraploid counts of $n = 34$ have been made for *Gustavia superba* (Lecythidoideae) and of $n = 26$ for *Petersianthus macrocarpus* (Planchonioideae). A recent count of $n = 36$ for *Gustavia augusta* (Sarkar et al, 1978) indicates that this species is also a tetraploid. However, based on our counts of *Gustavia*, this count does not appear to be correct and probably is a miscount of $n = 34$.

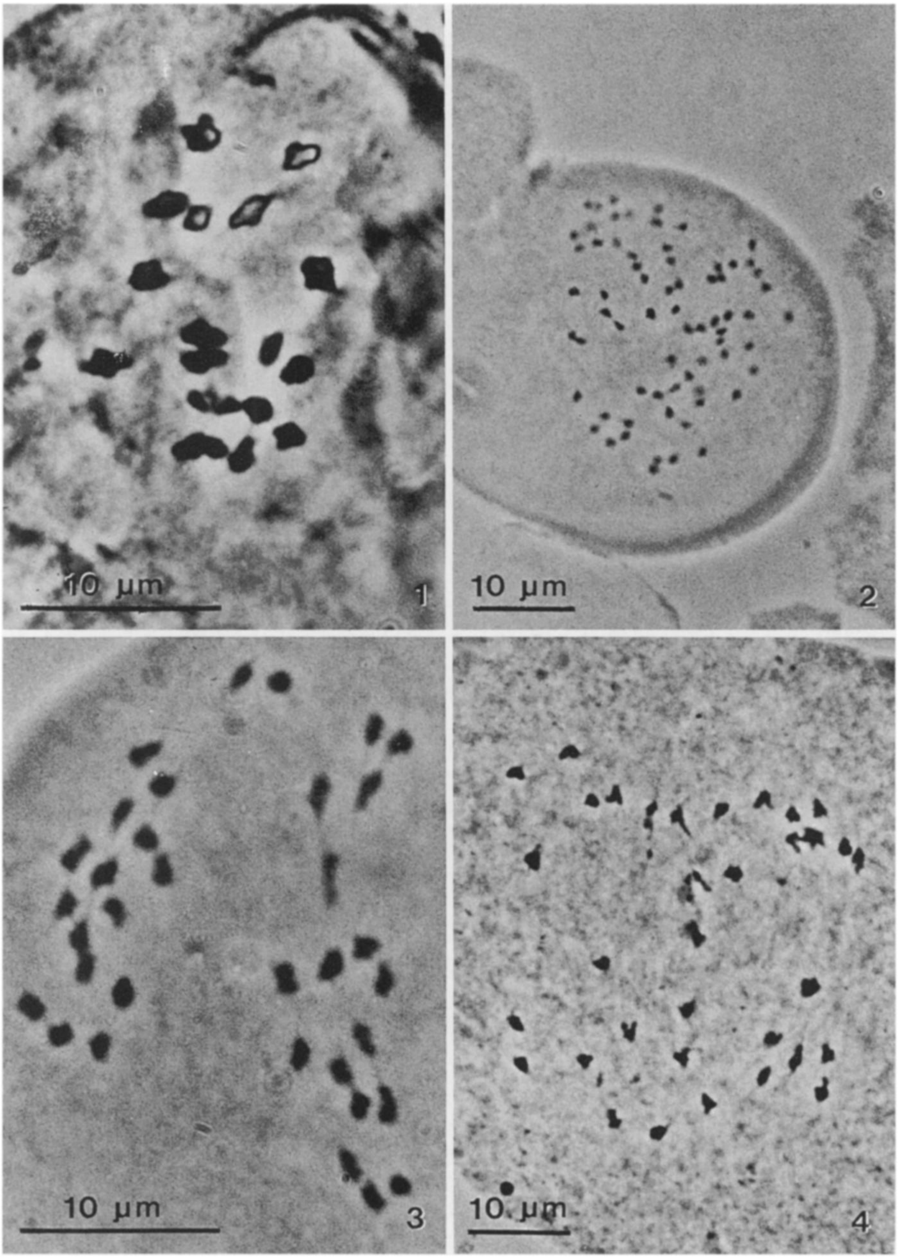


FIG 35. Meiotic chromosomes of *Gustavia, Eschweilera,* and *Couroupita:* 1, *Gustavia dubia,* metaphase I, $n = 17$ *(Mori 7720);* 2, *Gustavia superba,* anaphase II, $2n = 4x = 68$ *(Mori & Kallunki 5088);* 3, *Eschweilera pittieri,* anaphase II, an = 17 + 17 *(Mori & Kallunki 2875);* 4, *Couroupita guianensis,* anaphase I, $2n = 17 + 17$ *(Mori & Kallunki 2992).*

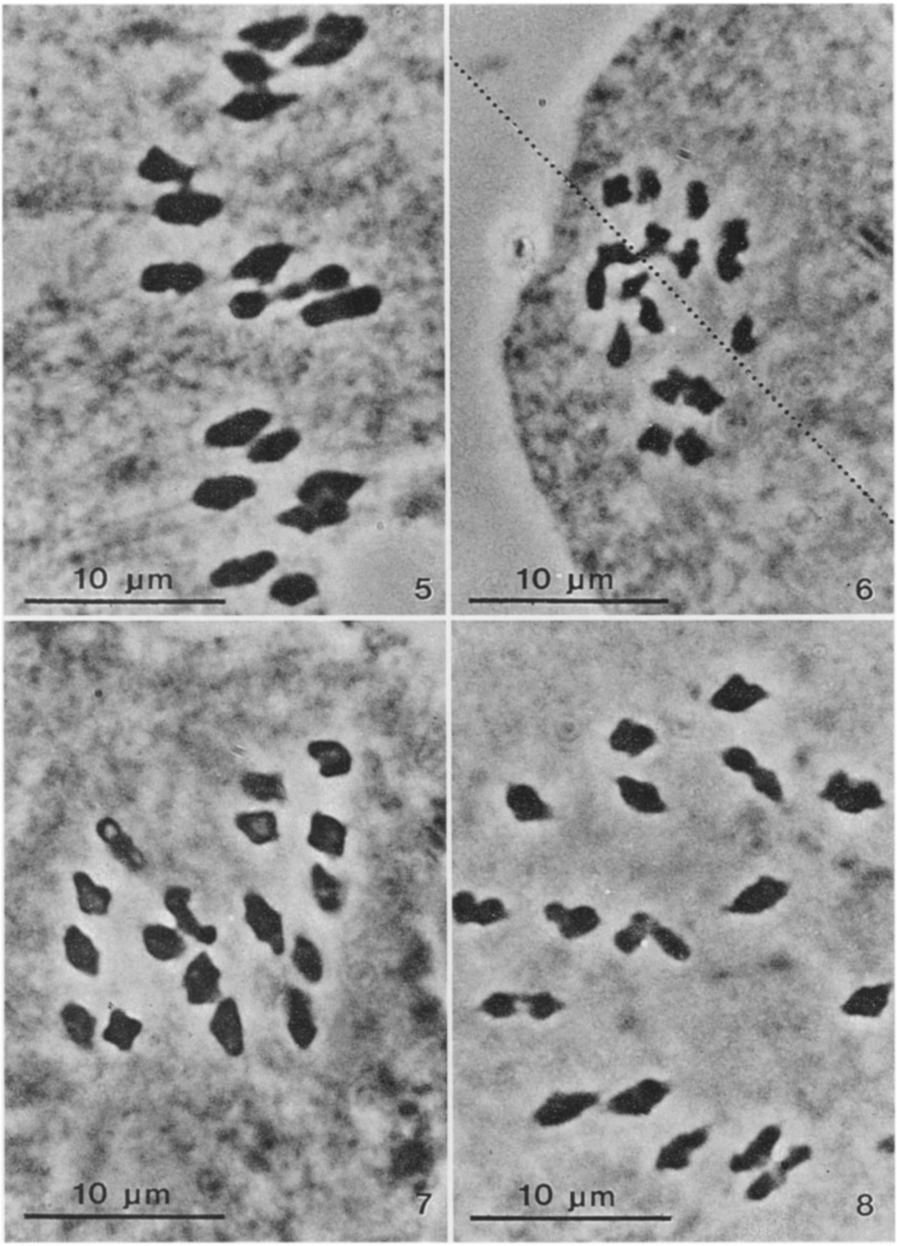


FIG 36. Meiotic chromosomes of *Grias, Lecythis,* and *Eschweilera:* 5, *Grias cauliflora,* metaphase I, *n* = 17 *(Mori & Kallunki 5773);* 6, *Lecythis minor,* metaphase II, *n* = 17, two photographs spliced along dotted line *(Nee 7713);* 7, *Eschweilera* species 1, metaphase I, *n* = 17 *(Mori & Kallunki 3771);* 8, *Eschweilera* species 3, metaphase I, *n* = 17 *(Mori et al 6905).*

Table X
Chromosome Numbers of Lecythidaceae Subfamily Lecythidoideae

Species	Geographic location and date of collection	Gametic chromosome number	Voucher (reference)
Gustavia			
G. angustifolia Benth.	Ecuador, Guayas, at Km 14 on Guayaquil-Salinas Road. 27-28 Jul 1977	17	*Iltis & Triviño E-595*
G. augusta L.	India, cultivated in Indian Botanic Garden, West Bengal	36[a]	(Sarker et al, 1978)
G. dubia (Kunth) Berg	Panama, Panama, El Llano-Carti Road, 11 km from Pan American Hwy. Ca 300 m alt. 13 Aug 1975	17	*Mori 7720* (Kowal et al, 1977)
G. superba (Kunth) Berg	Panama, Canal Zone, across from Summit Gardens, on U.S. Navy Station Property. 18 Mar 1975	34	*Mori & Kallunki 5088* (Kowal et al, 1977)
Grias			
G. cauliflora	Panama, Canal Zone, Río Petitpie, extreme NW corner of Canal Zone near coast. 30 Apr 1975	17	*Mori & Kallunki 5773* (Kowal et al, 1977)
Couroupita			
C. guianensis	Panama, Canal Zone, cultivated in Summit Gardens. 5 Nov 1974	17	*Mori & Kallunki 2992* (Kowal et al, 1977)
Lecythis			
L. corrugata Poit.	Guyana, Yarowkabra, ca 50 km SSW of Georgetown on Linden-Soesdyke Hwy. 6 Sep 1976.	17	*Mori & Bolten 8278*
L. minor Jacq.	Panama, Canal Zone, cultivated at Summit Gardens. 1 Nov 1973	17	*Nee 7713* (Kowal et al, 1977)
L. tuyrana Pittier	Panama, Canal Zone, across from Balboa Railroad Station. 28 Apr 1975	17	*Mori & Kallunki 5772* (Kowal et al, 1977)
L. usitata Miers	Guyana, Mazaruni-Potaro District. Bartica-Potaro Road, 24 miles S of Bartica. 16 Aug 1976.	17	*Mori & Bolten et al 8106*
Corythophora			
C. alta R. Knuth	Brazil, Amazonas, Reserva Ducke, Manaus-Itacoatiara Road, Km 26. 22 Nov 1975	17	*Prance 23700*

Table X—continued

Chromosome Numbers of Lecythidaceae Subfamily Lecythidoideae

Species	Geographic location and date of collection	Gametic chromosome number	Voucher (reference)
Bertholletia			
B. excelsa Humb. & Bonpl.		17	(Mangenot & Mangenot, 1958, 1962)
	Estrada do Aleixo, Manaus, Amazonas, Brazil.	17	*Prance & Ramos sn*
Eschweilera			
E. pittieri R. Knuth	Panama, Panama, El Llano-Carti Road, ca 10 km from the Pan American Hwy. Ca 350 m alt. 30 Oct 1975.	17	*Mori & Kallunki 2875* (Kowal et al, 1977)
E. aff *sessilis* A. C. Smith	Panama, Panama, Cerro Jefé, Ca 3 km NE of Cerro Azul by air 1000 m alt 5 Jun 1975	ca 16-19	*Mori & Kallunk 6516* (Kowal et al, 1977)
Species 1	Panama, Panama, Gorgas Memorial Labs yellow fever research camp, Campamento Cuatro, 5-10 km NE of Altos de Pacora, ca 18 km NE of Cerro Azul by air. Ca 700 m alt 23 Nov 1974	17	*Mori & Kallunki 3440* (Kowal et al, 1977)
Species 1	Panama, Panama, Cerro Jefé, along trail on ridge running NE from Summit, ca 3 km NE of Cerro Azul by air. Ca 1000 m alt 18 Dec 1974	17	*Mori & Kallunki 3771* (Kowal et al, 1977)
Species 2	Panama, Colón, on Santa Rita Ridge trail, beyond end of Santa Rita Ridge (Panamanian Hwy R20D), 17-35 km from Boyd Roosevelt Hwy, ca 40 km E of Colón. Ca 500 m alt 23 May 1975	17	*Mori & Crosby 6352* (Kowal et al, 1977)
Species 3	Panama, Panama, vicinity of Altos de Pacora, 15-20 km ENE of Cerro Azul. Ca 800 m alt 30 Jun 1975.	17	*Mori et al 6900 & 6905* (Kowal et al, 1977)
Species 4	Brazil, Amazonas, Manaus-Caracarai Road, km 60, Reserva INPA-SUFRAMA. 31 Mar 1975	17	*Prance & Ramos 23345*
Species 5	Brazil, Amazonas, 1-2 km behind Cachoeira Tarumazinho, Manuas. 22 Nov 1975.	17	*Prance 23695*
Species 6	Brazil, Amazonas, Manaus, Cachoeira baixa do Tarumã. 25 Nov 1975.	17	*Monteiro 3* (INPA herb. no. 53574)

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[a] Probably a miscount of $n = 34$, see text.

X. USES

Neotropical Lecythidaceae are best known economically for the edible seeds of *Bertholletia excelsa* and *Lecythis usitata.* The seeds of the former are marketed throughout the world as "Brazil nuts" (Paranuss, Maranhãokastanie, Chataigne du Brésil, Juriánuss, Amazonenmande) and those of the latter as Sapucaia, Paradise, or cream "nuts." The edible product is the seed (minus the seed coat) which is produced within a large circumscissile capsule (pyxidium), and, therefore, the correct botanical name of the product is Brazil seed or Sapucaia seed instead of nut.

There has been some discussion as to whether there are one or two species of Brazil "nut." Miers (1874) described *B. nobilis,* and separated it from *B. excelsa* by a number of weak characters which were later listed and discussed by Young (1911). Miers believed the principal difference between the two "species" was that the operculum of *B. excelsa* fell from the fruit and that of *B. nobilis* fell into the fruit at maturity. Young (1911) maintained that the Brazil "nut" of commerce was *B. nobilis* because opercula are frequently found in shipments of seeds, thereby suggesting that they had been within the fruit when harvested. Nevertheless, our studies and those of others (Sands, 1926; Knuth, 1939b) indicate that there is only one species, *B. excelsa,* the Brazil "nut" of commerce.

Brazil "nuts" are of economic importance in Amazonian Brazil, Peru and Bolivia. Until recently Brazil "nuts" were second only to rubber as an export crop in Amazonian Brazil (Knuth, 1939b, Dias, 1959). They are still a most important crop in the overall economy of the region. The economic importance of Brazil "nuts" is not as great in Peru and Bolivia as in Amazonian Brazil. However, in certain areas, such as the Department of Madre de Dios, Peru, where 20% of the department is covered by forests rich in individuals of *B. excelsa* and nearly two-thirds of the population is engaged in the exploitation of Brazil "nuts" the seeds are economically important (Sánchez, 1973). The economy of many Amazonian towns, such as Puerto Maldonado, Peru (Sánchez, 1973) and Marabá, Brazil (Dias, 1959) is based on the harvest of Brazil "nuts." Most of the seeds exported from Brazil are sent to the United States, England and West Germany.

Trees of *B. excelsa* occur in natural stands of 50-100 individuals, each separated from one another by distances of up to a kilometer, known as "manchales" in Peru (Sánchez, 1973) and "castanhais" in Brazil (Dias, 1959). Diniz & Bastos (1974) studied climatological data from 13 localities and have identified some of the climatic conditions under which Brazil "nut" trees grow. The annual mean temperature ranges between 24.3 and 27.2° C, annual rainfall from 1400 to 2800 mm per year, and mean annual relative humidity between 79 and 86%. They also noted that at least some months have less than 60 mm rainfall, i e there is a water balance deficit for 2 to 7 months depending on the locality. Densities as low as one tree per six hectares and as high as 15-20 trees per hectare have been reported (Sánchez, 1973). Forest trees first produce fruits at 12-16 years but do not reach maximum production until 25 years whereas cultivated trees may produce fruit after 8 years, probably due to the greater light intensity in plantations. The Brazil "nut" trees are light demanding and grow up only in natural clearings in the forest. Initial production is only 30-60 fruits annually but a high yielding mature tree produces 200 to 400 fruits, each weighing 1/2 to 3/4 kilograms and containing 12-25 seeds. These high yielding trees produce as much as 100-120 kilograms of unshelled seeds per tree per year (Knuth, 1939b; Sánchez, 1973). However, yearly variation in fruit production is high with good yield in one year usually followed by poor yield the following year.

Throughout the species range mature fruits fall between November and August. In the Department of Madre de Dios, Peru the fruit ripens in January and February and is collected from March through May (Sánchez, 1973), whereas on the middle Tocantins River of Pará, Brazil the harvest begins in November and December (Dias, 1959). At maturity the entire fruit falls, and the seeds are retained within the pericarp because the diameter of the opercular opening is smaller than that of the seeds. The harvest is dangerous because of the possibility of being hit by a fruit falling from as high as 50 meters. Consequently, the fruits are usually gathered after most have fallen from the trees. Almost all Brazil "nuts" are gathered from native trees which are connected by a trail system known as an "estrada." After a sufficient quantity of fruits is gathered, they are split open, and the seeds are removed, washed and dried. Depending on the ultimate use of the seeds, the seed coat may or may not be removed. In the former case the seeds are soaked for 12 to 24 hours and then broken with a machine that processes one seed at a time. After the seed coat is removed, the seeds are dried, sorted, and packed for sale. Properly dried and aerated seeds with the seed coat intact may be stored for 1-1 1/2 years, and those with the seed coat removed for 2 to 3 years (Sánchez, 1973). Without proper processing the fruits and seeds of *B. excelsa* are susceptible to a number of fungal and bacterial diseases, a number of which have been isolated by Spencer (1921) and Holubova-Jechova (1970).

Brazil "nuts" are eaten raw, roasted, or used in confectionary. The volatile flavor compounds responsible for the distinctive aroma of the raw seeds have been studied and partially identified by Clark and Nursten (1976). The oil extracted from the seed is bright yellow, nearly odorless and with a pleasant nut taste. It has a specific gravity of 0.9165 at 15°C, solidifies at −4°C and does not become rancid easily (Knuth, 1939b). First extraction of oil from the seeds yields an excellent cooking oil, and the second extraction produces an oil suitable for making soap and burning in lamps.

The residue left after pressing the seeds can be used as animal feed. Table XI compares the properties of seeds of *Bertholletia excelsa* from Peru and Brazil and cotton seed (Knuth, 1939b; Sánchez, 1973). Zucas et al (1975) and SUDAM (1976) report that the average protein content in defatted Brazil "nut" flour is about 46% and that all of the essential amino acids are present. However, the former author's studies with white rats reveal that the nutritional value of Brazil "nut" flour is less than that of casein.

Propagation of *B. excelsa* is by seed. Unless the seed coat is softened, sclarified, or removed, the seed may not germinate for one or even several years and then only 30% may germinate (Sánchez, 1973; Barbosa et al, 1974). Because *B. excelsa* is a primary forest species, the seeds should be germinated under 70% shade. Barbosa et al (1974) reports that slightly higher rates of germination are obtained after treating the seeds with 15% and 25% sulphuric acid solutions during 7 and 18 hours respectively. Experiments are needed to

Table XI
Properties of Brazil "nuts" and cotton seed

	B. excelsa **seeds from Peru (Sánchez, 1973)**	***B. excelsa*** **seeds from Brazil (Sánchez, 1973)**	***B. excelsa*** **seeds from Brazil (SUDAM, 1976)**	***B. excelsa*** **seeds Probably from Brazil (Knuth, 1939b)**	**Cotton seed**
oil	65.0	67.0	70.0	67.45	24.9
protein	17.0	17.0	13.9	15.48	19.9
ash	3.0	4.0	—	3.89	6.0
crude fiber	0.9	—	—	3.21	21.8
water	4.0	5.0	2.0	5.94	—
carbohydrates	10.1	7.0	—	3.83	17.8
ash/fiber/ carbohydrates	—	—	14.1	—	—
	100.0	100.0	100.0	99.80	89.6

determine if germination time is lowered artificially by breaking the seed coat. Sánchez (1973) reported that seedlings free from fungal and insect attacks reached 50 cms after one year's growth. According to Knuth (1939b) seedlings reach 80 cm after one year; 5 meters in 5 years and 25 meters × 0.8 meters at breast height after 60 years. All attempts at vegetative propagation have failed (Sánchez, 1973).

Although equally as delicious and nutritious as the Brazil "nut," the Sapucaia "nut," *L. usitata* and close relatives, has not reached the economic importance of the former. At maturity the fruit of the Sapucaia "nut" (Fig 19A, B) opens via an operculum much larger in diameter than that of the seeds. Consequently, the seeds are usually removed from the fruit by animals before they fall (see chapter on fruits, seeds, and seedlings) or they fall to the ground where they are readily carried away by terrestrial animals. In addition the seed coat of *L. usitata* is relatively thin in comparison to the indurate one of *B. excelsa* and is not as effective in protecting it against disease and insect attack. These features combine to make the Sapucaia "nut" very difficult to harvest and store and, therefore, have restricted its commercial exploitation.

In contrast to the long dormant period of *B. excelsa,* the seeds of *L. usitata* germinate in 7-10 days (Knuth, 1939b). Knuth (1939b) reported that plants of *L. usitata* reach 60 cm after one year, about 4 meters after 5 years and first set fruit between 16 and 18 years. The seeds weigh about 5.5 grams each, and mature individuals produce close to 80 kilograms of seeds annually. Sands (1925, 1936) gave data on seed production of two trees of *L. usitata* planted in 1926 at the Central Experiment Station in Serdang, Malaya. By 1936 the trees had reached a height of 12 meters with a crown spread of 10 meters. As with most Lecythidaceae grown outside natural forest conditions, branching commenced close to the ground, and no central leader had developed. In March and early June of 1934, one of the trees produced flowers and in January and February of 1935 ripened 12 fruits, each weighing about 1 kilogram and with 25-30 seeds. In 1936 the same tree flowered but did not set fruit. Finally, in 1937 both trees flowered, and the first individual produced 81 fruits, and the second, which had flowered for the first time, produced 21 fruits. Each fruit weighed about 2.3 kilograms and contained 41-49 seeds which amounted to a production of 10.7 kilograms of cleaned seeds from the two trees. Projecting this yield to a stand of 55 trees/acre gives 294 kg/acre. Yield per acre would increase with further maturity of the trees.

The seeds of *L. usitata* are eaten raw, roasted, or used in confectionary. The oil extract is light yellow, with a specific gravity of 0.920 at 15°C, and solidifies into a whitish-yellow mass at 4°C (Knuth, 1939b). Before the oil is extracted, the seed coats must be removed because they are harmful if consumed (Knuth, 1939b). Analysis of the seeds by Friese (1933) gave the following results: protein, 16.10; oil, 63.55; carbohydrates and crude fiber, 8.22; water, 2.80; ash, 3.85%.

Two closely related species of *Lecythis, L. ollaria* and *L. minor* (Prance and Mori, 1977), also have edible seeds which have proven to be toxic under some circumstances. Jacquin (1763) in his protologue of *L. minor* states that the seeds tasted agreeable to him but half an hour after consuming one he felt nausea, great anxiety, and giddiness. Dickson (1969) attributes the temporary loss of hair and fingernails that he experienced after eating 300-600 seeds of *L. minor* (misidentified as *L. elliptica*) to toxic elements in the seeds. Throughout northern Colombia, *L. minor* is said to be poisonous, a characteristic which is denied by Romero-Castañeda (1961). Loss of fingernails and hair, nausea, vomiting, diarrhea, muscle pains, convulsions, dizziness and even death have been attributed to consumption of the seeds of these species, and the death of a two year old Venezuelan boy to poisoning by *L. ollaria* (Kerdell-Vargas, 1966). Seed extracts from *L. ollaria* were administered both orally and intraperitoneally to mice, rats, and hamsters by Kerdell-Vargas (1966). In control animals a rounded hair-free zone 1.5 cm in diameter grew back to normal within 7 days, whereas in experimental animals there was no hair replacement at the end of 7 days. Other symptoms of the experimental animals were atrophy and disappearance of sebaceous glands, marked atrophy of the epidermis, edema and intra-alveolar hemorrhage of the lungs, necrotic foci of the liver and spleen, and intense sinusoidal congestion of the adrenals. Kerdell-Vargas (1966) identified the active substance causing these symptoms as the selenium-containing analog of the sulphur amino acid, cystathionine, with the following formula:

$$\mathrm{HOOC\text{-}CH\ (NH_2)\text{-}CH_2\text{-}Se\text{-}CH_2CH\ (NH_2)COOH}$$

Dried de-fatted seeds and whole de-shelled seeds have been reported to contain 2.23% and 0.58% selenium by weight respectively (Kerdell-Vargas, 1966). Mori (1970) reports that seeds examined from the same crop and tree as those eaten by a Honduran poisoning victim contained between 520 and 560 ppm selenium. Selenium concentrations above 10 parts per million are considered toxic (Kerdell-Vargas, 1966), and the concentrations found in *L. ollaria* and *L. minor* are well above these levels. Apparently these species of *Lecythis,* when grown on soils high in selenium, accumulate the element in their seeds at toxic levels but, when grown on soils low in selenium, do not accumulate the element and their seeds are then safe to eat.

Kask (1969) reports that, after subsisting on a diet of Brazil nuts, pineapple juice, and Cayenne peppers, he had excessive hair loss and softening of the fingernails. He adds that these signs disappeared without any change in diet but he had great difficulty in maintaining weight and that his muscular strength and endurance decreased. When he substituted fresh papaya for the pineapple juice all of the preceeding symptoms disappeared. These observations are the first to suggest that excessive consumption of the seeds of *Bertholletia excelsa* may also result in hair and fingernail loss. Seaber (1933) reported high concentrations of barium and Smith (1971) reported abnormally high concentrations of radium in the seeds of *B. excelsa.* The accumulation of elements in the seeds of *B. excelsa* may have ecological as well as medicinal importance. Brinkman (1972) has demonstrated that nutrient loss from Amazonian Brazil through Brazil nut export is considerable. He suggests that fertilization may be needed to restore elements, such as P, K, S, Mg, and Ca, in areas where Brazil nuts have been harvested over many years.

Seed production of *Bertholletia excelsa* and *Lecythis usitata* is compatible with a multicrop agricultural system which mimics the natural vegetation of *terra firme* forest. Smith (1977) pointed out that the Arara Indians of Brazil cultivate 19 varieties of plants belonging to 13 species. A species of *Cucurbita* and sweet potato *(Ipomoea batatas* Poir.) cover the soil, the shrub layer is occupied by the principal crop, manihot (*Manihot esculenta* Crantz), the next story is preempted by bananas (*Musa* spp), papaya (*Carica papaya* L.) and soursop (*Anona nitida* Ruíz & Pav.), and other crops are interspersed with these staple plants. Although not mentioned by Smith (1977), Brazil "nuts" are perfect candidates for occupying the emergent layer in this modified rain forest agricultural system.

The mesocarps of several species of *Gustavia* and *Grias* are edible (Romero-Castañeda, 1961; Mori, 1974). *Gustavia speciosa* subsp *speciosa* is cultivated for the yellowish pulp that surrounds the seed and which is either sucked raw from the fruit or cooked with meat and/or rice. At Mariquita in the Magdalena Valley of Colombia, fruit and vegetable vendors informed Mori that fruits of *Gustavia speciosa* reach the market twice each year, once in January and again in July and August. Several trees of *G. speciosa* were observed in the back yards of residents of Mariquita. Under certain conditions the pulp of *G. speciosa* may be somewhat toxic. Humboldt and Bonpland (in Kunth, 1824) reported that the skin of young children becomes yellowish after consuming too much pulp but that the color disappears after 24-48 hours without medical attention. According to Duke (1970), the mesocarp of *G. superba* is eaten and also used as grease in which to cook rice by the Chocó Indians of Panama. Romero-Castañeda (1961) reported that the pulp of the fruit of *G. nana* is edible.

The mesocarps of *Grias haughtii* (Romero-Castañeda, 1961), *G. neuberthii* (fide label data), *G. peruviana* (fide label data), and *G. cauliflora* (Sloane, 1725) are edible. Romero-Castañeda (1961) reported that the pulp of *G. haughtii* is eaten raw or cooked in syrup and suggests that its exploitation should be studied because it appears to be rich in vitamins and is not difficult to transport.

The timbers of Lecythidaceae are used locally for general construction, cabinet making, railroad ties, levers, paddles, tool handles, and marine pilings but have never been exported to any extent. *Cariniana pyriformis,* which forms relatively dense stands in northern Colombia (fide Curran in Record and Hess, 1943), has been exported to the United States and Europe as Colombian Mahogony or Abarco, but without success, possibly because the high silica content of the wood is said to dull saws. *Cariniana pyriformis* has been used successfully for reforestation in tropical humid areas of Colombia (Betancur and Raigosa, 1973). Timber of *B. excelsa* has occasionally been exported when stands have had to be cut down for other reasons. However, the value of the seeds exceeds that of the timber, so trees are only felled when necessary.

The high silica content of some, but not all species, of Lecythidaceae (Ter Welle, 1976) apparently provides the wood with resistance to marine borers (Wangaard et al, 1954). Pilings of Manbarklak (*Eschweilera odora* and/or *E. subglandulosa*), supporting the railroad bridge across the Saramacca Canal at Beekhuizen, Surinam, were installed in March 1904 and were still sound and fit for further use when they were removed in March 1921 (Record and Hess, 1943). Because of the strength and resistance of the wood several species of Lecythidaceae, especially *Lecythis usitata, Eschweilera odora,* and *E. jarana,* make excellent railroad cross ties (Horn, 1948; Wangaard et al, 1954). Lobato (1976) describes the use of the wood of *Holopyxidium (=Eschweilera) jaranum* for ties on the Belém-Bragança railroad. He pointed out that the local population of this species was completely decimated by the construction of the railroad.

Two studies have been made to test the feasibility of using species of Lecythidaceae as paper pulp. Melo and Alves (1974), in an investigation of 7 Amazonian species of trees in 6 families, found that *Allantoma lineata* has excellent properties for making paper pulp. In contrast, Melo and Huhn (1974) report that *Eschweilera odora* was the least favorable of 6 species in 6 families of Amazonian trees for making bleached paper pulp.

The properties and possible uses of the wood of various species of Lecythidaceae have been discussed in detail by Wangaard et al (1954), Japing (1957) and Mogollón (1973).

The bark of several species of Lecythidaceae, especially those of *Couratari, Eschweilera* and *Lecythis* is used for caulking boats, cigarette paper, native clothing, cordage, tinder, and tanning, and the empty fruits are utilized as pipe bowls (*Cariniana* spp), canisters (especially species of *Lecythis*), and for making souvenirs.

The use of the roots, bark, leaves, fruits, and seeds of Lecythidaceae in folk medicine has been reported by several authors, but no scientific studies of the efficacy of these treatments are known to us. Mori (1970) has observed that fruits and seeds of *Lecythis ampla* and *L. tuyrana* are used by the Cuna Indians of Panama for treatment of the following maladies:

Pneumonia
The pericarp is ground into a powder and then taken dissolved in water.
Liver ailments
The seeds are pulverized and taken with water.
Diarrhea

The fruit is ground into a powder and taken with water.
As an aid to childbirth
The opercular rim is ground into a powder and taken with water.

Penna (1946) and Pittier (1927) report that the roots, bark, fruits, and seeds of many different species of Lecythidaceae are used to cure colds, inflammations of the urinary system, kidney infections, running at the nose and eyes, asthma, whooping cough, siphilitic tumors, gout, liver infections, rheumatism, diarrhea, uterine hemorrhages and stomach acidity. We have observed the fruits of *L. ollaria* being sold in Caracas, Venezuela as medicine and were told by one informant that water steeped in the empty fruits of this species, when applied to young males over a long period, inhibits growth of facial hair at an older age. Nevertheless, the pharmacological properties of the Lecythidaceae appear to be minimal and as yet poorly studied.

The seeds of *Gustavia hexapetala* have been reported by Niedenzu (1892) to be used in making fish poison, a use which has also been reported for the seeds and bark of species of *Barringtonia,* which is, in many ways, the closest Old World relative of *Gustavia.*

The handsome growth form, showy flowers, and curious fruits of Lecythidaceae make this group appropriate for cultivation in tropical botanical gardens and in tropical conservatories. *Couroupita guianensis, Lecythis pisonis, Bertholletia excelsa,* and *Gustavia augusta* are currently the most widely cultivated species. Most species of Lecythidaceae used as ornamentals are propagated from seeds, however, Bose and Monal (1970) have demonstrated that *Gustavia augusta* is easily propagated vegetatively, especially if the cuttings are treated with indole butyric acid.

XI. THE FOSSIL RECORD

The fossil record of Lecythidaceae is sparse and most specimens are of dubious affinity. It thus provides little data to elucidate possible migratory routes, present day distributions or evolutionary trends in the family.

The fossil reports of Lecythidaceae known to us are:

Berry (1924a, b) described *Lecythidoanthus kugleri* a fossil flower impression found in a deposit of naturally burnt clay known as porcellanite from the Miocene of Trinidad. This is almost certainly of lecythidaceous affinity. It was illustrated again in Knuth (1939b).

Milanez (1935) provided a detailed description of the wood anatomy of a well preserved fossil wood from the Cretaceous which is of obvious lecythidaceous affinity. It was described as *Lecythioxylon brasiliense* and was collected from Alegre Manga in the State of Piauí, Brazil.

Huertas (1969) described *Lecythidopyxion girardotanum* as a new genus and species of Lecythidaceae based on fossil fruit from the Department of Cundinamarca, Colombia. This is undoubtedly an *Eschweilera* because of the bilocular ovary and the shape of the fruit. It bears a remarkable resemblance to present day species of the genus. Unfortunately Huertas does not give a date for these fruits which diminishes the value of his report. It is possible that these fruits are of recent origin.

The three fossil records above are almost certainly of lecythidaceous affinity. There have also been a few reports of fossil leaves which are far more questionable. Hickey and Doyle (1977) comment on the serious problem of misidentification of many Cretaceous angiosperm megafossil remains by early paleobotanists. Some of the authors cited by Hickey and Doyle, as having incorrectly placed megafossils to family, have also described species of Lecythidaceae based on fossil leaves. For completness these leaf fossils are cited below, however, we are not confident that any of them belong to Lecythidaceae.

Englehardt (1891) described *Lecythis neriifolia* based on a leaf impression from Tertiary sediments near Coronel, Chile. In 1895 the same author described *Couratari tertiaria* from Tertiary deposits of Ecuador. Berry (1923) described *Lecythidophyllum* as a new genus from southern Mexico. Hollick and Berry (1924) described *Couroupita ovata* from Tertiary deposits of Bahia, Brazil and Berry (1936) described another *Couroupita, C. santandersensis* from leaf impressions of Miocene deposits of the Magdalena valley in Santander, Colombia.

The Asiatic genus *Barringtonia,* or its ancestors, has been reported several times as fossils. These Barringtoniads appear to be based on more reliable reports. Shallom (1960) described *Barringtonioxylon deccanense* from the upper Cretaceous to early Eocene flora of the Deccan Intertrappean beds of Muhurzari in India, and Prakash and Dayal (1965) described a second species, *Barringtonioxylon eopterocarpum,* from the same deposits. Venkatachala and Kar (1968) found a pollen similar to that of *Barringtonia* in Eocene lake sediments of Kutch in India, which they described as *Rostriapollenites kutchensis.* Wolfe (1972) reported fossil leaves of *Barringtonia* from Eocene deposits of Alaska. Muller (1972), in a review of the pollen of Lecythidaceae, concluded that the earliest pollen grains that can be attributed to the Lecythidaceae came from Paleocene and Eocene of India. The fossils, with the exception of the Alaskan Record of *Barringtonia,* were all collected from within the present day range of Lecythidaceae.

The fossil record of Lecythidaceae is too meager to provide useful data for understanding the evolution of the family.

XII. GEOGRAPHIC DISTRIBUTION

The Lecythidaceae sensu lato are pantropical in distribution. Members of the Planchonioideae range from Africa into Australia, and those of the Foetidioideae from Madagascar into Malaya. The Napoleonaeoideae has one species, *Asteranthos brasiliensis,* in the neotropics and two genera *Napoleonaea* and *Crateranthus,* in West Africa. The genetic distributions of members of the above subfamilies are summarized in Table III.

The fourth subfamily, Lecythidoideae, which is confined to the New World, ranges from the Atlantic to the Pacific coasts and between 19° N and 25° S latitudes. The only species with part of its distribution outside of the tropics is *Cariniana estrellensis* which has been collected at stations several

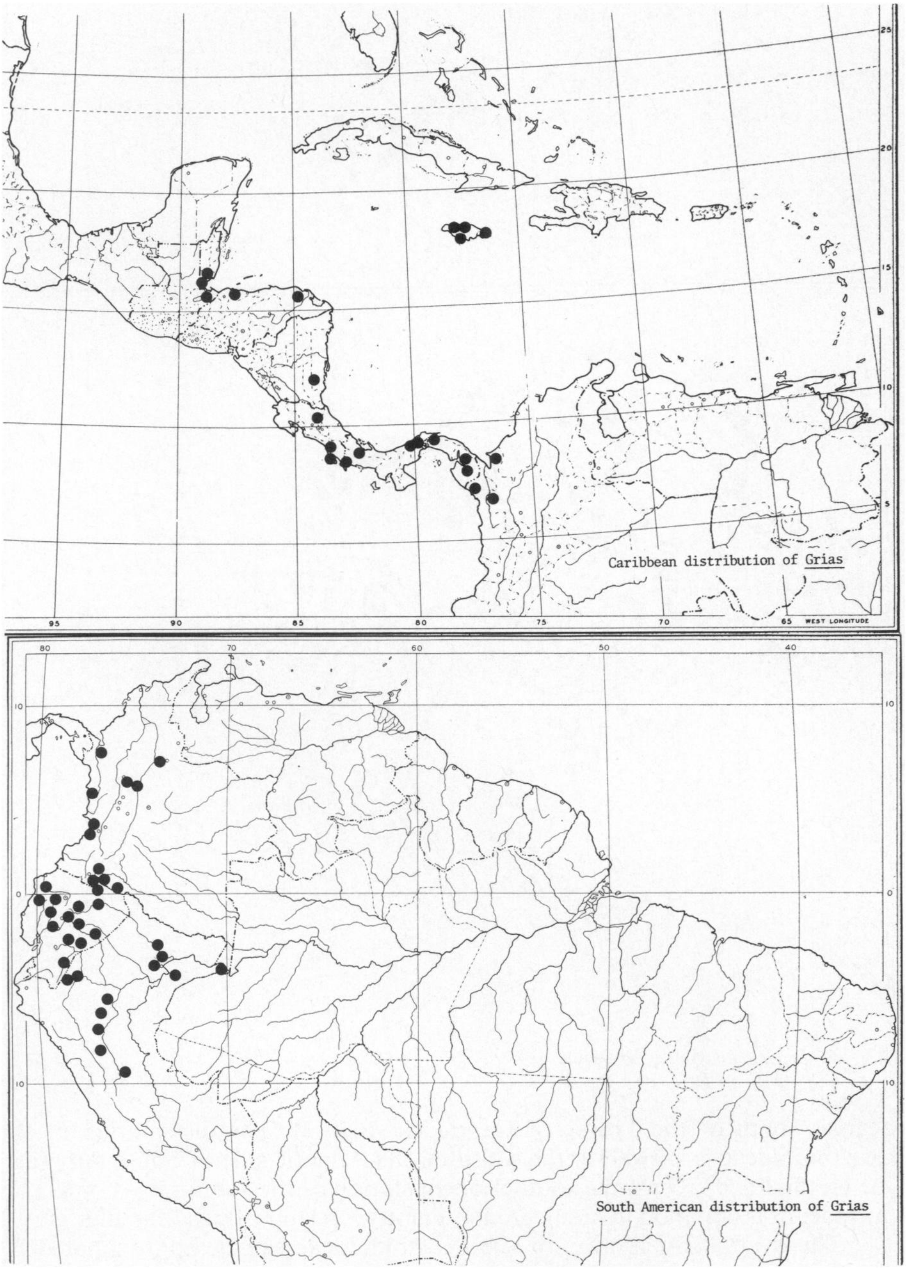

FIG 37. Generic distribution of *Grias*.

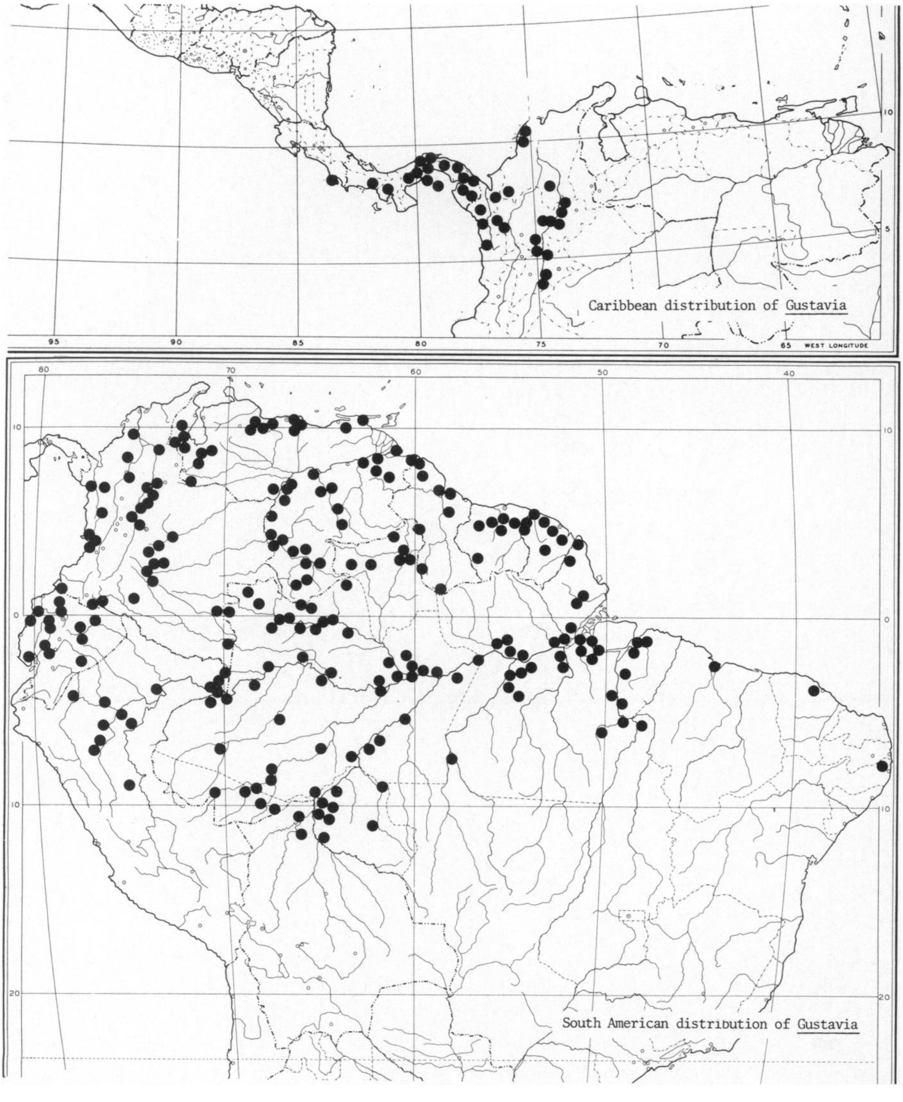

FIG. 38. Generic distribution of *Gustavia*.

degrees south of the Tropic of Capricorn (Fig 73). The distribution of the Lecythidoideae is skewed to the south on the Atlantic side of South America, for on the Pacific coast the southernmost station of the subfamily is only 3° S latitude, as is common in many predominantly lowland tropical families.

The overall distribution of the Lecythidoideae can be approximated by combining the generic distribution maps of *Grias, Gustavia,* and *Cariniana* (Figs 37, 38, 39). No other species of other genera fall outside the general distributions of these three genera.

FIG. 39. Generic distribution of *Cariniana*.

Detailed distributions of the genera treated in this monograph, i e *Asteranthos brasiliensis* (subfamily Napoleonaeoideae), the actinomorphic-flowered Lecythidoideae *(Gustavia, Grias, Allantoma),* and the slightly zygomorphic-flowered Lecythidoideae *(Cariniana)* are given below.

Asteranthos brasiliensis, the only Napoleonaeoid species in the New World, is restricted to blackwater, seasonally flooded forests on white sand between 64° and 68° W longitude and 1° S and 3° N latitude (Fig 41).

Gustavia, a widespread genus of 41 species, ranges from coast to coast and from 11° N to 12° S latitudes (Fig 38). There is an especially high number of species of this genus north and west of the Andes and in the inter-Andean valleys (27 species). For example, eight species are known between the Canal Zone and the Panamanian-Colombian border and twelve species from the Magdalena Valley of Colombia. There are fourteen species in Amazonia but only three in the Guianas. One species, *G. superba,* reaches Costa Rica, and none are native to the islands of the Caribbean.

Grias, a genus of 6 species is restricted to northwestern South America, Central America and the Caribbean (Fig 37). Two of the six species are western Amazonian, while the remainder are Caribbean, Pacific coastal South America, or of the inter-Andean valleys. *Grias cauliflora* reaches Jamaica.

Allantoma lineata, the only species of the genus, is a riverine tree which has been collected along the upper Río Orinoco, along the Rio Negro, and along the Amazon and several of its tributaries as far east as Belém (Fig 63). It has not yet been collected on the Rio Solimões, i e Rio Amazonas above its junction with the Rio Negro.

Cariniana, a widespread genus of 15 species, ranges from coast to coast and from 11° N to 28° S latitudes (Fig 39). However, only one species, *C. pyriformis* has been collected north or west of the Andes and none from the Guianas. The genus is most diverse in Amazonia (9 species) but also has seven species with all or part of their distributions south of the Amazon Basin.

XIII. SYSTEMATIC TREATMENT

LECYTHIDACEAE Poiteau, Mém. Mus. Hist. Nat. **13:** 141-165. 1825 (sub Lécythidées); Myrtaceae tribus Lecythideae Rich. ex DC., Prodromus **3:** 288-291. 1828; Myrtiflorae subord Lecythideae Endlicher, Gen. Pl. 1233-1234. 1840; Myrtaceae subtribus Eulecythideae Benth. & Hook., Gen. Pl. **1**(2): 720-725. 1865; Lecythidaceae subfam Lecythidoideae Niedenzu in Engler & Prantl, Nat. Pflanzenfam. **3**(7): 26-41. 1892.

Small to large trees, leaves alternate, simple, estipulate or with minute, caducous stipules, without pellucid punctations. Flowers actinomorphic or zygomorphic; petals usually present, less frequently absent; stamens numerous, connate at the base into a staminal ring, the ring actinomorphic or prolonged on one side into a strap-like structure which arches over the summit of the ovary, some apetalous species with the outermost stamens modified into a petaloid corona; intrastaminal disc present or absent; ovary inferior to half-inferior. Fruits fibrous berries, dry drupes, or woody circumscissile capsules with one to many seeds. Seeds with or without cotyledons.

Type genus. *Lecythis* Loefl.

Key to Subfamilies of Lecythidaceae

1. Pollen syntricolpate. Cortical bundles with reversed orientation (i e, xylem outside, phloem inside). Secondary xylem without crystal chains. Principally Asian, with 1 sp in East Africa and 2 spp. in Madagascar. subfam I. Planchonioideae.
1. Pollen tricolpate or tricolporate. Cortical bundles with reversed or normal orientation. Secondary xylem with or without crystal chains. New or Old World.
   2. Flowers apetalous, without a corona of staminal origin; filaments weakly fused at the base. Ovules horizontal, situated in a vertical ring on a thick shield-like placenta; funicle

and micropyle directed outwards. Cortical bundles with reverse orientation. Secondary xylem with crystal chains. Madagascar, India, Malaysia. subfam II. Foetidioideae.

2. Flowers with or without petals, if without then possessing a corona of staminal origin; filaments fused at base to form distinct staminal ring. Ovules in rows, hanging or ascending from a central columnar placenta, if horizontal then with the micropyle facing inwards. Cortical bundles with normal orientation. Secondary xylem with or without crystal chains. West Africa or the Neotropics.
   3. Flowers without petals, actinomorphic; outer row of filaments fused to form a petaloid corona. Fruits indehiscent. Secondary xylem without crystal chains. West Africa (except for *Asteranthos brasiliensis*). subfam III. Napoleonaeoideae.
   3. Flowers with petals, actinomorphic or zygomorphic; outer row of filaments not forming a petaloid corona. Fruits dehiscent in all but *Couroupita, Grias,* and *Gustavia.* Secondary xylem with crystal chains. Neotropics. subfam IV. Lecythidoideae.

I. **Lecythidaceae** subfam **Planchonioideae** Niedenzu in Engler & Prantl, Nat. Pflanzenfam. **3**(7): 30-33. 1892.

Myrtaceae tribus Barringtoniae DC., Prodromus **3**: 288-296. 1828. *pro parte;* Barringtoniaceae Lindley, Vegetable Kingdom 716-730. 1846. *pro parte;* Myrtaceae subtribus Barringtonieae Benth. & Hook., Gen. Pl. **1**(2): 720-725. 1865, *pro parte.*

Flowers actinomorphic; petals present, corona of staminal origin absent, inner or outer whorl of stamens sometimes staminodial, the base of the stamens fused into a distinct staminal ring except in *Petersianthus* where they are weakly fused; intrastaminal disk present, pollen syntricolpate; ovary 2-4 locular, placenta columnar. Fruit indehiscent; fibrous berries *(Planchonia)* or dry drupes which contain from one (all species of *Barringtonia*) to many (some species of *Planchonia*) seeds; cotyledons present in *Planchonia* and *Petersianthus,* absent in *Barringtonia, Careya* and *Chydenanthus.* Secondary xylem without crystal chains in parenchyma, cortical bundles reversely oriented with the xylem on the outside. $x = 13$.

A subfamily of 55 species in 6 genera (Table III) distributed throughout tropical Asia, Malaysia, northern Australia, and the Pacific Islands. Tropical Asia and the islands to the south and east have the greatest number of species of this subfamily.

Type genus. *Planchonia* Blume

II. **Lecythidaceae** subfam **Foetidioideae** Niedenzu in Engler & Prantl, Nat. Pflanzenfam. **3**(7): 29-30. 1892; Barringtoniaceae tribus Foetidieae Knuth, Pflanzenreich IV. **219a**: 62-65. 1939; Foetidiaceae Airy Shaw in Willis, J. C. A Dictionary of Fl. Pl. and Ferns ed. 8, 465. 1973.

Flowers actinomorphic; petals absent, corona of staminal origin absent, staminodes absent, the base of the stamens only weakly fused and not forming a staminal ring; intrastaminal disk present; pollen tricolpate; ovary 4 locular, placenta peltate. Fruit indehiscent; cotyledon type unknown. Secondary xylem with crystal chains in the parenchyma, cortical bundles reversely oriented. Chromosome number unknown.

The 5 species of the single genus, *Foetidia,* of this subfamily are distributed in Madagascar, India, and Malaysia.

Type genus. *Foetidia* Commerson ex Lamarck

III. Lecythidaceae subfam **Napoleonaeoideae** Niedenzu in Engler & Prantl, Nat. Pflanzenfam. **3**(7): 33-34. 1892; Napoleonaeaceae Beauv., Fl. Oware Benin Afr. **2**: 29. 1810 (sub Napoleonées); Myrtaceae subtribus Napoleoneae Benth. & Hook., Gen. Pl. **1**(2): 723-727. 1865; Barringtoniaceae tribus Napoleoneae R. Knuth, Pflanzenreich IV. **219a**: 67-73. 1939.

Belvisiaceae R. Brown, Trans. Linn. Soc. London **13**: 222-223. 1821.
Asteranthaceae R. Knuth, Notizbl. Bot. Gart. Berlin-Dhalem **11**(110): 1034-1036. 1934.
Barringtoniaceae tribus Craterantheae R. Knuth, Pflanzenreich IV. **219a**: 65-67. 1939.

Flowers actinomorphic; petals absent, corona of staminal origin present, staminodes present in *Napoleonaea* absent in *Crateranthus* and *Asteranthos,* the base of the stamens fused into a distinct staminal ring except in *Asteranthos* where they are weakly fused; intrastaminal disk present in *Napoleonaea* absent in *Crateranthus* and *Asteranthos;* pollen tricolpate; ovary 3 or 5 locular, placenta columnar. Fruit indehiscent, berry in *Crateranthus,* drupe in *Napoleonaea,* capsule ? in *Asteranthos;* cotyledons present. Secondary xylem without crystal chains in parenchyma, cortical bundles normally oriented with phloem on the outside. $x = 16$ in *Napoleonaea.*

A subfamily of 12 species in 3 genera of West Africa and the upper Rio Negro region of Amazonia. *Crateranthus* and *Napoleonaea* are distributed in western Africa, and *Asteranthos* is confined to the periodically flooded 'caatinga' forest of the upper Rio Negro in Colombia, Venezuela and Brazil.

Type genus. *Napoleonaea* Beauv.

Key to the Genera of Napoleonaeoideae

1. Calyx distinctly 3 or 5 lobed; pseudocorollas 1 or 3, if 1 then campanulate; seeds several to many per fruit, exalbuminous.
    2. Calyx lobes 5; pseudocorolla 3-rowed, rotate, staminodes present; ovary inferior, 5 locular. *Napoleonaea.*
    2. Calyx lobes 3; pseudocorolla 1-rowed, campanulate; staminodes absent; ovary semi-inferior, 3 locular. *Crateranthus.*
1. Calyx dentate but not distinctly lobed; pseudocorolla 1, radiate; seed one per fruit, albuminous. *Asteranthos.*

IV. Lecythidaceae subfam **Lecythidoideae** Niedenzu in Engler & Prantl, Nat. Pflanzenfam. **3**(7): 34-41. 1892.

Myrtaceae tribus Barringtonieae DC., Prodromus **3**: 288-296. 1828, *pro parte, typus exclusus;* Barringtoniaceae Lindley, Vegetable Kingdom 716-730. 1846. *pro parte, typus exclusus;* Myrtaceae subtribus Barringtonieae Benth. & Hook., Gen. Pl. **1**(2): 720-725. 1865. *pro parte, typus exclusus.*
Lecythidaceae subfam Lecythidoideae tribus Griadeae Pichon, Notul. Syst. (Paris) **12**: 195. 1945.

Small, unbranched to huge, much-branched emergent trees. Leaves alternate, exstipulate or with minute caducous stipules, simple, pinnately nerved, the margins usually entire, sometimes crenulate to serrate, very large and clustered at the branch ends in *Grias* and some species of *Gustavia,* medium-sized and not clustered in the remaining species. Inflorescences simple racemes, panicles with 2 or 3 orders of racemose or spicate branches or fascicles, suprafoliar (then either terminal or subterminal), axillary, or cauline. Flowers actinomorphic or zygomorphic, inferior or half-inferior, perfect; calyx entire or of 2 to 6 triangular to broadly ovate lobes; petals 4, 6, or 8, infrequently 12 or 18; stamens arising from a connate staminal ring in *Gustavia, Grias,* and *Allantoma,* the staminal ring slightly expanded on one side in *Cariniana,* and markedly expanded into a strap-like ligule with an enlarged hood at the apex in the remaining genera, the hood appendages with or without anthers; ovary usually 2, 4, or 6-locular, with 2-115 anatropous ovules per locule, the axile placentae at the apex, base, or throughout the length of the locule. Fruits indehiscent, then somewhat fleshy and berry-like *(Grias, Gustavia)* or with a thin, ligneous exocarp *(Couroupita),* or dehiscent via a circumscissile operculum, then often very large and woody; seeds winged in *Cariniana* and *Couratari,* without wings in the remaining genera, with or without arils; embryos undifferentiated, or with fleshy, plano-convex or foliaceous cotyledons. Secondary xylem with prominent crystal chains in the parenchyma, cortical bundles normally oriented. $x = 17$.

A subfamily of about 212 species in 10 genera endemic to the neotropics.

Type genus. *Lecythis* Loefl.

Key to the Genera of New World Lecythidaceae (including *Asteranthos* of the Napoleonaeoideae)

1. Androecium actinomorphic.
  2. Flowers solitary in leaf axils, without petals; outer row of stamens fused to form a radiate, petaloid corona. Embryo J-shaped, embedded in ruminate endosperm. 1. *Asteranthos.*
  2. Flowers in multi-flowered inflorescences, infrequently with a single flower, with 4-8(-18) separate petals without a petaloid corona. Embryo not J-shaped, without endosperm.
    3. Flower buds globose, the flowers large, 2.5-20 cm in diameter at anthesis; ovules on the upper 1/2 of the septum. Fruits indehiscent, the seeds released via deliquescence of the pericarp or by fragmentation of the opercular region.
      4. Petals 6-8(-18); stamens 500-1200, the anthers linear, 2-5 mm long, dehiscing by apical pores; placentae expanded, the ovules 7-93 per locule, horizontal or slightly descending. Fruits usually with 2 or more seeds; embryo with plano-convex, fleshy cotyledons. 2. *Gustavia.*
      4. Petals 4; stamens 85-210, the anthers globose, less than 1 mm long, dehiscing by longitudinal slits; placentae not expanded, the ovules 2-4, pendulous. Fruits with a single seed; embryo undifferentiated. 3. *Grias.*
    3. Flower buds globose or oblong, the flowers smaller, less than 2.5 cm in diameter at anthesis; ovules on the lower 1/2 of the septum. Fruits dehiscent, the seeds freely falling.
      5. Calyx rim-like or with 5 inconspicuous broadly triangular lobes at anthesis; petals 5. Seeds not winged, the embryo undifferentiated. 4. *Allantoma.*
      5. Calyx with 6 triangular lobes at anthesis; petals 6. Seeds uni-laterally winged, the embryo with 2 foliaceous cotyledons. 5. *Cariniana.*
1. Androecium zygomorphic.
  6. All of the hood appendages bearing anthers.
    7. Ovary 6-locular; ovules 30-115 per locule, on bilamellar placentae throughout the

length of the locule. Fruit globose, indehiscent. Embryo with 2 foliaceous, highly convoluted cotyledons. 6. *Couroupita.*

7. Ovary 2-3(-5)-locular; ovules 5-8 per locule, placentae not bilamellar, attached towards the base of the locule. Fruit campanulate or cylindric, dehiscent. Embryo undifferentiated or with 2 foliaceous cotyledons, these not highly convoluted.
  8. Androecium elongated on one side into a strap-like structure which bends over the summit of the ovary; ovary 2(-5)-locular. Seeds without wings, the embryo undifferentiated. 7. *Corythophora.*
  8. Androecium elongated on one side but not forming a conspicuous strap-like structure which bends over the summit of the ovary; ovary 3-locular. Seeds unilaterally winged, the embryo with foliaceous cotyledons. 5. *Cariniana.*

6. Usually with all of the hood appendages sterile or, less frequently, with less than half of the hood appendages bearing anthers.
  9. Buds enclosed by calyx except for a horizontal slit at the apex; calyx with 2 lobes at anthesis, the style greater than 10 mm long. Fruit appearing indehiscent but with a small inwardly falling operculum, the seeds being retained within the fruit until the pericarp disintegrates. Seeds with a thick, boney integument. 8. *Bertholletia.*
  9. Buds not enclosed by calyx; calyx with 6 lobes at anthesis, the style less than 10 mm long. Fruit dehiscent, with a relatively large, outwardly falling operculum, the seeds being released at maturity. Seeds with a thinner, non-boney integument.
    10. Androecium hood coiled inwards, with an outwardly extended flap at the apex of the coil. Fruits cylindric or campanulate. Seeds with a wing around the circumference, the embryo with 2 foliaceous cotyledons. 9. *Couratari.*
    10. Androecium hood flat, or if coiled inwards without an outwardly extended flap at the apex of the coil. Fruits usually globose. Seeds without wings, the embryo undifferentiated.
      11. Androecium coiled inwards, with blunt-tipped appendages at the apex of the coil, these differentiated from the more abundant, echinate hood appendages; ovary usually 2-locular. 10. *Eschweilera.*
      11. Androecium flat or expanded at the apex but not coiled inwards, all hood appendages more or less equal; ovary usually 4-locular.
        12. Ovary 2-locular, the style not differentiated from the summit of the ovary, the summit umbonate. 7. *Corythophora.*
        12. Ovary 4-locular, the style differentiated from the summit of the ovary, the summit truncate. 11. *Lecythis.*

ASTERANTHOS
by
G. T. PRANCE

1. Asteranthos Desfontaines, Mém. Mus. Hist. Nat. **6:** 9, *t 3.* 1820; R. Brown, Trans. Linn. Soc. London **13:** 222. 1821; de Candolle, Prodr. **7:** 55. 1828; Endlicher, Gen. Pl. 745. 1839; Meisner, Pl. Vasc. Gen. 125. 1839; Lindley, Veg. Kingdom 716-730. 1846; Bentham, J. Linn. Soc., Bot. **3:** 80-81. 1859; Benth. & Hook., Gen. Pl. **1:** 724. 1865; Miers, Trans. Linn. Soc. London II. **1:** 17-19. 1875; Knuth, Notizbl. Bot. Gart. Berlin **11:** 1034-1036. 1934, Pflanzenreich IV. **219b:** 1-3. 1939.

Asteranthus Spreng., Linn. Syst. Veg. ed. 16. **2:** 568. 1825; Reichenbach, Consp. Veg. 137. 1828; Eichler, Mart. Fl. Bras. **12**(1): 496-500. 1889; Niedenzu in Engl. & Prantl, Nat. Pflanzenfam. **3**(7): 34. 1892.

Medium sized trees. Leaves alternate, entire, appearing glabrous, but with minute clustered hairs on lower surface visible only with high power magnification; with minute caducous stipules visible only on the youngest leaves. Flowers hermaphrodite, actinomorphic, 3.5-4.5 cm diameter, solitary in leaf axils. Receptacle conical-campanulate with a radiate circular accrescent calyx with crenate margin. Corolla absent. The outer whorl of stamens developed into a corona or corolla-like structure with 24-28 conspicuous veins from center to margin, pleated and unfolding like a parasol, the margins irregularly dentate and ciliate; the fertile stamens numerous, free, inserted in several rows attached in a circle around the base of the sterile outer whorl; anthers 2 locular, longitudinally dehiscent, basally attached. Style erect and thin, the stigma 5-8 lobed. Ovary semi-inferior, 5-8 locular with 4 ovules in each loculus. Fruit an oblong-pyramidal capsule; semi-inferior ±2 cm long with enlarged persistent calyx persisting around middle, the fruiting calyx coriaceous, to 3.5 cm diameter, the lower portion of fruit smooth unribbed, O.5 cm long, upper part above calyx 1.5 cm long deeply 6 ribbed and tapered to a pointed apex, unilocular with a single cone-shaped seed within, with abundant ruminate endosperm; embryo curved on lower portion to form a J-shape, with 2 membranous cotyledons at apex.

Type species. *Asteranthos brasiliensis* Desf. The name *Asteranthos* is derived from the Greek compound word *αδτηϱ* = aster (= star) and *αυϑοs* = andos (= flower) referring to the star-like flower.

Distribution. 1 species confined to the upper Rio Negro region of Colombia, Venezuela and Brazil.

Niedenzu (1892) and Hutchinson (1969) pointed out that the fused outer row of staminodes was mistaken for a corolla by many previous authors. We agree with Hutchinson that *Asteranthos* is apetalous but has a corolla- or corona-like row of staminodes. This forms a complete fused circle and the inner rows of stamens are fused to it at their bases. This interpretation is important in relating *Asteranthos* to the Lecythidaceae a family in which many remarkable structures have developed from the staminal tissue.

Taxonomic History

Asteranthos was described by Desfontaines (1820) who related it to the genus *Napoleonaea.* The genus was based on a single fragmentary collection without collectors information which was sent to Paris from Portugal but was of Brazilian origin. This was one of the A. R. Ferreira Brazilian collections. From the scrappy material Desfontaines reconstructed the plant and described *A. brasiliensis* and provided a surprisingly accurate illustration. Desfontaines placed *Asteranthos* in the Jussieuan family Symploceae. In fact *Asteranthos* had been mentioned in the literature by Palisot de Beauvois (1810) ten years prior to its formal description. Palisot de Beauvois when he described the new African genus *Napoleonaea* referred to an undescribed and related genus from Brazil which is in fact *Asteranthos.*

Robert Brown (1821) described the new family, Belviseae, to accommodate the two genera *Belvisia* and *Asteranthos. Belvisia* is a later homonym of *Napoleonaea* and is consequently illegitimate. Brown was thus linking *Napoleonaea* and *Asteranthos* together. He stated that he was uncertain of the exact relationship of his family Belviseae which was described in a footnote of a work discussing the Rafflesiaceae.

Sprengel (1825) placed *Asteranthos* in the Linnaean group Polyandria monogynia. Reichenbach (1828) treated it together with 'Napoleona'[4] in his group Asterantheae which was placed between Olacinae and Aquifoliaceae.

Lindley moved the Belvisiaceae around in his different works as his thoughts developed. In the first edition of his Natural System (1830), he placed Belvisiaceae between Styracaceae and Sapotaceae in the second edition of the same work (1836) he moved the Belvisiaceae to his Alliance Campanales and placed it between the Sphenocleaceae and Columelliaceae. In 1846 Lindley was the first worker to suggest that the Belvisiaceae was related to the Myrtaceae and Lecythidaceae. He placed Belvisiaceae in his order Myrtales between Rhizophoraceae and Melastomaceae. The order also contained Myrtaceae, Lecythidaceae, Onagraceae and four other families.

De Candolle (1838) in his *Prodromus* placed the family 'Napoleoneae' between Columelliaceae and Vaccinieae. The family contained the two genera *'Napoleona'* and *Asteranthos.*

Meisner (1839) considered the Belvisieae as a family which was placed between the Passifloraceae and Loasaceae. Also in 1839, Endlicher, considered *Asteranthos* as part of his class Petalanthae and in the 'Order' Ebenaceae in the group Symploceae. However, it is placed together with 'Napoleona' in "Genera dubiae affinitatis."

Bentham (1859) discussed *Asteranthos* in light of further material collected by Spruce which ended the doubt that the original material was from Brazil. He suggested affinity with the Myrtaceae (including Barringtoniae and Lecythidaceae) and thus follows Lindley (1846). A few years later *Asteranthos* was again included in the Myrtaceae by Bentham and Hooker (1865) who placed it in their tribe Lecythidaceae together with *Barringtonia, 'Napoleona'* and the South American genera of the family. The early confusion about the position of *Asteranthos* was partially due to the poor type material. Since Bentham drew attention to the Spruce material it has generally been placed near to or within the Lecythidaceae in the more recent systems.

Le Maout & Decaisne (1873) placed *Asteranthos* and *'Napoleona'* in the family 'Napoleoneae' between the families Myrtaceae (including Lecythidaceae) and 'Melastomaceae.' Baillon (1877) treated the 'Napoleoneae' as one of his 'series' of the Myrtaceae.

Miers (1875a) did not agree that *Asteranthos* is related to Myrtaceae. He studied the Spruce material and suggested a close relationship with *Rhododendron,* based mainly on the false assumption that *Asteranthos* had a fully superior ovary. This affinity has not been adopted by later workers. Miers' suggestion that there is more than one species of the genus is certainly unfounded judging by the more recent material studied here. In the same work Miers placed *Napoleonaea* in a unigeneric family Belvisiaceae.

Eichler (1889) treated the Napoleonaeaceae for Martius' *Flora Brasiliensis* as it was not included with the Myrtaceae in Berg's (1858) earlier account of that family which included the Lecythidaceae. Eichler did not agree with a myrtaceous affinity for Napoleonaeaceae and he discussed the various affinities

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[4] The correct orthography of the generic name is *Napoleonaea* (see Liben, 1971). Most later authors have misspelled the name as 'Napoleona.' In this account the orthography used by each author is given, but between quotation marks where is is incorrect.

suggested by previous authors, he rejected them all and rather hesitantly suggested a relationship to *Mesembrianthemum* or Cactaceae.

Niedenzu (1892) in the first edition of Engler's *Pflanzenfamilien* treated the genera *'Napoleona'* and *Asteranthos* as the subfamily 'Napoleonoideae' of the Lecythidaceae.

Knuth (1934, 1939c) treated *Asteranthos* in a separate family Asteranthaceae. He considered *'Napoleona'* as a separate tribe of the family Barringtoniaceae. Hutchinson (1969) followed Knuth and recognized the Asteranthaceae with some hesitation. Other more recent phyllogenetic systems e g Cronquist (1968), Takhtajan (1969) have included *Asteranthos* within the Lecythidaceae.

The Systematic Position of *Asteranthos*

The historical review above shows that there has been considerable disagreement about the systematic position of *Asteranthos.* Table XII summarizes the most important placings of *Asteranthos.*

The majority of workers starting with Desfontaines (1820), who described the genus, have related it to *Napoleonaea,* although the exact position and taxonomic status has varied widely from author to author. In the last detailed monograph of the Lecythidaceae Knuth (1939a, b, c) placed *Asteranthos* in a separate family, and *Napoleonaea* as a separate tribe in his family Barringtoniaceae.

In the introductory material to the present work it is shown that *Asteranthos* is undoubtedly most closely related to the African *Napoleonaea.* The main reason that some authors have been reluctant to relate the two genera is geographical rather than morphological. There are many examples of relationships between African and American genera and species and the geography does not pose any real problems. However, *Asteranthos* remains as the most isolated and distinct genus within the Lecythidaceae. It is close enough to *Napoleonaea* to be included in the same subfamily, but is obviously more primitive with only one staminal whorl developed into a fused corolla-like structure and the rest of the stamens free but attached to the outer whorl. In *Napoleonaea* there are four whorls of staminal origin, the outermost corolla-like, the inner 3 coronas are smaller with staminodes on the second and third rows and with the fertile stamens borne on the innermost corona. In *Asteranthos* the fruit is reduced to a single seeded capsule but as the flower has a multilocular ovary it is easy to relate to the many seeded drupe of *Napoleonaea.* The endosperm of *Asteranthos* is its most important difference from other Lecythidaceae, i e no other Lecythidaceae possess endosperm in the mature seeds.

Asteranthos brasiliensis Desfontaines, Mém. Mus. Hist. Nat. **6:** 9, *t 3.* 1820; de Candolle, Prodr. **7:** 5551. 1838; Miers, Trans. Linn. Soc. London II. **1:** 17-19. 1875; Eichler; Mart. Fl. Bras. **12**(1): 497-500. 1889, sub *Asteranthus;* Knuth, Pflanzenreich IV. **219b:** 3. 1939. Figs 7, 16A-D, 40, 41.

Tree to 15 m tall, the young branches glabrous. Leaves with laminas coriaceous, oblong, 4-13 cm long, 2-4.5 cm broad, almost glabrous on both

Table XII
Proposed relationship of *Asteranthos*

Relationship proposed	**Author**
near *Napoleonaea* family Symploceae	Desfontaines 1820
Fam. Belviseae with *Belvisia* =*Napoleonaea*	R. Brown 1821
Asterantheae with *Napoleonae*	Reichenbach 1828
Belvisiaceae near Styracaceae & Sapotaceae	Lindley 1830
Belvisiaceae in Alliance Campanales	Lindley 1836
Belvisiaceae in order Myrtales	Lindley 1846
Fam. Napoleoneae between Columelliaceae & Vaccinieae	de Candolle 1838
Fam. Belvisieae between Passifloraceae & Loasaceae	Meisner 1839
Myrtaceae tribe Lecythidaceae	Bentham & Hooker 1865
Fam. Napoleoneae next to Myrtaceae (incl. Lecythidaceae)	Le Maout & Decaisne 1873
Myrtaceae series Napoleoneae	Baillon 1877
near *Rhododendron*	Miers 1875a
Napoleonaceae with *Napoleonaea* related to *Mesembrianthemum* or Cactaceae	Eichler 1889
Lecythidaceae subfam Napoleonoideae	Niedenzu 1892
Asteranthaceae including only *Asteranthos*	Hutchinson 1969
	Knuth 1934, 1939c
Lecythidaceae subfam Napoleonoideae tribe Asterantheae	Pichon 1945
Lecythidaceae subfam Napoleonoideae tribe Asterantheae	Melchior 1964

surfaces, lower surface with minute clustered hairs visible only at very high magnification, acuminate at apex, the acumen 4-15 mm long, cuneate at base; midrib more or less plane above or slightly raised near base, prominulous or prominent beneath; primary veins plane and rather inconspicuous on both surfaces; leaves subsessile or with very short petioles to 3 mm long. Stipules minute and caducous. Flowers borne solitarily on long axillary pedicels, the pedicels 12-18 mm long, glabrous; bracteoles 2, small, caducous, inserted at base of pedicels. Receptacle conical with a circular accrescent calyx, crenate margin, glabrous. Pseudo-corolla (outer row of staminodes) a single united radiate unit with 24-28 conspicuous veins from center to margin, the margins ciliate, colored yellow. Stamens numerous with thin free filaments to 7 mm long, arranged in several rows around the interior rim of the pseudo-corolla; anthers small. Style to 5 mm long, glabrous. Fruit to 2 cm long, the persistent calyx expanding and forming a circular rim around the fruit, smooth below rim, deeply costate above rim, the costae coming to a pointed apex. The single seed obconical-pyriform with swollen base and pointed apex filling the interior of the loculus, the other loculi abort and are not apparent in the mature fruit.

Type. *Ferreira sn* (ex herb. Lusitan. comm. Geoffroy), Brazil, Amazonas, Rio Negro fl (holotype, P).

Distribution. Flooded forest on sand beside black water rivers of the upper Rio Negro region of Colombia, Venezuela and Brazil. Where this geographically restricted plant does grow it often grows in great abundance even though the lack of collections indicate otherwise.

COLOMBIA. Guainía: Río Guainía; between Maroa and Victorino, *Maguire & Wurdack 35585* fl (COL, F, IAN, MICH, NY, US, frag INPA), Puerto Colombia, opposite Maroa,

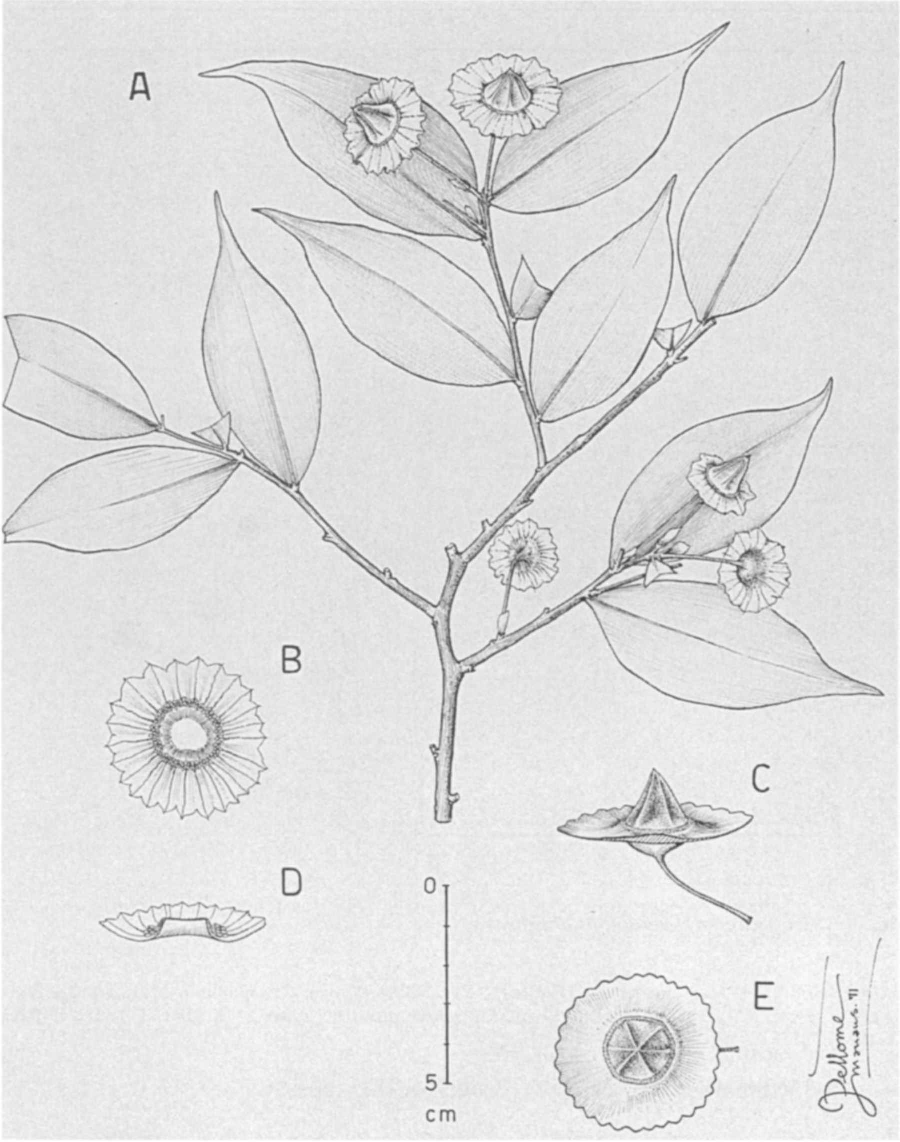


FIG 40. *Asteranthos brasiliensis (Prance et al 15798):* A, Habit. B, Top view of corona and stamens which fall as a unit. C, Fruit with persistent calyx. D, Longitudinal section of B.

Schultes, Baker & Cabrera 18214 fl (BM), *Maguire, Wurdack & Keith 41834* fl (NY). VENEZUELA. Terr. Amazonas: Río Guainía, above mouth of Río Casiquiare, *Spruce 3500* fl (BM, CGE, E, F, G, MG, NY, OXF, P); between Caño San Miguel and Maroa, *Wurdack & Adderley 43265* fr (F, G, NY, US, VEN). BRAZIL. Amazonas: Rio Negro; Cucuí, *Ducke 39* fl (F, NY, US), mouth of Rio Curicuriarí, *Ducke 57* fl (F, G, NY, P, RB 23883), *57a* fr (G, NY, RB 23883); Tapuruquara, *Monteiro 1450* fl (INPA, NY), *1452* fl (INPA, NY), *1455* fl (INPA, NY),

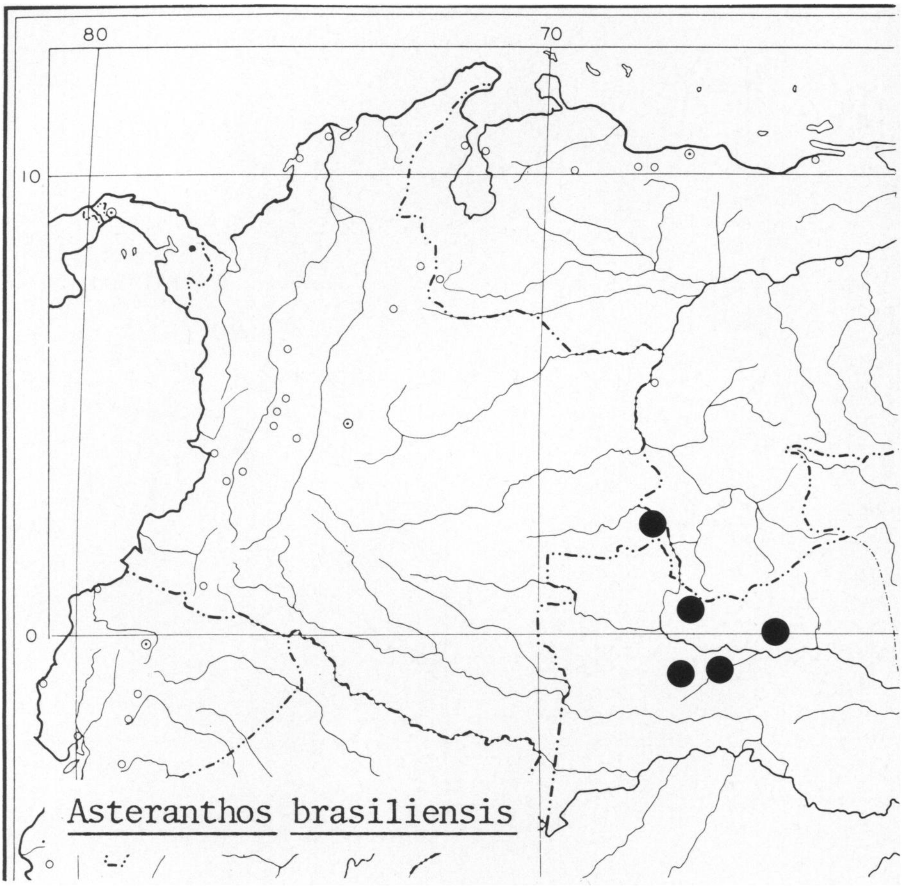


FIG 41. Distribution of *Asteranthos brasiliensis.*

1456 fl (INPA, NY), *Prance et al 15798* fl (INPA, MG, NY, U); Rio Uneiuxi, Matozinho, *Fróes 22359* fr (IAN, NY, P, US, VEN), 100-200 km above mouth, *Prance et al 15481* fl fr (F, INPA, MG, NY, S, U, US).

No local names or uses are recorded for this species.

GUSTAVIA
by
SCOTT A. MORI

2. **Gustavia** Linnaeus, Pl. Surinam. **12:** 17-18, *t sn 1775, nom. conserv.;* Miers, Trans. Linn. Soc. London **30**(2): 175-188, *t 33.* 1874; Knuth, Pflanzenreich IV. **219a:** 28-33, *fig 6.* 1939; Macbride, Publ. Field Mus. Nat. Hist., Bot. Ser. **13**(4): 230-236. 1941; Woodson, Ann. Missouri Bot. Gard. **45:** 117-122, *figs 36-37.* 1958.

Iaparandiba Marcgrave, Historiae Rerum Naturalium Brasiliae, Caput 28. 1648.
Japarandiba Adanson, Fam. **2:** 448. 1763, *nom. rejic.*
Pirigara Aublet, Hist. Pl. Guian. **1:** 487. 1775.
Teichmeyeria Scopoli, Introd. p 267. 1777.
Spallanzania Necker, Elem. p 79. 1790.
Perigaria Spanoghe, Linnaea **15:** 204. 1841.

Trees, small to medium sized, to 30 m tall; growth form either single stemmed or few branched with clusters of large leaves at ends of thickened branches (pachycaul) or with a single dominant trunk and a much branched crown with smaller leaves at ends of slender branches (leptocaul); leaves always more or less congested at ends of branches. Leaves petiolate or sessile, glabrous, infrequently pubescent on abaxial surface, chartaceous to coriaceous, entire to serrate, the blades relatively small to extremely large, the largest leaves occurring in pachycaul species and the smallest ones in leptocaul species. Inflorescences suprafoliar, axillary, or cauline, solitary or racemose, the rachis contracted to very long; pedicels subtended by a single bract and with 2 opposite or subopposite bracteoles variously inserted along the length of the pedicel. Flowers symmetrical, showy, to 20 cm in diameter; calyx entire or 4 or 6 lobed; petals 6 or 8 (12 or 18 in *G. romeroi*); androecium with 500-1210 stamens, all fertile, fused at their bases into a symmetrical ring, this adnate to the bases of the petals and the summit of the ovary, the filaments somewhat dilated and then sharply constricted at the apex, the anthers 2-5 mm, basifixed, dehiscing by 2 apical pores; ovary inferior, with or without costae, 4 or 6(-10)-locular, each locule with 7-93 anatropous ovules; placentation axile, the placenta occupying only the upper one-half of the septum; style less than 5 mm long. Fruits berry-like, sometimes becoming woody, normally releasing the seeds by deliquescence of pericarp, in some species appearing dehiscent because of rotting away of weaker fruit summit, usually globose, sometimes cylindric or obconic, with calyx lobes persistent or absent, with or without costae; mesocarp white, sometimes orange, often becoming mushy at maturity. Seeds of two types, without well developed funicles or with yellow, expanded, contorted funicles. Embryo with large, fleshy, plano-convex cotyledons and minute hypocotyl and plumule. Seedlings with cataphylls. $x = 17$.

Type species. *Gustavia augusta* L. The genus was named by Linnaeus in honor of King Gustavius III of Sweden.

Distribution. *Gustavia* includes 41 described species which are widely distributed in Central and South America from southwestern Costa Rica to northern Bolivia (Fig 38).

Taxonomic History of *Gustavia*

The first description and illustration of a species of *Gustavia* to appear in the literature is in Marcgrave's *Historiae Rerum Naturalium Brasiliae* (1648, see also Taxonomic History of the Lecythidaceae). He described the species as a tree with large white flowers with somewhat fleshy petals, many incurved stamens, and apple-sized fruits which contain almond-sized seeds borne on a

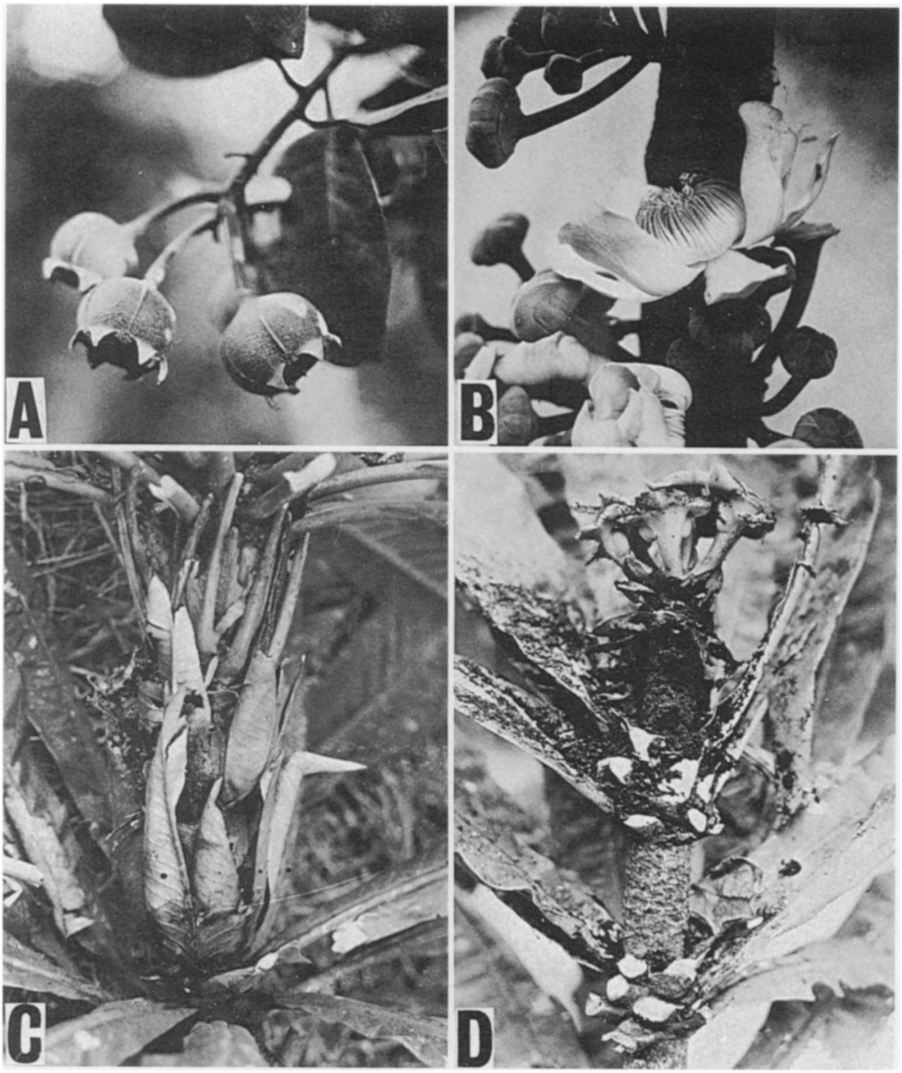


FIG 42. Vegetative, flowering, and fruiting characteristics of selected species of *Gustavia:* A, Fruits of *G. dubia (Mori et al 4085),* note the 6 persistent calyx lobes and the costae on the hypanthium which are characteristics of *Gustavia* section *Hexapetala;* B, Inflorescences, buds and flowers of *G. superba* (unvouchered); C, Stem of *G. grandibracteata (Mori 836),* note the persistent leaf-like bracts which once subtended a flower cluster; D, Cluster of young fruits of *G. monocaulis (Mori & Kallunki 5600),* note the suprafoliar position of the fruits and the absence of leaf-like bracts.

thick funicle. The description and illustration clearly refer to *G. augusta*. L. Berg (1858) suggested that the description and illustration were of *G. brasiliana (G. hexapetala).* However, the entire calyx, clearly depicted in the illustration, of *G. augusta* differs markedly from the 6-lobed one of *G. hexapetala*. The Portuguese common name, "Jeniparanduba," given for the plant by Marcgrave still persists as "Jeniparana," especially for *G. augusta* in northeastern Brazil.

In 1775 two species of *Gustavia* were published under two different genera. *Gustavia augusta* was published by Linnaeus in *Plantae Surinamenses* and *Pirigara hexapetala* by Aublet in his *Histoire des Plantes de la Guiane Française*. Aublet's work was published in 4 volumes which included 72 parts. The first part appeared on June 10, 1775 and the last in September of the same year (Stafleu, 1967). The description of *Pirigara* is in the second volume and most likely appeared after the June 23rd publication of *Plantae Surinamenses*. Aublet's genus was later reduced to synonymy under *Gustavia* by Smith (in Rees' *Cyclopaedia,* 1819). In addition, *Gustavia* has recently been conserved over *Pirigara* (Lanjouw, 1966).

The actinomorphic flowers of *Gustavia* have prompted some early workers to place the genus in the subfamily Planchonioideae. For example, A. P. de Candolle (1828), Lindley (1836, 1846), and Thompson (1927) aligned *Gustavia* with their tribe Barringtoniae, family Barringtoniaceae, and series Barringtoniaceae respectively. Nevertheless, the monographers of the family (Miers, 1874; Knuth, 1939b; Mori, 1974; Prance and Mori, 1977) recognize the affinities of *Gustavia* with other Lecythids. Moreover, the chromosome number of *Gustavia* unequivocally relates it to other Lecythids rather than the Planchonioids. Gametic counts of $n = 17$ have been reported for *G. dubia* and *G. angustifolia* and $n = 34$ for *G. superba*. In contrast, known counts of Planchonioids are either $n = 13$ or $n = 26$ (Kowal et al, 1977). In addition, the tricolpate pollen of *Gustavia* supports its relationship to the other, uniformly tricolpate Lecythidoid genera rather than to the uniformly syntricolpate Planchonioids (Muller, 1972, 1973).

Key to Sections of *Gustavia*

1. Leaf blades usually less than 30 cm, never over 50 cm long. Flowers with 6 calyx lobes and 6 petals; hypanthium with strongly developed costae persisting on the fruit; calyx lobes with an adaxial, inverted "Y-shaped" thickening (Figs 42A, 43). I. Hexapetala.

1. Leaf blades various, 17-136 cm long. Flowers with entire calices or with 4 (infrequently 6) calyx lobes and 8 (infrequently 6) petals *(G. romeroi* has 12 or 18 petals), if with 6 calyx lobes or petals then without thickened calyx lobes and costae on the hypanthium; hypanthium smooth or with 4(-6) obscure costae; calyx lobes without adaxial "Y-shaped" thickenings.
   2. Monocaulous or few-branched trees. Inflorescences suprafoliar, subtended by the terminal whorl of large (35-100 cm long), tightly compacted leaves; pedicels subtended by a large bract 25-115 × 10-35 mm and with 2 large bracteoles 13-65 × 6-48 mm inserted just below the hypanthium. II. Grandibracteata.
   2. Few-branched to many-branched trees. Inflorescences cauline, axillary, or suprafoliar when suprafoliar not subtended by a terminal whorl of large compacted leaves; pedicels subtended by a small, scale-like, usually caducous bract or normal leaves and with 2 variously inserted, scale-like bracteoles. III. Gustavia.

Key to the Species of Section *Hexapetala*

1. Fruits "pseudoperculate" (i e the operculum is removed piecemeal by fragmentation or by insects before fruits fall and does not fall as a unit). Fresh fruits brown at maturity. Seeds with yellow, expanded funicles. When fruits not present use distributions and frequency of occurence as aids for identification.
    2. Leaves chartaceous, 10-20 × 3.5-7 cm. Fruits cylindrical, 25 × 20 mm; costae decurrent on pedicel. Eastern Chiriqui, Panama and the Osa Peninsula, Costa Rica. Rare. 1. *G. brachycarpa.*
    2. Leaves coriaceous, 15-27 × 5-8 cm. Fruits globose, 20 × 20 mm; costae not decurrent on pedicel. Magdalena Valley, Colombia. Rare. 2. *G. longifuniculata.*
1. Fruits non-operculate (i e the operculum persists until after the fruits fall). Fresh fruits bright, yellowish brown at maturity. Seeds with straight, inconspicuous funicles. When fruits not present use distributions and frequency of occurence as aids for identification.
    3. Leaves chartaceous. Fruits with costae absent or, if present, not decurrent to base. Eastern Panama and Magdalena Valley, Colombia. Common within restricted range. 3. *G. dubia.*
    3. Leaves usually coriaceous, sometimes chartaceous, especially when young. Fruits with costae decurrent to base (costae absent in one collection of *G. hexapetala* (Prance & Silva 58863) which has distinctly coriaceous leaves). Amazonia, the Guianas and northern Venezuela. Widespread and common. 4. *G. hexapetala.*

Key to the Species of Section *Grandibracteata*

1. Leaf blades pilose abaxially, especially on the veins. Flowers with 6 calyx lobes and petals; ovary with 6 obscure costae. Ecuador. 5. *G. pubescens.*
1. Leaf blades glabrous or minutely puberulous abaxially. Flowers with 4 calyx lobes and 8 petals; ovary without costae.
    2. Leaves petiolate, the petiole 20-78 mm. Flower cluster subtended by sterile leaf-like bracts (Fig 42C), these often persistent for several years, the two bracteoles on the pedicel 45-65 × 34-48 mm. Central Panama eastward into the Magdalena Valley of Colombia. 6. *G. grandibracteata.*
    2. Leaves sessile (one leaf of *G. monocaulis* has been found with a petiole 85 mm long). Flower cluster without subtending, sterile, leaf-like bracts, the two bracteoles on the pedicel 15-22 × 6-19 mm.
        3. Leaf blades entire, 71-88 × 13-15 cm. Flowers with pedicels 40-50 mm; calyx lobes triangular, 8 × 15 mm; connate androecium base 4 mm high, outermost filaments 11 mm. Southern Chocó, Colombia. 7. *G. sessilis.*
        3. Leaf blades serrulate to serrate towards the apex, 92-120 × 18-33 cm. Flowers with pedicels 30-40 mm; calyx lobes very widely ovate, 16-25 × 23-40 mm; connate androecium base 9 mm high; outermost filaments 22-25 mm. Central Panama Province, Panama. 8. *G. monocaulis.*

Key to the Species of Section *Gustavia*

1. Inflorescences mostly arising above the leaves (i e suprafoliar).
    2. Abaxial leaf surface pubescent (use × 10 magnification), at least on the veins. Ovary usually obscurely 4 costate. Plants of coastal Ecuador and southwestern coastal Colombia.
        3. Petioles absent to 30 mm long; leaf bases acute. 9. *G. angustifolia.*
        3. Petioles 100 mm long, never absent; leaf bases obtuse. 10. *G. petiolata.*
    2. Abaxial leaf surface glabrous (use × 10 magnification). Ovary with or without costae. Only *G. dodsonii* of coastal Ecuador, the remaining species of the Andes, Interandean Valleys, Amazonia, or the Guianas.
        4. Seeds with well developed, thickened, yellow, contorted funicles. Mostly Amazonian, only *G. santanderiensis* extra-Amazonian.

5. Petioles 50-95 mm long. Calyx with 6 shallowly rounded lobes. Magdalena Valley, Colombia and extreme western Amazonia. 11. *G. santanderiensis.*

5. Petioles 5-40 mm long. Calyx entire or of 4 shallow lobes. Amazonia and the Guianas.

6. Leaf blades elliptic, 11-28 x 4-9.5 cm. Fruits cylindrical, 17-30 mm in diameter. Plants of *terra firme*, restricted to central Amazonia. 12. *G. elliptica.*

6. Leaf blades oblanceolate, 16-48 x 4-13 cm. Fruits globose, 30-80 mm in diameter. Plants mostly of *várzea* or river margins, infrequently of *terra firme*, widespread and common throughout Amazonia and the Guianas. 13. *G. augusta.*

4. Seeds without well developed, thickened, yellow, contorted funicles. Mostly extra-Amazonian, only *G. terminaliflora* and *G. macarenensis* Amazonian.

7. Leaves sessile; blades 78-90 x 20-27 cm, with 36-37 pairs of lateral veins. Plants of coastal Ecuador. 14. *G. dodsonii.*

7. Leaves petiolate; blades 13-72 x 5-10 cm, with 10-27 pairs of lateral veins. Plants of the Andes, Interandean Valleys, Amazonia, or Panama.

8. Petioles indistinct, less than 5 mm long. Known only from one locality in Amazonas, Peru. 15. *G. terminaliflora.*

8. Petioles distinct, 5-80 mm long. Plants of the Andes, Interandean Valleys, western Amazonia, or Panama.

9. Calyx entire. Plants of the Magdalena Valley, Colombia into the Darien of Panama. 16. *G. verticillata.*

9. Calyx 4-lobed. Plants not of the Magdalena Valley and the Darien of Panama.

10. Flowers 5-8 cm in diameter; hypanthium costate. Plants of eastern Venezuela. 17. *G. parviflora.*

10. Flowers 13-18 cm in diameter; hypanthium smooth. Plants not of eastern Venezuela.

11. Leaf blades distinctly serrate. Plants of Barro Colorado Island, Panama. 18. *G. fosteri.*

11. Leaf blades entire to serrulate. Plants of the Andes, Interandean Valleys, and western Amazonia.

12. Summit of ovary glabrous; style 4-5 mm long. Fruits truncate at apex. Plants of western Amazonia and western Venezuela. 19. *G. macarenensis.*

12. Summit of ovary white puberulous to white tomentose; style 1.5-3(-4) mm long. Fruits bulging upward at apex, more or less umbonate. Plants of Interandean Valleys, sometimes cultivated outside of native range. 20. *G. speciosa.*

1. Inflorescences mostly arising among or below the leaves, i e axillary or cauline.

13. Largest leaf blades less than 30 cm long.

14. Petals 12 or 18. 21. *G. romeroi.*

14. Petals 6 or 8.

15. Petioles greater than or equal to 50 mm long. 22. *G. nana.*

15. Petioles less than 50 mm long.

16. Known only from the state of Zulia, Venezuela. Inflorescences cauline. 23. *G. tejerae.*

16. Plants of Amazonia, the Guianas, or the Chocó, if from the state of Zulia, Venezuela then with axillary inflorescences.

17. Leaves often in several distinct verticils at the branch ends. Inflorescences axillary, infrequently cauline.

18. Leaf blades acute at base. Inflorescence with more than one flower, the rachis greater than 10 mm long. Petals rose to red. Plants of Antioquia and Chocó, Colombia. 24. *G. gentryi.*

18. Leaf blades auriculate at base. Inflorescence usually with one flower, the rachis less than 10 mm long. Petals white with tinges of pink. Plants of Amazonia and coastal Venezuela. 25. *G. poeppigiana.*

17. Leaves aggregated at branch ends but not in distinct verticils. Inflorescences mostly cauline, infrequently axillary.

19. Leaf blades with 12-13 pairs of lateral veins. Petals 6. 26. *G. longepetiolata.*

19. Leaf blades with 14-23 pairs of lateral veins. Petals 8.

20. Leaf blades obovate or oblanceolate. Seeds with a distinct, yellow contorted funicle. Inflorescences more commonly suprafoliar than cauline. Common and widespread throughout the Guianas and Amazonia. 13. *G. augusta.*

20. Leaf blades mostly elliptic or infrequently oblanceolate. Seeds not know. Inflorescences always cauline. Restricted in distribution.

21. Leaf margins distinctly serrate. Known only from Manabi, Ecuador. 27. *G. serrata.*

21. Leaf margins entire. Known only from the Rio Orinoco watershed. 28. *G. acuta.*

13. Largest leaf blades equal to or greater than 30 cm.

22. Inflorescence axillary, or if cauline, solitary, without a rachis and in the axils of leaf scars directly below the leaves.

23. Leaf blades 2-3.5 cm wide. 29. *G. gracillima.*

23. Leaf blades 4-18 cm wide.

24. Inflorescence a single flower in the leaf axils or in axils or leaf scars, without a rachis; pedicels 90-100 mm long. Seeds without well developed funicles. Plants of southwestern Colombia and northwestern Ecuador. 30. *G. foliosa.*

24. Inflorescences of more than one flower or if of one flower then arising from a reduced rachis which in turn arises from a leaf axil; pedicels 10-75 mm long. Seeds with a well developed, contorted, yellow funicle. Plants of northern Venezuela, the Guianas, and Amazonia.

25. Leaf blades spathulate, the bases somewhat auriculate. Inflorescences strictly axillary, the rachis reduced, 1-7 mm long, usually with 1, less frequently with 2 or 3 flowers. 25. *G. poeppigiana.*

25. Leaf blades obovate or oblanceolate. Inflorescences mostly suprafoliar, less frequently axillary or cauline, the rachis 10-70 mm long, usually with 2 or more flowers. 13. *G. augusta.*

22. Inflorescences cauline, always with more than one flower and with a distinct rachis, variously inserted on the trunk and branches.

26. Plants of the Guianas and Amazonia.

27. Leaf blades with scattered hairs abaxially. Fruits red. 12a. *G. erythrocarpa.*

27. Leaf blades glabrous abaxially. Fruits brown.

28. Leaf blades with 14-22 pairs of lateral veins. Inflorescences mostly suprafoliar, infrequently cauline. Calyx entire or 4 lobed. 13. *G. augusta.*

28. Leaf blades with 21-49 pairs of lateral veins, if with 21 or 22 pairs then the calyx with 6 lobes. Inflorescences always cauline.

29. Calyx with 6 lobes; hypanthium usually obscurely 4-costate. 31. *G. pulchra.*

29. Calyx with 4 lobes; hypanthium with or without costae.

30. Leaf blades with 25-28 pairs of lateral veins.

31. Petioles 15-25 mm long. Calyx of 4 very broadly triangular lobes; petals 80 × 45 mm. 32. *G. coriacea.*

31. Petioles 40-60 mm long. Calyx entire; petals 52 × 27 mm. 33. *G. inakuama.*

30. Leaf blades with (27-)30-49 pairs of lateral veins.

32. Leaves sessile. 34. *G. acuminata.*

32. Leaves petiolate, some of the petioles as short as 4 mm.

33. Inflorescences with the rachis 15-70 mm long. Petals pink to dark red or purple. 35. *G. longifolia.*

33. Inflorescences with the rachis 40-130 mm. Petals white. 36. *G. gigantophylla.*

26. Plants of Andean Valleys or west or north of the Andes.

34. Leaf blades 2-3.5 cm wide. 28. *G. gracillima.*

34. Leaf blades 4-31 cm wide.
    35. Leaf blades with 12-23 pairs of lateral veins.
        36. Calyx entire.
            37. Leaf blades with 17-19 pairs of lateral veins, the margins entire. Hypanthium rusty-tomentose; ovary 4-locular. Rare. 37. *G. latifolia.*
            37. Leaf blades usually with more than 19 pairs of lateral veins, the margins serrate to serrulate. Hypanthium puberulous; ovary 6-locular. Common. 38. *G. superba.*
        36. Calyx of 4 very broadly triangular or rounded lobes.
            38. Leaf blades mostly narrowly ovate or lanceolate, infrequently elliptic. Rachis of the inflorescence equal to or less than 50 mm long. Ovary 4-locular. Plants of eastern Panama and northwestern Colombia. 22. *G. nana.*
            38. Leaf blades mostly obovate or oblanceolate, infrequently elliptic. Rachis of the inflorescence greater than 50 mm long. Ovary 6-locular. Plants of north central Venezuela. 39. *G. flagellata.*
    35. Leaf blades with 24-60 pairs of lateral veins.
        39. Leaf blades with 24-36 pairs of lateral veins. Ovary 6-locular. Common. 38. *G. superba.*
        39. Leaf blades with 60 pairs of lateral veins. Ovary 4-locular. Rare. 40. *G. excelsa.*

I. **Gustavia** sectio **Hexapetala** Mori, sect nov Figs. 5, 42A, 43.

Gustavia sect *Augustae* R. Knuth in Engler, Pflanzenreich IV. **219a:** 13. 1939, *pro parte.*
Gustavia sect *Speciosae* R. Knuth in Engler, Pflanzenreich IV. **219a:** 14. 1939, *pro parte.*

Arbores usque ad 25 m altae. Folia laxe ad apicem ramorum aggregata; laminae 8-31(-45) × 3-13 cm. Flores: lobi calycis et petala (5-)6(-8) et ovarium 6-costatum, 6-loculatum. Fructus plerumque costatus, ad summum lobis calycis persistentibus ornatus. Semina carunculo et funiculo 1-9 mm longo instructa.

Type species. *Gustavia hexapetala* (Aublet) Smith

The 6-merous flowers, the persistent calyx lobes with adaxial "Y-shaped" thickenings, the costate ovary, and the carunculate seeds readily separate the species of this section from all other species of *Gustavia.*

All species of section *Hexapetala* have the leptocaul growth form whereas species outside the section are either leptocauls or pachycauls. In addition, the petioles of the species of this section have a system of vascularization unique in the genus. A cross section of the petiole at its junction with the blade reveals two diagnostic features: 1) the adaxial fourth of the petiole is occupied by longitudinal rows of parenchyma cells that are not penetrated by vascular bundles and 2) the secondary vascular bundles (there is one large primary bundle and 4 or 5 slightly smaller secondary bundles) are always adaxial to the primary bundle (Fig. 5). In other species of *Gustavia* the entire petiole is penetrated by vascular bundles and there is more than one primary bundle or, if only one primary bundle is present, the secondary bundles are abaxial or completely surround it (Fig. 6).

The species of section *Hexapetala* form the most coherent, easily recognized section of the genus. However, specific and subspecific limits within the section are not clearly defined. I treat all collections east of the Andes as well as those in Venezuela north of the Andes as one common, widespread species, *G. hexapetala*. Although there are 3 species west of the Andes, one is common (*G. dubia*) and two are rare (*G. longifuniculata, G. brachycarpa*). Since interspecific differences are so slight, an argument could be made for treating all four species as subspecies of *G. hexapetala*.

1. **Gustavia brachycarpa** Pittier, Contr. U.S. Natl. Herb. **26**(1): 3-4. 1927; Woodson, Ann. Missouri Bot. Gard. **45**(2): 119-120, *fig 36*. 1958.

Figs 16F, 43, 44.

Gustavia microcarpa Pittier ex R. Knuth in Engler, Pflanzenreich IV. **219a**; 21. 1939 In synon.

Trees 5-15 m tall to 35 cm in diameter; trunk straight, branching diffuse, forming a rounded crown; leaf-bearing branches ca 3 mm in diameter, the leaves loosely grouped at their ends, the petiole scars 5-30 mm apart. Bark grayish, smooth. Leaf blades elliptic to narrowly obovate, 10-20 × 3-8 cm, glabrous, chartaceous, with 11-15 pairs of lateral veins; apices acuminate; bases acute, narrowly decurrent; margins crenulate on upper half of blade to entire on lower half. Petioles 4-20 × 2 mm, subterete in cross section, flattened adaxially; stipules triangular, acute, ca 4 mm, early caducous (fide Pittier), their scars not readily distinguishable on older twigs. Inflorescences suprafoliar or axillary, flowers in bract or leaf axils, puberulous, with 1 or 2 flowers at the branch ends; pedicels 30 mm, winged, subtended by a single caducous bract and bearing 2 variously inserted bracteoles ca 4 × 2 mm. Flowers 6-merous; calyx lobes triangular, 10 × 8 mm, slightly rusty-tomentose; petals 6, white, broadly oval, 40-45 mm long; fused androecium base ca 6 mm high; outermost filaments ca 8 mm; anthers 2-2.5 mm; ovary 6-costate, 6-loculate, glabrous at summit; style 2 mm. Fruits cylindrical, 25 × 20 mm, with 6 wings to 5 mm wide, with persistent calyx lobes. Seeds: "2 or 3 fertile seeds in each fruit, the remaining cells occupied by aborted seeds; funicle fleshy; seed ovoid about 12 mm long, with a brown perisperm, paler and torulose around the large apical micropyle" (fide Pittier).

Type. *Pittier 5269* (holotype, US 715480, photos NY, WIS; isotypes, GH, NY). Panama. Chiriquí, Eastern Chiriquí, vicinity of San Félix, collected in woods, 23 Dec 1911 (fr).

Distribution. A straight-boled tree ranging from the lowland forests and swamps of the Pacific watershed of Panama to the Osa Peninsula of Costa Rica.

COSTA RICA. Puntarenas: Playa Llorona, 30 m alt, 21 Sep 1975 (fr), *Poveda et al sn* (MO, NY). PANAMA. Chiriquí: W of Remedios, 24 Jun 1938 (fl), *Woodson et al 787* (A, MICH, MO, NY).

Gustavia brachycarpa has distinctive fruit and seed characteristics. The fruits, at maturity, lack an operculum and consequently appear to be dehiscent. Woodson (1958) notes this in his treatment of the Lecythidaceae for the Flora of Panama where he also claims to have seen the same condition in collections of *G. hexapetala* and cites Sandwith's report of dehiscence in *G. laciniosa (= G. augusta)*. However, I have never seen freely operculate fruits in

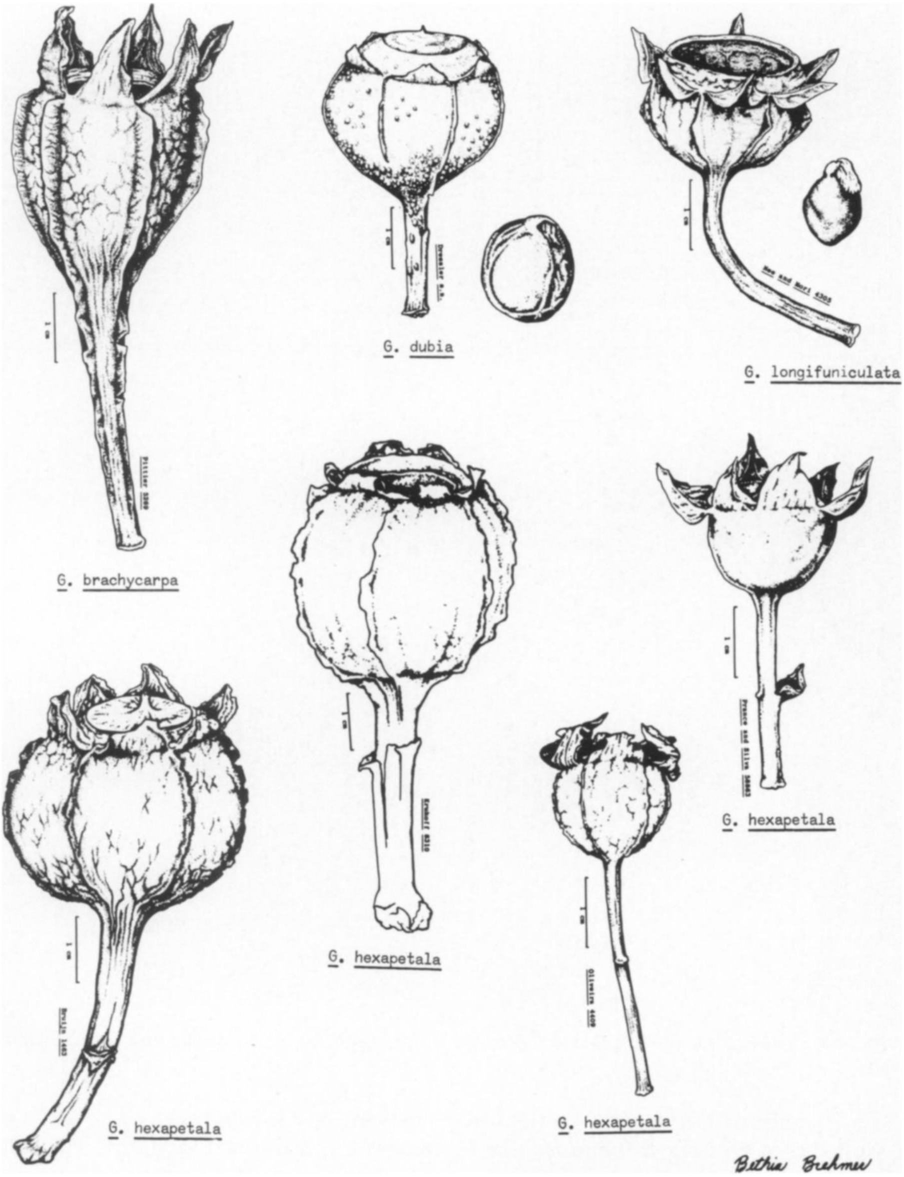


FIG 43. Fruits of *Gustavia* section *Hexapetala*. Note the costae and 6 persistent calyx lobes with their inverted "Y-shaped" thickenings. Costae are absent from Prance & Silva's collection *(58863)* of *Gustavia hexapetala*.

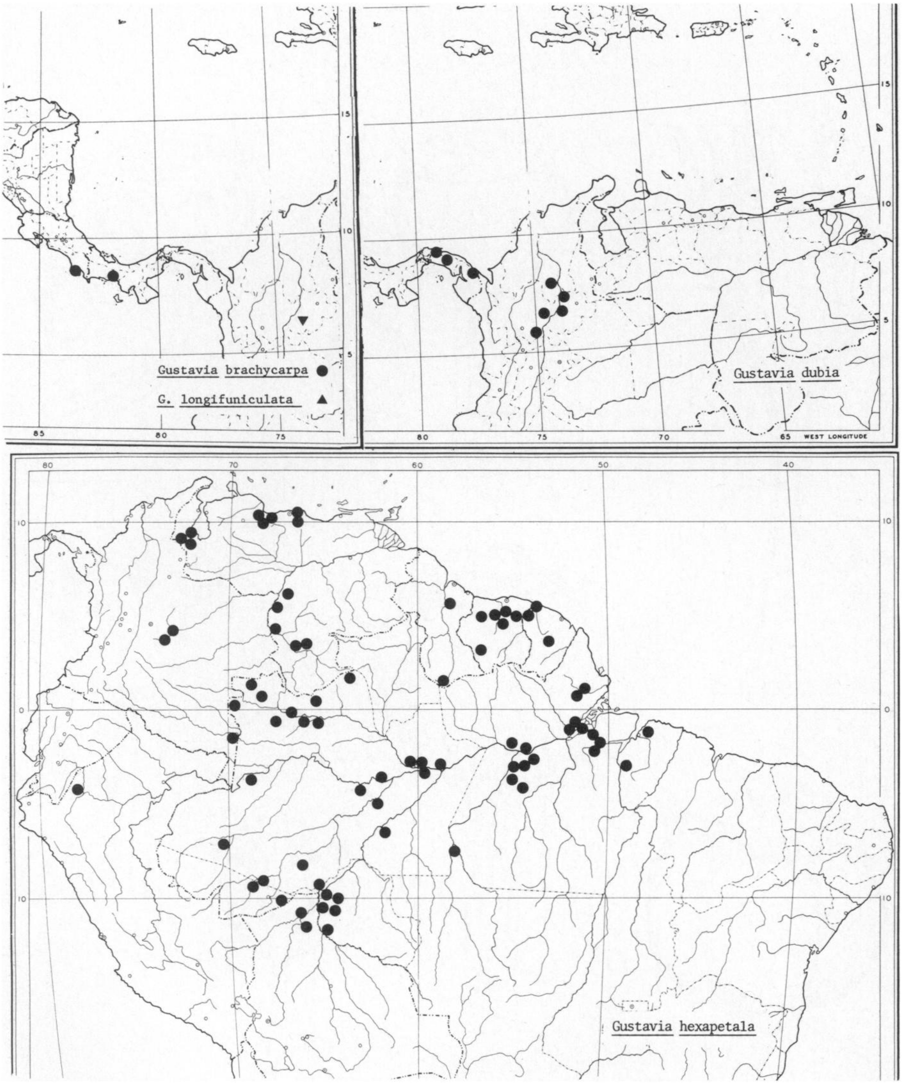


FIG 44. Distributions of *Gustavia brachycarpa, G. longifuniculata, G. dubia,* and *G. hexapetala.*

any species of *Gustavia.* My field observations of *G. longifuniculata* have revealed that *G. longifuniculata,* like *G. brachycarpa,* is pseudoperculate. In this species the opercular area is weak and easily removed by rotting and/or animals. I was able to find no intact opercula under the tree while many fruits with fragmented and partially removed opercular regions remained on the tree. I have also observed seedlings growing out of the opercular opening of a fruit of *G. augusta.* All other species of *Gustavia* release their seeds only after the pericarp has been opened by animals or rotted away. The reports of Woodson (1958) and of Corner (1976), who described the fruits of *Gustavia* as woody capsules, are erroneous. There are no freely operculate species of *Gustavia.*

The seed of *G. brachycarpa* possesses a well developed, fleshy funicle. Fleshy funicles are found in this section only in this species and *G. longifuniculata.* Pseudooperculate fruits and fleshy funicles are probably adaptations for dispersal by animals although we have no data to support this suggestion.

2. Gustavia longifuniculata Mori, sp nov. Figs 5, 43, 44.

Abores usque ad 20 m altae × 30 cm diametro, trunco erecto; folia ad extrema ramorum laxe aggregata cicatricibus petiolorum 5-10 mm inter se distantibus; rami infra folia 3-4 mm diametro. Cortex manifeste fissuratus, brunneus. Laminae elliptico-oblanceolatae, apice acuminatae, basi attenuatae, 15-27 × 5-8 cm, marginibus integro-crenulatae, glabrae, coriaceae, paribus venarum lateralium 12-14. Petioli 5-10 × 3 mm, in sectione transversali semicirculares, facie adaxiali complanati. Inflorescentiae suprafoliatae, in axillis foliorum vel bractearum exorientes, ferrugineae, tomentosae, floribus 2-5; pedicelli 35-45 mm, bractea caduca et bracteolis 2, sagittatis, 6-10 × 4-6 mm ad medium insertis suffulti. Flores ca 11 cm diametro; calycis lobi triangulari-sagittati, 7-10 × 6-7 mm, tomentosi, virides; petala 6, obovata, 50-60 × 30-40 mm, puberula, alba; androecii basis connata 10 mm alta, alba; antherae 3 mm, lutae; ovarium 6-costatum, extus ferrugineo-tomentosum, 6-loculare. Fructus globosi, ad apicem complanati, 6-costati, 20 × 20 mm, lobis calycis 6, triangulari-sagittatis, persistentibus ornati. Semina in sectione transversali semicircularia, 15 × 10 mm, 2-3 per fructum, caruncula lutea et funiculo carnoso expanso, ca 6 mm longo instructa.

Type. *Nee & Mori 4305* (holotype, COL; isotypes, BM, COL, F, MO, NY, P, US, VEN, WIS). Santander: Campo Capote (6° 38' N, 73° 55' W), compartment 82, alt 100-200 m, 9 Jul 1971 (fl, fr).

Distribution. This species is known only from the central Magdalena Valley of Colombia.

COLOMBIA. Santander: Campo Capote, 27 Mar 1971 (st), *Nee & Mori 3801* (F, NY, US, WIS).

Ecology. A medium to large sized tree of tropical lowland forests. Other tree genera in the forest of the type locality are: *Alchornea* (Euphorbiaceae), *Cariniana, Couratari, Eschweilera* (Lecythidaceae), *Cespedesia* (Ochnaceae), *Couma* (Apocynaceae), *Ormosia* (Fabaceae), and *Parkia* (Mimosaceae). *Gustavia longifuniculata* and *G. romeroi* are frequently found scattered among the understory trees of this floristically rich area.

Observations on *Nee & Mori 4305* have demonstrated that the opercular region does not dehisce but is removed piecemeal by insects and/or rotting. Fruits with all stages of fragmented opercula were observed on the tree and no complete opercula were found under it. From these observations I have concluded that the fruits are not freely operculate and that animals play a role in releasing the seeds from the fruits.

The six petals, six loculi, persistent calyx lobes on the fruit, costate ovary, leptocaul growth form, and leaf features clearly place this *Gustavia* in section *Hexapetala. Gustavia longifuniculata* is most closely related to the Panamanian *G. brachycarpa,* which likewise possesses expanded funicles and opercula that are pseudoperculate. It is distinct from *G. brachycarpa* in having coriceous instead of chartaceous leaves and by its globose fruits with wings to the base instead of cylindrical ones with wings onto the pedicel.

This new species is sympatric with *G. dubia* from which it differs in leaf, fruit, and seed characters (see Key to section Hexapetala).

3. Gustavia dubia (Kunth) Berg, Linnaea **27:** 446. 1856.

Figs 5, 15A-B, 42A, 43, 44.

Lecythis dubia Kunth, Synops. Plant. Aeq. **3:** 424. 1824; H.B.K., Nov. Gen. Sp. **7:** 259. 1825. Type. *Humboldt & Bonpland sn* (lectotype, P; isolectotypes, B in Herb. Willd. no. 10155 fide Knuth; F photo neg no 38304, GH photo). Colombia. On the shores of the Río Magdalena, without date (old fr).

Japarandiba dubia (Kunth) O. Kuntze, Rev. Gen. **1:** 240. 1891.

Gustavia pleurocarpa Pittier, Contr. U. S. Natl. Herb. **26**(1): 4. 1927; Woodson, Ann. Missouri Bot. Gard. **45**(2): 118-120. 1958. Type. *Pittier 3857* (holotype, US 678933; isotypes, BM, GH, NY). Panama. Colón: Loma de la Gloria, back of Fató (Nombre de Dios), alt 100 m or less, Jul 1911 (fl).

Trees to 30 m × 40 cm; crown elongate; leaf-bearing branches 2-4 mm in diameter, the branching radiate, the leaves loosely grouped at their ends, the petiole scars 5-15 mm apart. Bark slightly roughened, brown. Leaf blades elliptic, 8-20(-31) × 4-7(-12) cm, glabrous, chartaceous, with 10-14 pairs of lateral veins; apices acuminate; bases acute, somewhat decurrent; margins entire to serrulate. Petioles 2-25 × 2-3 mm, subterete in cross section, flattened slightly adaxially. Inflorescences suprafoliar, flowers in axils of bracts or leaves, densely rusty-tomentose, with 1-5 flowers at branch ends; pedicels 17-40 mm, subtended by a single caducous bract and bearing usually at or above the middle two ovate, acute bracteoles 4-9 × 4-8 mm. Flowers 6 cm in diameter; calyx lobes triangular-sagittate, 5-9 × 5-8 mm, rusty-tomentose; petals 6, obovate, 25-40 × 20-25 mm, puberulous within, white; fused androecium base 7 mm high; outermost filaments 10 mm, cream-colored; anthers 1.8-2.5 mm, yellow; ovary 6-costate or with costae lacking, densely rusty-tomentose, 6-loculate, puberulous at the summit; style 1-2 mm; stigma 6-lobed. Fruits globose, 6-costate or costae reduced to lacking, 15-20 × 17-30 mm, with persistent triangular calyx lobes, first green then bright yellowish-brown at maturity, the mesocarp pure white. Seeds 1-5 per fruit, carunculate, 15-17 × 12-15 mm, with a straight, little-developed funicle 1-2(-3) mm; cotyledons well developed, remaining in the testa upon germination. Seedlings with winged stems and inconspicuous caducous stipules (less than 0.5 mm) on the cataphylls; seedling leaves with caducous hairs at the tips of the marginal teeth (Fig 15A). $x = 17$.

Type. *Humboldt & Bonpland sn* (lectotype, P; isolectotypes, B in herb Willdenow no 10155 fide Knuth; F photo neg 38304, GH photo) Colombia, Rio Magdalena, no date.

Distribution. This species is found east of the Canal Zone in Panama into the Magdalena Valley of Colombia.

Representative specimens examined. PANAMA. Colón: Loma de la Gloria, back of Fató (Nombre de Dios), alt 100 m or less, Aug 1911 (fl), *Pittier 4104* (BM, F, GH, NY, US). Panama: El Llano-Carti, 5 to 6 miles N of El Llano, 1300 ft, 8 Sep 1972 (fl), *Gentry 5794* (MO), 8.2 km from Panamerican Hwy., 27 Dec 1974 (fr), *Mori et al 4085* (MO, NY). COLOMBIA. Antioquia: Río Cimitarra, near Quebrada Toroba, 3 Aug 1954 (fr), *Lamb 160* (US); San Luis de Cocorná, 3 km al sur de la confluencia del Río Cocorná con el Magdalena, 19 Nov 1963 (fr), *Romero-Castañeda 10058* (NY). Bolívar: 150 km N of Barrancabermeja (74° 4' W, 8° 15' N), Aug 1966 (fl), *Bruijn 1086* (NY). Santander. 15 leguas al SE de Barrancabermeja, a 3 km de la margen izquierda del Río Opón, 11 Oct 1954 (fr), *Romero-Castañeda 5033* (COL, US); Puerto Wilches and vicinity, 28 Nov-2 Dec 1926 (fl), *Killip & Smith 14904* (A, F, GH, NY, US).

Ecology. *Gustavia dubia* is a medium sized tree of wet forests from near sea level to 500 meters. I have observed numerous individuals of this species along the El Llano-Carti Road of eastern Panama where it flowers from July through September (middle wet season) and bears fruit from November through March (late wet season through most of the dry season). Most fruits reach maturity during the later part of the dry season.

Local names. COLOMBIA. Mula Muerta *(Areira 4-10),* Alma Negra *(Lamb 160).*

4. **Gustavia hexapetala** (Aublet) Smith in Rees, Cycl. **17:** 2. 1819; Pulle, Flora of Surinam **3**(1): 123-126. 1934; Lemée, Flore de la Guyane Française **3:** 115. 1953. Figs 5, 9, 11A-E, 15C, 43, 44.

Pirigara hexapetala Aublet, Hist. Pl. Gui. **1:** 490-491, *t 193.* 1775. Type. *Aublet sn* (BM photo neg. no. N.S. 398). Guyane Française. On the Sinemari River, 40 leagues from its Mouth, Oct (fl, fr).

Gustavia fastuosa Willdenow, Spec. Pl. **3:** 847. 1800 (based on *Pirigara hexapetala* Aubl.)

Gustavia pterocarpa Poiteau, Mém. Mus. Hist. Nat. **13:** 158-159, *t 5-6. 1825;* Hooker, W.J., Bot. Mag. **87:** *t 5239.* 1861. Lectotype. Poiteau *t 5* in lieu of known collection.

Gustavia brasiliana A. P. de Candolle, Prodr. **3:** 290. 1828. Type. *Martius 2668* (M). Brazil. Pará: Prope Gurupá, without date (fl.).

Gustavia brasiliana A. P. de Candolle var *minor* A. P. de Candolle, Prodr. **3:** 290. 1828. *ex char.* Type. Mart. herb. fide DC.

Gustavia fastuosa Willdenow var *angustisepala* Berg, Mart. Fl. Bras. **14**(1): 473-474. 1858. *ex char.* Syntypes. Guyane Française. Prope Sinemari (fide Berg, probably Aublet's collection of *Pirigara hexapetala).* Brazil. Ad Cameta prov. Paraensis, *Sieber sn* (fide Berg).

Gustavia fastuosa Willdenow var *latisepala* Berg, Mart. Fl. Bras. **14**(1): 474. 1858. Syntypes. Surinam. 1843 (fl), *Hostmann 1210* (US). Guyane Française. *Poiteau sn* (fide Berg).

Japarandiba brasiliana (A. P. de Candolle) O. Kuntze, Rev. Gen. **1:** 240. 1891.

Japarandiba fastuosa (Willdenow) O. Kuntze, Rev. Gen. **1:** 240. 1891.

Japarandiba hexapetala (Aublet) O. Kuntze, Rev. Gen. **1:** 240. 1891.

Japarandiba pterocarpa (Poiteau) Niedenzu in Engler & Prantl, Nat. Pflanzenfamilien 3(7): 37. 1892.

Gustavia microcarpa Pilger, Verh. Bot. Vereins Prov. Brandenburg **47:** 164. 1905. Type. *Ule 5610* (F photo neg. no. 29157, MG). Brazil. Amazonas: Rio Juruá, J. Miry, Jun 1901 (fl).

Gustavia eximia Pittier, Contrib. Fl. Venezuela decas **1:** 9-10. 1921. Type. *Pittier 9096* (holotype, US; isotypes, F photo neg. no. 29166, GH, NY, P). Venezuela. Carabobo: Guaremales, road from Puerto Cabello to San Felipe, alt 10-100 m, 4 Oct 1920 (fl).

Gustavia fustis-mortui Pittier, Arbol. y Arbust. Venez. decas 4 & 5. Bol. Ci. y Tecn. Mus. Com. Venez. **1:** 64-65. 1925. Type. *Pittier 10965* (holotype, US; isotypes, GH, NY). Venezuela. Zulia: Vegas del Río Lora, afluente del Santa Ana, 14 Dec 1922 (fl, fr).

Eschweilera carrii Standley, Trop. Woods **29:** 7-8. 1932. Type. *Monteiro da Costa 51 (holo*type, F herb. no. 648538; isotype, IAN). Brazil. Pará: Boa Vista, Tapajós River, 1931 (fl).

Gustavia longepetiolata Huber, sensu Knuth non Huber, in Engler, Pflanzenreich IV. **219a:** 23. 1939. *ex char.*

Trees, small to medium sized, 3-20(-25) m×5-15(-40) cm in diameter; leaf-bearing branches 2-5(-9) mm in diameter, the leaves loosely grouped at their ends; petiole scars 2-15 mm apart. Bark reddish brown. Leaf blades elliptic, oblanceolate, or obovate; (9-)10-24(-45)×3-13 cm wide, glabrous, chartaceous to coriaceous, with 9-13 pairs of lateral veins; apices acuminate to attenuate; bases acute to attenuate, narrowly decurrent; margins entire to serrulate. Petioles 2-17 mm long, (1.5-)2-3(-5) mm in diameter, subterete to semicircular in cross section, flattened somewhat adaxially. Inflorescences suprafoliar, rusty-white tomentose, the flowers in the uppermost leaf or in bract axils, with 1-4(-6) flowers at the branch ends; pedicels (6-)10-30(-50) mm, subtended by a single oblong, ovate, or lanceolate, keeled caducous bract 4-9(-12) ×2-8 mm and bearing at various points along the length of the pedicel 2 ovate-oblong bracteoles (2.5-)4-12×2-12 mm. Flowers 6-9(-16) cm in diameter; calyx lobes triangular, sagittate, or ovate, 4-12×3-9(-12) mm, rusty-tomentose, green; petals (5-)6(-8), obovate to oblanceolate, infrequently oblong, (20-)30-40(-80)×10-30(-50) mm, puberulous, white; androecium white, sometimes yellow at base, the connate base (4-)8-15 mm high; outermost filaments 8-18 mm, white; anthers 1.6-2.9(-3.8) mm, yellow; ovary 6-costate, rusty-tomentose, (5-)6(-8)-locular, glabrous to puberulous at summit; style 1-2(-3) mm; stigma with (5-)6(-8) lobes. Fruits globose, first green, then yellow-orange at maturity, brown when dried, (5-)6(-8) costate, 10-30×12-35 mm, with (5-)6(-8) persistent triangular, sagittate, or ovate calyx lobes. Seeds trigonous to semicircular in cross section, carunculate, 10-16×6-13 mm, 1-5 per fruit, with a straight non-expanded funicle, 1-5(-9) mm long.

Distribution. A very wide spread, common species throughout Amazonia, the Guianas and north central Venezuela.

Representative specimens examined. COLOMBIA. Meta: Puerto López, 2 Aug 1944 (fl), *Little & Little 8417* (US); Villavicencio, cerca al Río Ocoa, 24 Jul 1944 (fl), *Uribe-Uribe 1299* (COL). Vaupés: Monfort, 23 Sep 1943 (fl), *Allen 3112a* (US). Amazonas: Río Caqueta, La Pedrera, 1-4 Oct 1952 (fl), *García-Barriga 14579* (COL). VENEZUELA. Zulia: Perijá district, 60 km S of Machiques near mission Los Angeles de Tukuko, 14 Oct 1966 (fr), *Bruijn 1175* (NY, VEN). Falcón: Lado sur del Río Tocuyo, cerca de Tocuyo de la Costa, 22 Jan 1966 (fl, fr), *Steyermark 94490* (F, NY, P, VEN). Yaracuy: Yumare, 8 Feb 1959 (fr), *Bernardi 6948* (VEN); Taría, Dec 1946, *Brito 30* (VEN). Aragua: Ocumare Valley, 8 Aug 1937 (fl), *Pittier 9428* (VEN); Rancho Grande, 3 May 1938 (fr), *Williams 9427* (= 10046) (F, US, VEN). Distrito Federal: Between Los Caracas and Oritopo, 1 Nov 1962 (fl), *Steyermark 90968* (US, VEN). Miranda: Parque Nacional Guatopo, 41.5 km SE of Santa Teresa, 11 Sep 1960 (fr), *Steyermark 87093* (US, VEN); Bolívar: Río Parguaza, Dec 1955 (fl), *Wurdack & Monachino 41011* (NY). Amazonas: Orinoco River, southern part of Isla del Ratón (52° 2' N, 67° 46' W), 24 Nov 1965 (fl), *Breteler 4815* (VEN); Río Orinoco, Caño Yagual, 10 km above mouth of Río Atabapo, 30 May 1954 (fl), *Level 113* (NY); Cerro Sipapo, Caño Grande, Río Cuao, 21 Jan 1949 (Fl), *Maguire & Politi 28527* (NY, WIS); alto Río Orinoco between Tama-Tama and Esmeralda, 20 Sep 1957 (fl), *Maguire et al 41549* (NY). GUYANA. Rocky hilltop by Mapuera, 25 Oct 1952 (fl), *Forest Dept. British Guiana 7508* (NY); Winiperu, Essequibo River, 1 Aug 1952 (fl), *Forest Dept. British Guiana 7070* (NY). SURINAM. Brownsberg, 26 Mar 1917 (fr), *Boschwezen 2731* (MO, US); Kaboerie, 2 Oct 1920 (fl), *Boschwezen 4922* (MO, US); Sectie 0, 30 Jul 1915 (fl), *Boschwezen 713* (NY, US); Zanderij I, May 1944 (st), *Boschwezen 55* (BBS, GH, IAN, NY); Jodensavanne-Mapane Kreek area (Surinam River), 30 Mar 1953 (fr), *Lindeman 3647* (BBS, VEN); Jamaike, 7 Aug 1937 (fl), *Rombouts 775* (NY); Falawatra, distr. Nickerie, 27 Oct 1971 (fr), *Jiménez-Saa 1524* (NY); Brokopondo distr., S of Gansee on Kentoegoni Island in Surinam River, 21 Jul 1964 (fl), *Donselaar 1470* (WIS). GUYANE FRANÇAISE. Rive droite Mana, a 300 m en forêt côté est de l'habitation Fecourt Plateau, 17 Dec 1954 (fr), *BAFOG 270M* (NY); placeau no. 3, carreau no. 62-route de Mana, 8 Mar 1956 (fr), *BAFOG 7345* (NY, P); Maroni-Charvein, Mar 1921 (fr), *Lemée sn* (P); Mana, Cayenne, without date (fl), *Martin sn* (BM, P); Karouany, 1856 (fl), *Sagot 950* (GH, P, W); Fleuve Approuague, Saut Couata, 19 Oct 1968 (fl), *Oldeman T233* (INPA); Godebert, without date (fl, fr), *Wachenheim 216, 275, 316* (P). PERU. Amazonas: Provincia de Bagua, rainforest along Río Santiago, 3-5 km above mouth, 8-13 Oct 1962 (fl), *Wurdack 2173* (F, GH). BRAZIL. Roraima: Serra da Lua, 2° 25-29' N; 60° 11-14' W, vic of Dormida, 25 Jan 1969 (fr), *Prance et al 9496* (INPA, NY); Posto Mucajaí, Rio Mucajaí, vic of Mucajaí airstrip, 14 Mar 1971 (fr), *Prance et al 10950* (INPA, NY). Amapá: Rio Amapari, slopes of Curuca oil body toward Igarapé Sentinela, 9 Nov 1954 (fr), *Cowan 38184* (NY); Rio Araguari, Porto Platón 0° 44' N, 51° 22' W, 16 Aug (fl), *Pires et al 50354* (MG, NY, WIS); between Monguba and Serra do Navio, 0° 44' N, 51° 45' W, 25 Sep 1961 (fl), *Pires et al 51183* (INPA, MG, NY, WIS). Amazonas: Manaus, Reserva Florestal Ducke, 3 Oct 1968 (fl), *Alusio & Coêlho 204* (WIS); Taperinha bei Santarém, 25 Aug 1927 (fl), *Eingeborner 562* (F); Rio Negro, Macará, 30 Sep 1947 (fl), *Fróes 22482* (IAN); Rio Negro, Padauiry, Castanha, 9 Oct 1947 (fl), *Fróes 22568* (IAN, SP); Rio Purus, Bom Lugar, Jun 1904 (fl), *Huber 4717* (MG); basin of Rio Juruá, near mouth of Rio Embira (trib. of Rio Tarauacá), lat. 7° 30' S, long. 70° 15' W, 6 Jun 1933 (fl, fr), *Krukoff 4691* (A, NY); basin of Rio Madeira, municipality Humaitá, near Tres Casas, 14 Sep-11 Oct 1934 (fr), *Krukoff 6226* (A, F, MO, NY, US); basin of Rio Solimões, municipality São Paulo de Olivença near Palmares, 11 Sep-26 Oct 1936 (fr), *Krukoff 8310* (A, F, MO, NY); Cachoeira do Jurupari, Rio Ayari, 17 Oct 1928 (fl), *Luetzelberg 23604* (R); Vaupés, beira da estrada do campo de aviaçao, 15 Oct 1960 (fr), *Oliveira 2294* (IAN); Ega (= Tefé), 1831 (fl), *Poeppig 2508* (F, W); basin of Rio Demeni, vic of Tototobí, 25 Feb 1969 (fr), *Prance et al 10215* (INPA, NY); basin of Rio Negro, Rio Uneiuxi, Makú Indian village, 300 km above mouth, 24 Oct 1971 (fl), *Prance et al 15585* (INPA, NY, WIS); Rio Japurá, afluente do Rio Negro, Acanaui, 25 Nov 1959 (fr), *Rodrigues & Coêlho 1398* (WIS); margem setentrional do R. Amazonas na bôca do Rio Negro, Aug 1851 (fl), *Spruce 1019* (MG, P). Pará: Rio Pixuna, 40 km acima do bôca do Cupari, entre Sitio Prainha e Agua Boa, 22 Dec 1947 (fr), *Black 47-1958* (IAN); várzea do Rio Tajapura, Ilha São Sebastião e Nazaré, 21 Jul 1948 (fl), *Black 48-3020* (IAN, P); Monte Alegre, igarapé do furo do Paituna, 9 Sep 1953 (fl), *Fróes 30579* (IAN); Rio Curuáuna, planalto de Santarém, Oct 1954 (fl, fr), *Fróes 31307* (IAN); Fordlândia, Tapajós River region, Sep 1921 (fl), *Krukoff 1036* (A, MO, NY); upper Cupary River, plateau between the Xingu and Tapajós Rivers, Sep 1931 (fl), *Krukoff 1129, 1183* (A, MO, NY); Rio Tocantins, regiào de Itaquara, 19 Dec 1960 (fr), *Oliveira 1254* (IAN); Foz do Rio Juruena, margem direita, 1 Jan 1952 (fl, fr), *Pires 3716* (IAN, NY); perto do Igarapé Arapijó, mun. de Breves, 22 Oct 1955 (fl), *Pires et al 4965* (IAN); região do Rio Jarí, estrada do Monguba, 16 Jan 1969 (fr), *Silva 1644* (IAN). Acre: Km 242-246, vic. of Campinas, 20 Jul 1968 (fr), *Forero 6413* (INPA, NY); basin of Rio Purus, near mouth of Rio Macauhan (trib. of Rio Yaco), lat. 9° 20' S, long. 69° W, 21 Aug 1933 (fl. fr), *Krukoff 5587* (A, MO, NY, US); municipality of Sena Madureira, vic. of km 7, road Sena Madureira to Rio Branco, 28 Sep 1968 (fr), *Prance et al 7648* (INPA, NY); Rio Acre, Seringal Turistella, Mar 1911 (fl), *Ule 9653* (MG). Rondônia: Pôrto Velho to Cuiabá highway, 4 km S of Nova Vida, 15 Aug 1968 (fr), *Forero & Wrigley 7073* (INPA, NY); Rio Madeira Basin, south bank of Rio Madeira 2 km above Mutumparana, 6 Jul 1968 (fl, fr), *Prance et al 5668* (INPA, NY, US); N bank of Rio Abuña between Cachoeira Tres S and Fortaleza, 18 Jul 1968 (fr), *Prance et al 6171* (INPA, NY); Pacaás Novos, 7 Aug 1968 (fr), *Prance et al 6847* (INPA, NY). Mato Grosso: Margens do Guaporé, May 1919 (fr), *Rondon 2448* (R). Guanabara: Passeio Publico (Rio de Janeiro), arbusto cultivado, 10 Feb 1862 (fl), *Glaziou 139a* (P, R). BOLIVIA. Beni: Junction of Rivers Beni and Madre de Dios, Aug 1886 (fl), *Rusby 657* (PH, US); Río Ivory, 12 Feb 1922 (fl), *White 2365* (NY).

Ecology. A small to medium sized tree most common in well drained forests *(terra firme)* but also encountered in flood-plain forests *(várzea)*. This species infrequently assumes a shrub-like habit when found in secondary growth. In north central Venezuela *G. hexapetala* is found in the finger-like extensions of evergreen forest that penetrate into a region otherwise dominated by deciduous, semi-xerophytic woodland.

In the Guianas *G. hexapetala* blooms from July to December and bears fruit from October to April (the peak fruiting time is March and April). Collections from the lower Amazon (below the junction of the Rios Negro and Solimões) indicate a July to October blooming time and a September to December fruit set. Fertile specimens from the Rio Negro drainage system have been collected mostly in September and October, while those from the Solimões watershed have been collected mostly betwen February and September.

As in most wide-ranging species of plants, considerable variability is found in *G. hexapetala*. For example, some individuals have relatively small, chartaceous leaves whereas others have larger, coriaceous leaves. In addition, some individuals have only one seed per fruit in contrast to the 2-5 normally encountered and other individuals have the costae of the exocarp missing or nearly missing (Fig 43). Nevertheless, the variation is not sufficient to merit taxonomic recognition.

Local names. COLOMBIA. Coral *(Little & Little 8417),* Titaquemú (Karijona language, *García-Barriga 14579).* VENEZUELA. Chupón de Muerto *(Brito 30),* Chupón Ventoso *(Pittier 9096),* Coco de Mono *(Steyermark 90090),* Motin *(Pittier 10965),* Muerto *(Bernardi 6948),* Palo de Muerto *(Pittier 10965).* GUYANA. Chawanaime *(British Guiana Forest Dept. 7508).* SURINAM. Lannaballi Hohorodikoro *(Boschwezen 55),* Lannaballi Djarmo *(Boschwezen 55),* Hoogland Konikonioedoe *(Jiménez-Saa 1524).* GUYANE FRANÇAISE. Bois Puant *(Melinon 9),* Tapouhoupa (Paramaka language, *BAFOG 7345, 7351, 7597).* BRAZIL. Lalouch (Makú language, *Prance et al 15585);* Geniparana *(Cowan 38184; Eingeborner 562; Oliveira 2294, 2547, 2953, 3046, 3573, 4409; Krukoff 1036, 1129; Silva 1644; Williams & Silva 18221);* Matamataica *(Black 47-1958);* Abiurana *(Krukoff 1243);* Hicodi (Uaicá-Mucajaí language, *Prance et al 10950).*

II. **Gustavia** sectio **Grandibracteata** Mori, sect nov

Figs 1A, 15F, 42C, D, 45, 46.

Arbores parvae, usque ad 7.5 m altae, 1-caules vel pauciramosae; folia ad apicem ramorum arcte aggregata; cicatrices petiolorum continguae. Laminae 35-100 × 10-33 cm, paribus venarum lateralium 30-62. Inflorescentia suprafoliares, ad anthesin rosula foliorum terminalium subtentae; pedicelli singula bractea magna 30-115 × 14-40 mm suffulti et 2 bracteolis oppositis 13-65 × 6-48 mm secus longitudinem suam varie insertis instructi. Semina caruncula et funiculo destituta.

Type species. *Gustavia grandibracteata* Croat & Mori.

Species of this section are single stemmed or little branched trees. Their leaves are tightly congested in one to several whorls at the ends of stout branches (Fig 1A). Growth form in this section is of the pachycaul type.

The floral arrangement and associated bracts are the most distinctive features of this section. A whorl of sterile breacts subtends the subterminal inflorescences and may persist for several seasons after flowering at that particular region of the stem has occurred (Fig 42C). These sterile bracts are the largest and most leaf-like in *G. grandibracteata* and the smallest and least leaf-like in *G. pubescens.* Each flower is also subtended by a single large bract and its pedicel bears two large opposite bracteoles somewhere along its length. Although all species of *Gustavia* have a bract at the base of the pedicel and 2 pedicellary bracteoles, the size and persistence of those of section *Grandibracteata* separate its members from the remaining species of *Gustavia.*

The suprafoliar position of the flowers, which are subtended by the uppermost whorl of very large leaves, is also characteristic of this section. In all other species of *Gustavia* with suprafoliar inflorescences the trees are not so distinctly monocaulous, the leaves are smaller and less compacted, and the bract and bracteoles are small, nearly scale-like.

5. **Gustavia pubescens** Ruiz & Pavon ex Berg, Linnaea **27**: 442. 1856; Ruiz & Pavon, Flora Peruv. **4**: 306, *t 351,* vol. ined. Fig 45.

Japarandiba pubescens (Ruiz & Pavon ex Berg) O. Kuntze, Rev. Gen. **1**: 240. 1891.

Trees, 3-20 m tall; leaf-bearing branches 12-25 mm in diameter, the leaves tightly congested at their ends; leaf scars touching. Leaf blades oblanceolate to spathulate, narrowly attentuate at the base, subsessile, 35-80 x 10-22 cm, glabrous above, velutinous below, especially on the veins, with 30-62 pairs of lateral veins; apices acuminate; margins entire to serrulate-crenulate. Inflorescences terminal, racemose, rusty-tomentose; rachis 40-80 mm, sometimes with sterile ovate bracts 20-25 x 16-18 mm persisting at the base; pedicels 35-70 mm, subtended by a single lanceolate bract 25-35 x 10-14 mm and bearing above the middle 2 oblong bracteoles 13-15 x 9-13 mm. Flowers showy, to 17 cm in diameter; calyx with (5-)6, ovate to triangular lobes, 7-12 x 10-15 mm; petals 6, white to pink, ovate to oblong, 65-85 x 35-55 mm; fused androecium base 12 mm high, the outermost filaments 20 mm, the anthers 3 mm; ovary without costae, densely rusty-tomentose outside, white-puberulous at the summit, 6(-7)-locular, the style 3-4 mm, the stigma 5-6 lobed. Fruits and seeds unknown.

Type. *Ruiz & Pavon sn* (MA, not seen; GH photo, F photo neg. no. 29400, F leaf fragment, B fide Berg, probably not extant), Ecuador. Guayas: Guayaquil, without date (fl).

Distribution. This species is known only from northwestern Ecuador.

ECUADOR. Guayas: 2-4 km W of Bucay, alt ca 170 m, 31 Oct 1974 (fl) *Gentry 12298* (MO, NY). Los Ríos: Hacienda Monica, 12 km E of San Carlos, ca 180 m, 2-4 Nov 1967 (fl), *Sparre 19391* (S). Bolívar: Tablas de Telimbela, 22 Nov 1943 (fl), *Acosta-Solís 6948* (F).

Local names. Ecuador. Utugcama *(Acosta-Solís 6948);* Membrillo de Montaña *(Ruiz & Pavon sn).*

6. **Gustavia grandibracteata** Croat & Mori, Brittonia **26**(1): 22-26, *figs 1-3. 1974.* Figs 6, 15F, 42C, 45.

Gustavia superba (Kunth) Berg var *puberula* Dwyer, Ann. Missouri Bot. Gard. **52**(3): 351—352, *fig 1.* 1965. Type. *Duke 4881* (holotype, MO; isotypes, GH, NY). Panama. Darién: Río Chucunaque, ca 4 miles below Yaviza, 19 Jun 1963 (fr).

Trees, single-stemmed or few-branched, to 7.5 m tall x 17 cm in diameter; leaf-bearing branches 13-35 mm in diameter, with clusters of leaves tightly

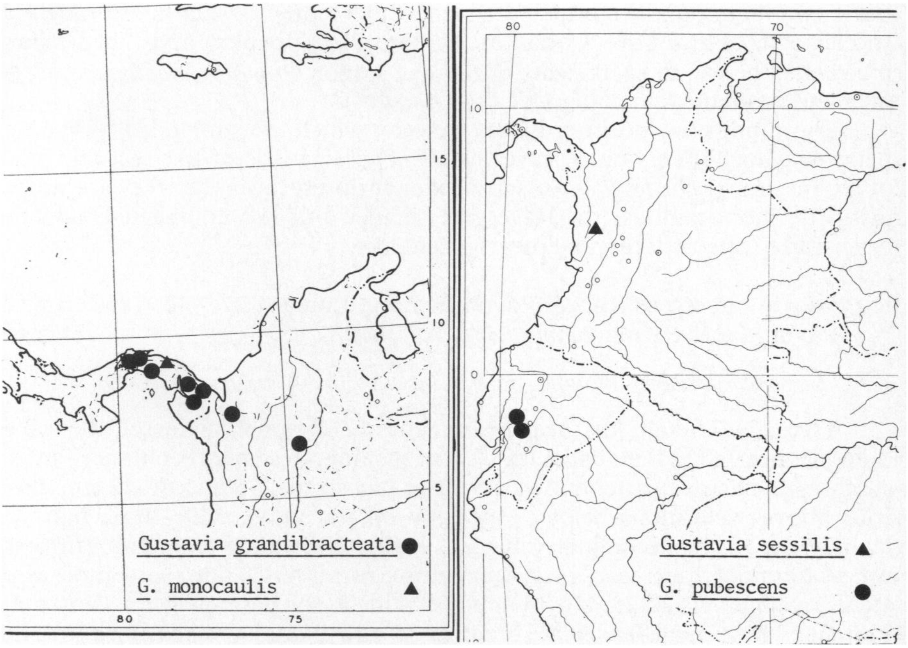


FIG 45. Distribution of species of *Gustavia* section *Grandibracteata. G. grandibracteata, G. monocaulis, G. sessilis,* and *G. pubescens.*

grouped at their ends, and persistent bracts ca 115 × 50 mm subtending each flush of growth; petiole scars touching. Bark slightly fissured, brown. Leaf blades oblanceolate, tapered from the middle to an acute base, 73-100 × 10-21 cm wide, glabrous to minutely puberulous, with 45-54 pairs of lateral veins; apices acute-acuminate; margins serrate. Petioles 20-78 × 4-6 mm, semicircular in cross section. Inflorescences suprafoliar, the flowers solitary in bract axils, clustered near branch apex within a cup formed by the leaves, appearing terminal; pedicels 35-70 mm, subtended by a single oblanceolate floral bract 80-105 × 30-35 mm and bearing directly below the hypanthium 2 rounded-ovate bracteoles 45-65 × 34-48 mm. Flowers to 20 cm in diameter; calyx lobes 4, ovate to oblong, 29-55 × 24-55 mm, puberulous; petals 8(-9), narrowly obovate to oblanceolate, 74-90 × 27-45 mm wide, glabrous, mostly white with tinges of pink and red; connate androecium base 22-25 mm in diameter, ca 10 mm high, the outermost filaments 20-24 mm, white at the base, pink at the apex; anthers 2-5 mm, yellow; ovary without costae, puberulous, 6-locular, the summit puberulous with glabrous spots; style ca 1 mm long; stigma with 6(-7) lobes. Fruits globose, without costae, summit slightly bulged upward, 4.7-6 × 5.5-6.5 cm in diameter, with persistent ovate-oblong, tattered calyx lobes; endocarp a distinctive orange. Seeds more or less trigonous in cross section, 22-26 mm in diameter, mostly 1 per loculus, without distinctive funicle.

Type. *Croat 11690* (holotype, MO; isotypes, BM, F, DUKE, NY, PMA, US, WIS). Panama. Canal Zone: Along edge of lagoon 3 miles W of Gamboa, along Panama RR tracks at marker 25-13, 1 Aug 1970 (fl).

Distribution. This species is found from the Canal Zone east and south into the lower Cauca and Magdalena Valleys of Colombia.

Representative specimens examined: PANAMA. Canal Zone: 1 km NW of Gamboa, 19 Jul 1971 (fr), *Mori 836* (US, WIS); vicinity of Salamanca Hydrographic Station, Río Pequeni, ca 80 m alt, 28-29 Jul 1938 (fr), *Woodson et al 1582* (MO). Panama: Pacora, Apr 1933 (fl), *Paul 341* (US). Darien: Río Pucro, 25 Jan 1975 (st), *Mori & Gentry 4403* (MO, NY); vicinity of Río Paya, trail between Paya and Pucro, 12 Jun 1959 (fr), *Stern et al 410* (GH). COLOMBIA. Antioquia: Carare and Puerto Berrío, without date (st), *Daniel 2083* (US); near Río León, approximately 20-30 km upstream and S of the river mouth and approximately 15 km W of Chigorodó (probable lat. ca 7° 45' N, long. 76° 50' W), alt less than 100 m, 18 Mar 1962 (fl), *Feddema 1950* (US).

Ecology. *Gustavia grandibracteata* is found in tropical moist to tropical wet forests. In both vegetation types it is locally common at the margins of lagoons and wet season swamps and in river flood plains. However, it also grows on more well drained sites. In Panama, *G. grandibracteata* flowers from March through May (late dry-early wet seasons) and fruits in June and July (middle wet season).

The stem of this species produces a group of sterile, sessile, foliaceous bracts; then a group of flowers, each of which is subtended by a floral bract; and then a tightly compacted group of petiolate leaves (Fig 42C). At anthesis the flowers are clustered within the rosette formed by the leaves of the previous growth flush. At this time the cluster of solitary flowers appears as a single terminal inflorescence. The rosette of leaves conceals the flowers from view from the ground and also holds the rotting floral parts, and other debris in place. This mass of flowers, rotting floral parts, and debris forms an ideal habitat for many kinds of insects and other animals. As the fruits mature their weight bends the branch downward making them visible from the ground. With the expansion of the next flush of petiolate leaves the fruits assume a lateral position.

The Panamanian collections are finely puberulous on the abaxial leaf surface whereas the Colombian material is glabrous. The hairs are simple, unicellular, thick walled, and sharply pointed.

The fact that *Gustavia superba* var *puberula* is synonymous with *G. grandibracteata* was not discovered until after the latter species was published. The holotype collection of *G. superba* var *puberula* is mixed and hence a source of confusion. The herbarium sheet of the holotype contains a packet with *Eschweilera* flowers as well as *Gustavia* leaves on the sheet itself. The isotype fruit collection at MO has a fruit rachis of *G. nana* along with the fruits of the correct species. Because of the mixed fruit collection I was led to believe that the fruits of *G. superba* var *puberula* arose from below the leaves and therefore I thought the taxon to be completely unrelated to *G. grandibracteata*. Later examination of the GH material revealed the true nature of the fruit and inflorescence thereby enabling me to bring it into synonymy with *G. grandibracteata*.

Another source of confusion is found in the protologue of *G. superba* var *puberula* (Dwyer, 1965). In Figure 1 a photograph of the fruits of the paratype of *G. superba* var *puberula (Stern et al 410)* is labelled *"Gustavia pittieri."*

7. Gustavia sessilis Mori, Brittonia **28**(3): 291-293, *fig 2.* 1976. Figs 6, 45, 46.

Tree, 5 m tall, with slender trunk; leaf bearing branches 11-14 mm in diameter, the leaves in a compact rosette at their summit; petiole scars touching. Leaf blades sessile, oblanceolate, 71-88 × 13-15 cm, glabrous, chartaceous, with ca 40 pairs of lateral veins; apices acuminate; margins entire. Inflorescence terminal, racemose, puberulous, 4-5 flowered; rachis 45 mm, with distinct downward-curving floral bract scars; pedicels 40-50 mm, subtended by a single, lanceolate, parallel-veined, greenish-white bract 75-100 × 10-25 mm and bearing directly below the hypanthium 2 oblong, acute-tipped bracteoles 16-22 × 6-8 mm. Calyx of 4 well-developed, triangular lobes, 8 × 15 mm; petals rusty-white–pubescent in bud; connate androecium base 4 mm high; outermost filaments 11 mm; anthers 3 mm; ovary without costae, densely rusty-pubescent, 6-locular; stigma 6-lobed. Fruits unknown.

Type. *Killip 35417* (holotype, US; isotypes, BM, NY, WIS photo). Colombia. Chocó: Dense forest S of Río Condoto between Quebrada Guarapo and Mandinga, Alt 18-120 m, 28 Apr 1939 (fl).

Distribution. Known only from the type collection.

8. Gustavia monocaulis Mori, Brittonia **28:** 289-291, *fig 1A,* 1976.
Figs 1A, 42D, 45.

Trees, usually unbranched, to 5 m tall, the leaves in 1-5 clusters at the branch ends, the terminal cluster with 16-28 tightly congested leaves. Leaf blades oblanceolate to spathulate, 82-120 × 18-33 cm, glabrous, with 34-45 pairs of lateral veins; apices acuminate; bases acute to rounded; margins serrulate to serrate towards the apex. Petioles usually missing or infrequently to 80 mm. Inflorescences suprafoliar, the flowers solitary in bract axils, 6-8 flowers clustered near branch apex within cup formed by the terminal cluster of leaves, appearing terminal but continued vegetative growth is monopodial; pedicels 30-40 mm, subtended by a single oblong to spathulate bract to 115 × 33 m (these bracts diminishing distally) and bearing slightly below the hypanthium 2 oblong to ovate, cucullate bracteoles 15-20 × 14-19 mm. Flowers ca 13 cm in diameter; calyx lobes 4, very widely ovate, 16-25 × 23-40 mm, imbricate, somewhat auriculate at bases; petals 8, narrowly obovate, 55-60 × 27-35 mm; connate androecium base ca 9 mm high, the outermost filaments 22-25 mm, pubescent; anthers 2.5-3.5 mm; ovary puberulous, 5-8-locular, each locule with 50-93 ovules, the summit white-tomentose; style 2 mm. Fruits globose, 50 × 70 mm, brown with white speckles, with 4 persistent calyx lobes, the mesocarp creamy-white. Seeds 2-5 per locule, to 22 × 18 mm.

Type. *R. L. Leisner 1312* (holotype, MO, 233058; isotypes, MO, NY). Panama. Panama: Primary forest along newly cut road from El Llano to Carti-Tupile, continental divide to 1 mile from divide, alt 300-500 m, 30 Mar 1973 (fl).

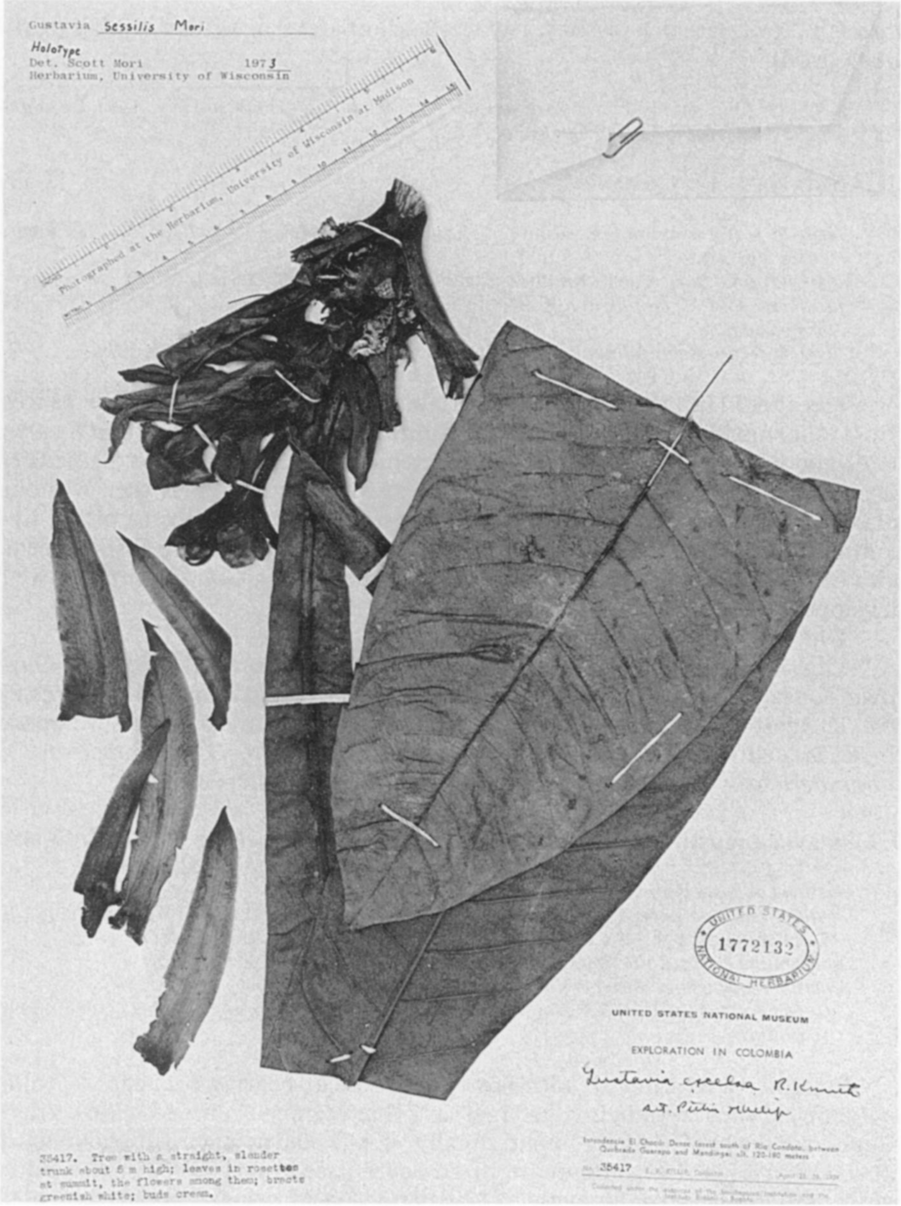


FIG 46. Holotype of *Gustavia sessilis (Killip 35417),* note lanceolate floral bracts and suprafoliar position of the inflorescence.

Distribution and ecology. This species is confined to tropical wet forest at about 350 meters in the low mountains of east-central Panama. It is a small tree most commonly found along streams. Flowering occurs from late March through April (late dry season-early wet season) and fruits ripen in May (early wet season).

PANAMA. Panama: El Llano-Carti road, 9.6 km from Pan American Hwy, *Mori & Kallunki 1856, 6382* (MO), *5598, 5599, 5600* (MO, NY).

III. **Gustavia** sectio **Gustavia** Figs 47-58.

Gustavia sectio *Augustae* R. Knuth in Engler, Pflanzenreich IV. **219a:** 13. 1939 (char. emend. Mori).
Gustavia sectio *Speciosae* R. Knuth in Engler, Pflanzenreich IV. **219a:** 14. 1939. *pro parte.*
Gustavia sectio *Macrophyllum* R. Knuth in Engler, Pflanzenreich IV. **219a:** 14-15. 1939. *pro parte.*
Gustavia sectio *Magnifolium* R. Knuth in Engler, Pflanzenreich IV. **219a:** 15. 1939.

Trees to 30 m tall. Leaf blades variable, 11-136 × 3-31 cm. Inflorescences suprafoliar, axillary, or cauline, when suprafoliar then with less than 6 calyx lobes and with a scale-like bract and bracteoles subtending and on the pedicel respectively. Calyx entire or with 4-6 lobes, when with 6 lobes then without adaxial "Y-shaped" thickenings on the lobes and prominent costae on the hypanthium. Fruits usually without, infrequently with, 4-6 obscure costae. Seeds with or without caruncles and funicles, some species (e g *G. augusta)* with well developed, tortuous, yellow funicles.

Type species. *Gustavia augusta* Linnaeus.

This section is a heterogeneous group to which belong all species of *Gustavia* not possessing the characters of sections *Hexapetala* and *Grandibracteata.* The major dichotomy in the section is the possession of a well developed, tortuous, yellow funicle in some species (e g *G. augusta, G. poeppigiana, G. santanderiensis,* and *G. elliptica)* and its absence in other species.

9. **Gustavia angustifolia** Bentham, Bot. Voy. Sulph. 99. 1844. Figs 47, 48.

Gustavia angusta Ruiz ex Berg, Linnaea **27:** 444. 1856. In synon.
Gustavia ruiziana Berg, Linnaea **27:** 444. 1856. Type. *Ruiz & Pavon sn* (MA, GH photo, B fide Knuth, probably not extant). Ecuador. Guayas: Guayaquil, without date (fl).
Japarandiba angustifolia (Bentham) O. Kuntze, Rev. Gen. **1:** 240. 1891.
Japarandiba ruiziana (Berg) O Kuntze, Rev. Gen. **1:** 240. 1891.
Gustavia corymbosa Ruiz & Pavon ex R. Knuth in Engler, Pflanzenreich IV. **219a:** 26. 1939. In synon.

Small trees to 4 m tall, with few branches; leaf-bearing branches 5-7 mm in diameter, the leaves tightly grouped in 2-3 clusters at their ends. Bark gray, rough, somewhat fissured longitudinally. Leaf blades narrowly oblong to narrowly oblanceolate, attentuate to an acute base, 26-41 × 7-9.5 cm, velutinous throughout abaxially, with 25-32 pairs of lateral veins; apices acuminate; margins serrulate to serrate. Petioles absent to 30 mm long, 3-6 mm thick, semi-circular in cross section. Inflorescences suprafoliar, racemose, buff-rusty tomentose, with 4-10 flowers, the rachis 20-60 mm; pedicels 35-100 mm, subtended by a single caducous bract and bearing at or above the middle 2 ovate to lanceolate, cucullate bracteoles 2.5-6 × 2-4 mm. Flowers 10-14.5 cm in diameter; calyx with 4 rounded to triangular lobes, 3-5 × 9-12 mm; petals 8 narrowly elliptic to oblong, 50-65 × 20-25 mm wide, densely gray-pubescent in bud, puberulous at maturity, white, sometimes rose-red outside; connate androecium base 10-15 mm high; outermost filaments 18 mm, rose-red; anthers 3-4 mm, yellow; ovary obscurely 4-costate, buff-rusty-tomentose, 4-locular, the summit entirely white-tomentose to merely puberulous in lines; style 1-2 mm; stigma with 4 lobes. Fruits globose, truncate at summit, obscurely 4-costate, 25 × 28 mm, possibly larger, with 4 broadly triangular lobes 3 × 11 mm. Seeds without expanded fleshy funicles. $x = 17$.

Type. *Sinclair sn* (lectotype, K, here designated). Ecuador. Without date (fl).

Distribution. This species has only been collected from northwestern Ecuador and southwestern Colombia.

COLOMBIA. Valle: San Francisco de Raposo, Río Raposo, 27 May 1949 (fl), *Patiño 16* (F). ECUADOR. In the forests of the coastal plain near foot of the cordillera, 1931 (fl), *Rimbach 52* (F, GH). Manabi: El Recreo, without date (fl), *Eggers 15438* (F, US). Guayas: Between Palme and Daule, 30 Sep 1952 (fl), *Fagerlind & Wibom 422* (S); 1 km E of entrance to toll road to Salinas, ca 5 km W of Guayaquil, near sea level, 30 Oct 1974 (fl), *Gentry 12242* (MO, NY); Guayaquil, Cerro Azul, 100-150 m, 22 Oct 1958 (fl), *Harling 3038* (S); near top of Cerro Azul, a calcareous outlier of Cerros de Chongon, at Km 14 on Guayaquil-Salinas road, ca 18 Km W of Guayaquil, 27-28 Jul 1977 (fl), *Iltis & Triviño E-595, E-607* (WIS); Guayaquil, 20 Oct 1918 (fl), *Rose & Rose 23503* (GH, NY, US), 31 Oct 1933 (fl), *Schimpf 368* (MO), *1964* (fl), *Valverde 511* (US), Nov 1963 (young fr), *Valverde 1813* (MO). Chimborazo: Prov. Riobamba, without date (fl), *Rimbach 187* (US).

Ecology. *Gustavia angustifolia* is a tree of the dry seasonally deciduous forests of the coastal plain of Ecuador and Colombia. Although it is common in the vicinity of Guayaquil it is poorly collected and little is known of its ecology. Valverde (collection no. *511)* reports that it blooms in October and fruits in November. All flowering collections from the vicinity of Guayaquil have been gathered between July and October.

This species is easily recognized by its pubescent abaxial leaf surface as most species of *Gustavia* have glabrous leaves.

Ruiz and Pavon were the first to recognize this species, providing it with two illegitimate names. The first, *G. corymbosa,* appears on their collection label and the second, *G. angusta,* is an unpublished manuscript name not to be confused with *G. augusta* of Linnaeus. Berg (1856) published *G. ruiziana* based on the Ruiz and Pavon material. However, this name is synonymous with *G. angustifolia* which was published in 1844 by Bentham.

Local names. ECUADOR. Membrillo de Monte *(Rimbach 52);* Membrillo de Montaña *(Ruiz & Pavon sn).*

10. Gustavia petiolata Mori, sp nov Fig 48.

Arbor usque ad 8 m alta; folia in aliquot verticillis disposita; rami infra folia 11 mm diametro. Laminae oblanceolatae, apice acuminatae, basi obtusae, 45 × 14 cm, marginibus serratae, velutinae in pagina abaxiali, glabrae in pagina adaxiali, chartaceae, paribus venarum lateralium 27. Petioli 100 × 4 mm, in sectione tranversali subteres. Inflorescentiae suprafoliares, racemosae, bubalino- vel ferrugineo-tomentosae, floribus 4, rhachidi 65 mm; pedicelli 55-70 mm, bractea et bracteolis 2 lanceolatis 7.5 × 4 mm infra hypanthium insertis

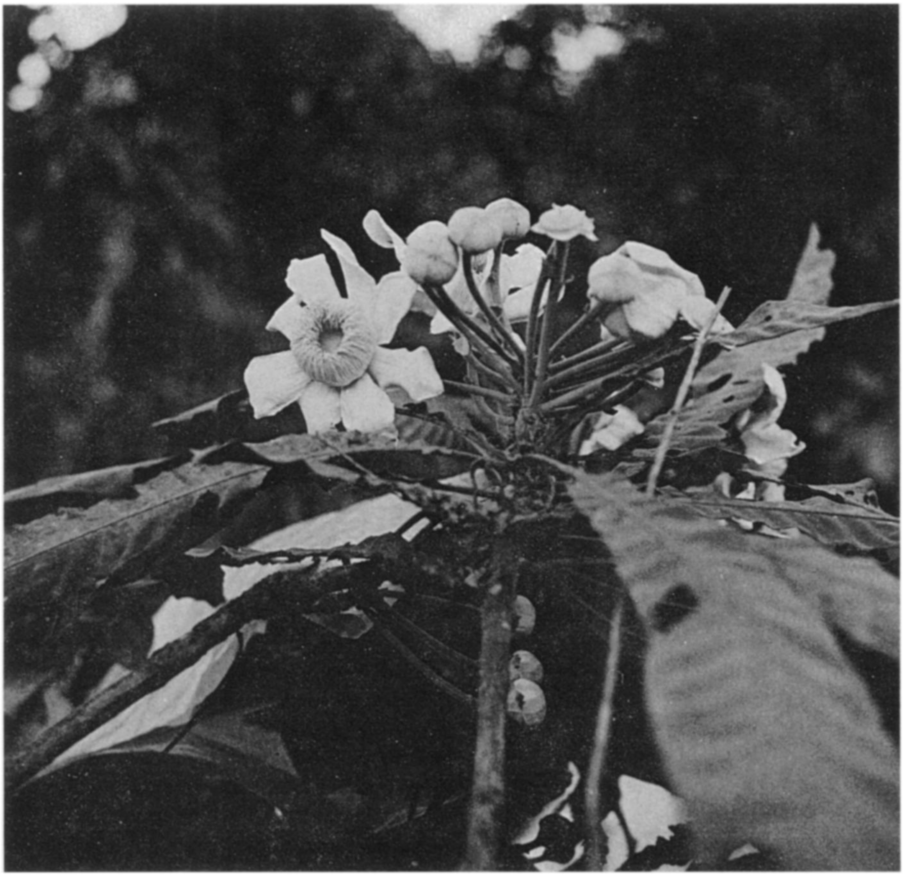


FIG 47. *Gustavia angustifolia (Iltis & Trivino E-595).* Photo by Hugh H. Iltis.

suffulti. Flores ignoti. Fructus immaturi, 4-costati, lobis calycis 4, perisistentibus, late triangularibus, 8 × 14 mm instructi. Semina ignota.

Type. *Romero-Castañeda 5170* (holotype, COL 65309). COLOMBIA. Nariño: Tumaco, vereda de Santa Maria, Río Rosario en el bosque situado detras del Caserío, 18 Jun 1955 (young fr).

Distribution. This species is known only from the type locality.

The type of *G. petiolata* consists of a branch end with 2 leaves, an inflorescence, and 4 immature fruits. However, this material is sufficient to distinguish it from its closest relative, *G. angustifolia,* from which it differs by having longer petioles, more obtuse leaf bases, and a smaller leaf length to width ratio. On the other hand its terminal inflorescence and costate hypanthium are indicative of its relationship to *G. angustifolia.*

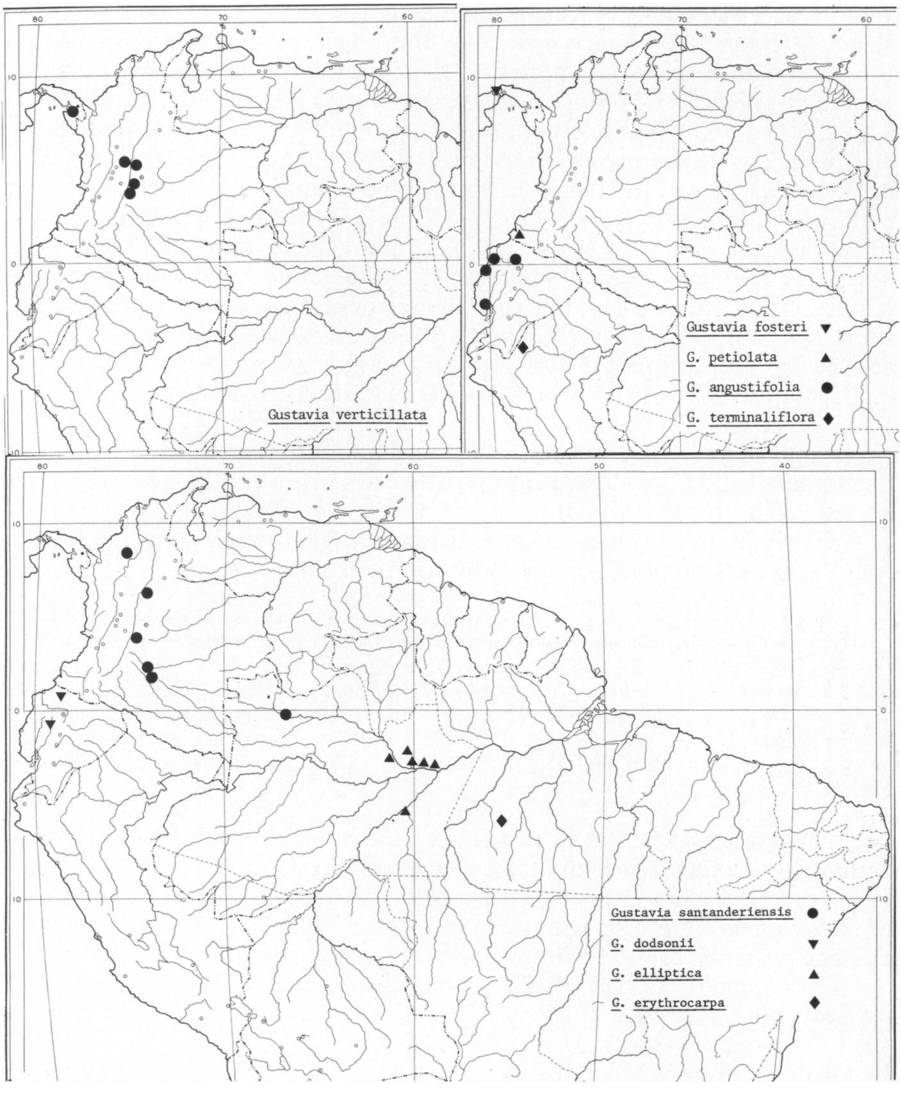


FIG 48. Distributions of *Gustavia verticillata, G. fosteri, G. petiolata, G. angustifolia, G. terminaliflora, G. santanderiensis, G. dodsonii, G. erythrocarpa,* and *G. elliptica.*

11. Gustavia santanderiensis R. Knuth in Engler, Pflanzenreich IV. **219a:** 24. 1939. Fig 48.

Trees to 5 m tall; leaf-bearing branches 3-7 mm in diameter, the leaves tightly grouped at their ends. Leaf blades narrowly ovate to elliptic to oblanceolate, 15-29×6-12.5 cm, glabrous, chartaceous, with 13-17 pairs of lateral veins; apices acuminate to long acuminate; bases acute; margins entire to serrulate. Petioles 50-95 mm, slender, 2-4 mm thick, subterete in cross section. Inflorescences suprafoliar, racemose, pubescent, with 1-5 flowers, the rachis 10-30 mm; pedicels 17-35 mm, subtended by a single lanceolate keeled bract 3 x 1.5-2 mm and bearing anywhere from the middle to directly below the hypanthium 2 ovate slightly keeled bracteoles 2-3 x 2-4 mm. Flowers 8-11.5 cm in diameter; calyx with 6 rounded, shallow lobes 2 mm x 5-6 mm, pubescent; petals (6-)8, oblanceolate, 35-45 x 15-25 mm, densely gray-pubescent in bud, puberulous at maturity, white; connate androecium base 10-12 mm high; outermost filaments 12 mm long; anthers 2-3 mm long, yellow; ovary without costae, pubescent, 4-5-locular, the summit densely white-woolly; style very short, 0.5 mm; stigma with 4-5 lobes. Fruits cylindrical, without costae, 40-45 x 30-35 mm, without persistent calyx. Seeds rounded in cross section, carunculate, 15-20 x 10-15 mm, 10 per fruit, with a narrow contorted funicle 10-15 x 2 mm.

Type. *Haught 1834* (holotype, B fide Knuth; isotypes, F, US). Colombia. Santander: Vicinity of Puerto Berrío, between Carare and Magdalena Rivers, alt 100-700 m, 10 Jul 1935 (fl).

Distribution. This species has a disjunct distribution between the Magdalena Valley of Colombia and northwestern Amazonia.

COLOMBIA. Córdoba: Municipio Ayapel, Corregimiento de San José, 24 Feb 1944 (fl), *García 470* (COL). Cundinamarca: Entre Nilo y la quebrada de agua de Diosito, alt 530 m, 3 Aug 1961 (fr), *Murillo 297* (COL); Vaupés: Riberas del Río Inírida (long. 70° 30' W) alrededores del sitio llamado "Morichal," cerca de la boca del Río Papunáua, alt 200 m, 14 Feb 1953 (fl), *Fernández 2253* (COL); riberas del Río Papunáua, cinco km arriba de su desembocadura en el Inírida, alt 200 m, 18 Feb 1953 (fl, fr), *Fernández 2292* (US). BRAZIL. Amazonas: Serra de São Gabriel, mun. de Vaupés, 9 Oct 1962 (fr), *Oliveira 2199* (IAN); Vaupés, alto R. Negro, 24 Jul 1962 (fr), *Pires & Silva 8071* (IAN).

This species resembles *G. nana* in vegetative features. Both are small trees with long petiolate leaves and long petioles in relation to blade length. However, they are easily distinguished by inflorescence and seed characters. *Gustavia santanderiensis* has terminal inflorescences and funiculate seeds whereas *G. nana* possesses cauline inflorescences and seeds without funicles.

Local names. COLOMBIA: Membrillo *(García 470)*. BRAZIL: Geniparana *(Oliveira 2199)*.

12. **Gustavia elliptica** Mori, sp nov Figs 6, 48.

Arbores usque ad 22 m altae x 35 cm diametro, leptocaulinae; folia ad apicem ramorum laxe aggregata, cicatricibus petiolorum contiguis vel usque ad 20 mm inter se distantibus; rami infra folia 3-5 mm diametro, versus apicem arcuati. Cortex lenticellatus, leviter fissuratus. Laminae plerumque ellipticae interdum oblanceolatae, apice breviter acuminatae, basi acuto-attenuatae leviter decurrentes, 11-28 x 4-9.5 cm, marginibus integrae vel subtiliter serrulatae, glabrae, chartaceae, paribus venarum lateralium 13-19. Petioli 5-25 x 1.5-3 mm, in sectione transversali subteres. Inflorescentiae plerumque suprafoliares interdum caulinae, griseo-tomentosae, floribus 1-6, rhachidi 5-25 mm; pedicelli 25-60 mm, bractea lanceolata 5-10 x 2-4 mm plerumque persistenti et bracteolis 2 lanceolatis, 3-8 × 2-5 mm varie insertis suffulti. Flores 7-9 cm diametro; calyx ex labio undulato 1-2 mm profundo constans; petala (7-)8, oblonga, 25-35 × 20-25 mm, in alabastro dense griseo-pubescens, sub anthesi albo-puberula; androecii basis connata 20 mm diametro, 7-9 mm alta; filamenta externa 11-15 mm; antherae 1.5-3 mm; ovarium ecostatum, 4(-6)-loculare, ad apicem albo-tomentosum; stylus 1-2 mm longus; stigma 4-lobatum. Fructus cylindricus infrequenter globosus, ecostatus, 17-30 × 17-30 mm. Semina carunculata, in sectione transversali rotundata, 12-15 × 5-7 mm, funiculo conspicuo flavo 7-13 × 3 mm instructa.

Type. *Fróes 22468* (holotype, IAN 32256). Brazil. Amazonas: Rio Negro, Tauapecaçu, 23 Sep 1947 (fl).

Distribution. This species is restricted to *terra firme* forests of central Amazonia and is especially common in the vicinity of Manaus.

BRAZIL. Amazonas: Reserva Florestal Ducke, 3 Dec 1969 (fl), *Aluízio 312* (WIS), 15 Oct 1957 (fl), *Ferreira 141/57* (NY, WIS), 5 Dec 1969 (fl), *Freitas et al sn* (INPA), 2 Oct 1965 (fl), *Loureiro sn* (WIS), 11 Nov 1965 (fl), *Loureiro sn* (NY, WIS), 12 Oct 1965 (fl), *Loureiro sn* (INPA), 23 Jun 1971 (st), *Mori 833* (COL, INPA, NY, WIS), 25 Jan 1962 (fr), *Rodrigues & Chagas 4138* (NY, WIS), 23 Nov 1963 (fl), *Rodrigues 5131* (WIS), 23 Nov 1963 (fl), *Rodrigues 5531* (NY), 23 Jan 1965 (fl), *Rodrigues & Osmarino 6848a* (NY, WIS), 6 Jan 1966 (fr) *Rodrigues & Osmarino 7383* (NY, WIS), 5 Dec 1969 (fl), *Silva et al 8* (WIS); Manaus, Igarapé do Parque 10 de Novembro, 28 Nov 1955 (fr), *Coêlho sn* (INPA); Manaus, Igarapé do Passarinho, 12 Nov 1957 (fl), *Coêlho sn* (NY, WIS), 17 Nov 1955 (fl), *Mello sn* (INPA, MG); Região do Rio Madeira, Rio Canumá, 5 Oct 1957 (fl), *Fróes 33753* (IAN); Manaus estrada Manaus-Caracarai, km 60, 24 Feb 1972 (fl), *Honda & Mello sn* (WIS); Manaus, Igarapé da Agua Branca, 7 Nov 1955 (fl), *Mello sn* (WIS), 8 Jan 1962 (fr), *Rodrigues & Chagas 4063* (WIS); Lajes, Rio Amazonas just below junction with Rio Negro, 27 Dec 1974 (fl), *Prance & Ramos 23156* (INPA, NY); 11 Feb 1977 (fr), *Mori et al 8991* (INPA, NY); Mauá; Estrada do Aleixo, Km 12, 3 Mar 1975 (young fr), *Prance & Ramos 23307* (A, K, M, MO, NY, P, S, U); Manaus, estrada Manaus-Itacoatiara, km 55, 14 Oct 1960 (fr), *Rodrigues & Coêlho 1845* (IAN, MG, NY, WIS); Manaus, Ponte da Bolívia, 17 Oct 1961 (fl), *Rodrigues & Lima 3449* (NY, WIS); Manaus, Igarapé da Cachoeira Alta do Taruma, 8 Nov 1962 (fl), *Rodrigues & Chagas 4738* (WIS); Manaus, Igarapé do Tabatinga, 9 Jan 1963 (fr), *Rodrigues & Chagas 4958* (NY, WIS); Bôca do Rio Preto, 24 Apr 1964 (fr), *Rodrigues & Coêlho 5788* (NY); estrada Manaus-Itacoatiara, km 150, 16 Dec 1965 (fl), *Rodrigues & Coêlho 7384* (NY, WIS); Manaus, estrada do Aleixo, Porto Mauá, 23 Apr 1970 (fr), *Rodrigues 8809* (WIS).

Ecology. In June of 1971 I found *G. elliptica (Mori 833)* in *terra firme* forest of the Reserva Florestal Ducke some 26 kilometers east of Manaus on the road to Itacoatiara. Under the medium sized trees with very straight boles and much branched crowns were fruits in advanced stages of decay. Then in February of 1977 G. T. Prance and I found mature fruits of this species at Lajes near the mouth of the Rio Negro. These observations, along with label data, indicate that *G. elliptica* flowers from September to January, with a peak in November, and fruits from January to April.

Gustavia elliptica can be distinguished from the closely related, sympatric *G. augusta* by its elliptic versus oblanceolate leaves, cylindric rather than globose fruits, and its smaller flowers and fruit size. It is also characterized by the usually persistent, lanceolate, relatively long bract at the base of the pedicel. The straight bole and *terra firme* habitat of the new species also helps separate it from *G. augusta* which is usually a plant of the *várzea* and has a more branched trunk.

Gustavia elliptica may be separated from the little-knwon *G. longepetio-*

lata by its greater height, suprafoliar instead of cauline inflorescences, 8 versus 6 petals, and its entire versus 5-lobed calyx.

Local names. BRAZIL. Amazonas: Castanha-rana *(Rodrigues & Osmarino 6848a);* General *(Freitas et al sn, Mori 833, Rodrigues 5131, Silva et al 8);* Mucurão *(Aluísio 312);* Ripeiro *(Mello sn).*

12a. Gustavia erythrocarpa Mori, sp nov Fig 48.

Arbores 8-10 m altae × 8-10 cm diametro; rami infra folia 8-9 mm diametro; folia ad apicem ramorum laxe aggregata, 8-16 mm inter se distantes. Laminae oblanceolatae, apice acuminatae vel mucronatae, basi cuneatae, 51-69 × 17-22.5 cm, pagina abaxiali pilis inconspicuis conspersae, marginibus integrae vel inconspicue serratae, paribus venarum lateralium 17-25. Petioli 30-60 mm, in sectione transversali semicirculares. Inforescentiae caulinae? Flores ignoti. Fructus globosi, rubri, 4.5-5.0 × 5.5 cm, lobis calycis 4 inconspicuis ad summum instructi. Semina 13 per fructum, in sectione transversali angularia, brunnea, 20-25 × 15-20 mm, funiculo 15 × 5 mm instructa.

Type. *Prance et al 25419* (holotype, MG; isotypes, INPA, NY, others to be distributed). Brazil. Pará: BR 163, Km 1131, vicinity of Igarapé Natal, 15 Nov 1977 (fr).

Distribution. This species is known only from the type and one other collection from the vicinity of the type locality.

BRAZIL. Pará: BR 163, Km 1135, vicinity of Igarapé Natal, 16 Nov 1977 (fr), *Prance et al 25517* (INPA, MG, NY, duplicates to be distributed).

Ecology. *Gustavia erythrocarpa* is an understory tree of forest on *terra firme,* and is extremely common in the type locality.

Gustavia erythrocarpa is known only from leaves and separated fruits. However, since there are no inflorescences above or among the leaves I assume that the inflorescences are cauline. The only other species of *Gustavia* with large leaves and cauline inflorescences in the Guianas and Amazonia are: *G. augusta, G. pulchra, G. coriacea, G. inakuama, G. acuminata, G. longifolia,* and *G. gigantophylla.* However, the red fruits and sparsely pubescent abaxial leaf surface of *G. erythrocarpa* serve to distinguish it from the preceding species. Although *G. augusta,* especially from the southernmost part of its range, sometimes has reddish fruits it differs from *G. erythrocarpa* by having smaller leaves, shorter petioles, seeds round instead of angular in cross section, and a more developed funicle.

13. Gustavia augusta Linnaeus, Dissert. Fl. Surinam 17-18, *t 12.* 1775; Linnaeus, Amoen. Acad. **8:** 265, *t 5.* 1785; Pulle, Flora Surinam 122-123. 1934; Lemée, Flore Guyane Française 114-115. 1953.

Figs 6, 15D-E, 16G-H, 51.

Pirigara tetrapetala Aublet, Hist. Pl. Gui. **1:** 487-490, *t 192.* 1775. Type. Guyane Française. "Cet arbre crôit dans l'ile de Caïenne. Il vient aussi dans la terre ferme, surtoute sur la montagne de Courou, our je l'ai observé en fleur et en fruit dans le mois de Septembre." Aublet in Hist. Pl. Gui. (Lectotype, tab. 192, Hist. Pl. Gui., here designated in lieu of extant collection).

Gustavia meizocarpa Gaertner, De Fruct. et Sem. Plant. **2:** 264, *t 138.* 1791. *ex char.* Type. If extant probably at TUB.

Gustavia angusta J.F. Gmelin in Linnaeus, Syst. Nat. ed. 13. 1791. sphalm.

Gustavia urceolata Poiteau, Mém. Mus. Hist. Nat. **13:** 156-158, *t 5, 7.* 1825. *ex char.*

Gustavia tetrapetala (Aublet) de Candolle, Prodr. **3:** 290. 1828.

Gustavia augusta Linnaeus var *calycaris* Berg, Mart. Fl. Bras. **14**(1): 471. 1858. Type. *Spruce 1574* (lectotype, K, here designated; isolectotypes, A photo, F photo neg. no. 31633, K, W). Brazil. Amazonas: Mouth of Rio Negro, May 1851 (fl).

Gustavia augusta Linneaus var *guianensis* Berg, Mart. Fl. Bras. **14**(1): 471, *t 55, 56.* 1858. Type. *Schomburgk sn* (lectotype, K, here designated). Guyana. 1859 (st).

Gustavia augusta Linnaeus var *brasiliensis* Berg, Mart. Fl. Bras. **14**(1): 471. 1858. *ex char.* Type. B, sub *Gustavia insignis* in Willd. Herb. no. 12853 fide Berg, W fide Berg.

Gustavia augusta Linnaeus var *verrucosa* Mart. ex Berg, Mart. Fl. Bras. **14**(1): 471. 1858. Type. *Wullschlägel 205* (M fide Berg, W). Surinam. Paramaribo.

Gustavia insignis Willdenow ex Berg, Mart. Fl. Bras. **14**(1): 471. 1858. *in synon.*

Gustavia poeppigiana Berg var *rigida* Berg, Mart. Fl. Bras. **14**(1): 471. 1858. Type. *Martius sn* (M). Brazil. Amazonas: Rio Negro?, Oct (fl).

Gustavia insignis W. J. Hooker, Bot. Mag. **84:** *t 5069,* 1858. Type. Lectotype, *t 5069* in lieu of extant collection, here designated.

Gustavia membrillo Appun, Bot. Sam. Venez. 34. 1858. fide R. Knuth.

Gustavia theophrasta Linden, Illust. Hortic. **20:** 74. 1873. fide R. Knuth.

Gustavia antillana Miers, Trans. Linn. Soc. London **30**(2): 179. 1874. Type. *Guilding sn* (K). Antilles. St. Vincent.

Gustavia calycaris (Berg) Miers, Trans. Linn. Soc. London **30**(2): 185. 1874.

Gustavia laciniosa Miers, Trans. Linn. Soc. London **30**(2): 178-179. 1874. Type. *Spruce 1574* (lectotype, K, here designated; isolectotype, P). Brazil. Amazonas: Mouth of Rio Negro, May 1851 (fl).

Gustavia marcgraaviana Miers, Trans. Linn. Soc. London **30**(2): 183. 1874. Type. *Gardner 1022* (lectotype, K, here designated; isolectotypes, BM, OXF, W). Brazil. Pernambuco: Dec 1857 (fl).

Grias aubletiana Miers, Trans. Linn. Soc. London **30**(2): 299-300. 1874 (based on *Pirigara tetrapetala* Aublet).

Japarandiba augusta (Linnaeus) O. Kuntze, Rev. Gen. **1:** 240. 1891.

Japarandiba antillana (Miers) Niedenzu in Engler & Prantl, Nat. Pflanzenfamilien **3**(7): 37. 1892.

Japarandiba marcgraaviana (Miers) Niedenzu in Engler & Prantl, Nat. Pflanzenfamilien **3**(7): 37. 1892.

Grias tetrapetala (Aublet) Niedenzu in Engler & Prantl, Nat. Pflanzenfamilien **3**(7): 37-38. 1892.

Grias hexapetala Hooker ex Urban, Bot. Jahrb. Syst. **19:** 669. 1895. In synon.

Grias mexiana R. Knuth in Engler, Pflanzenreich IV. **219a:** 24. 1939. Type. *Mexia 6517* lectotype, F, here designated; isolectotypes, BM, MO, NY, US). Peru. Loreto: Distrito de Iquitos, Muena-caño, 10 Feb 1932 (fl).

Trees, often much branched, sometimes shrub-like, to 22 m tall; leaf-bearing branches 3-9 mm in diameter, the leaves aggregated at their ends. Leaf blades narrowly obovate to oblanceolate, 16-48 × 4-13 cm, glabrous, chartaceous, with 14-22 pairs of lateral veins; apices acuminate to long acuminate; bases acute to cuneate; margins entire to serrulate or infrequently serrate, the serration especially pronounced on upper one-half of blade. Petioles absent to 40 mm long, 2-6 mm thick, semi-circular in cross section. Inflorescences usually suprafoliar, infrequently axillary or cauline, racemose, puberulous to pubescent, with 1-8 flowers; rachis 4-60 mm, often with persistent bud scales at the base; pedicels 15-75 mm, subtended by a single ovate to lanceolate caducous bract 2-7 × 3-4 mm and bearing at various points along the length 2 ovate to broadly ovate or lanceolate bracteoles 2-8 × 2.5-7 mm. Flowers 9-20 cm in diameter; calyx usually an undulate rim 1-2.5 mm deep or less frequently of 4 shallow, broadly rounded or triangular lobes, the lobes 2-5×8-14 mm; petals (6-)8(-9), oblong, obovate, or oblanceolate, 25-95×15-50 mm, rusty-to-gray pubescent in bud, puberulous at anthesis, white inside and outside, with tinges of pink on the outside especially towards the apex; connate androecium base 8-19 mm high; outermost filaments 10-24 mm, white at base, often pink toward the apex; anthers 2-4 mm, yellow; ovary usually without costae, puberulous or pubescent, 4-7-locular, the summit white-pubescent to white-tomentose; style conical 1-3 mm long; stigma with 4-6 lobes. Fruits globose, truncate at apex, without costae, 30-70×30-80 mm, without persistent calyx lobes. Seeds rounded in cross section, black at maturity, 15-22×10-14 mm, with a distinctive yellow, contorted funcile, 14-35×4-12 mm. Seedlings with distinctive cataphylls, 4-5 mm long.

Type. Probably collected by Allamand and Solander between 1755 and 1770 (lectotype, LINN, microfiche no. 863.2, here designated; isolectotypes, LINN microfiche nos. 863.1, 863.4). Surinam.

Distribution. Common along river margins throughout the Guianas and Amazonia. Occasionally cultivated in botanical gardens.

Representative specimens examined. SINGAPORE (Cultivated). Lawn B in botanic gardens, 26 Oct 1929 (fl), *Nees sn* (BM, OXF). DOMINICA. Cultivated, Botanic Gardens Roseau, 30 May 1940 (fl), *Hodge 3935* (GH). MARTINIQUE. 1864 (fl, fr), *Hahn sn* (P); St. Pierre, Botanical Garden, 1854 (fl), *Duss sn* (NY). COLOMBIA. Amazonas: Trapecio Amazónico, entre los ríos Loretoyacu y Hamacayacu, 260 m, Nov 1945 (fl) *Duque-Jaramillo 2049, 2050* (COL), Fleuve Amazone, Lago el Badio, 2 km N de Leticia, 27 Jan 1969 (fr), *Sastre & Gómez-Pompa 515* (INPA); Trapecio Amazónico, Boiauassu River, Nov 1945 (fl), *Schultes 6818* (NY, US); Loretoyacu, alt 100 m, Mar 1946 (fl), *Schultes 7126* (GH, NY, US). VENEZUELA. Delta Amacuro: Caño del Corisal-Corisal, 26 Feb 1911 (fl), *Bond et al 196a* (PH, US); 15 km E de Los Castillos, 14 Jul 1960 (fl), *Little 17704* (VEN); Cerro Lucupanar, 20 Mar 1948 (fl), *Tamayo 27673* (VEN). Bolívar: Puerto Ordaz-San Félix, margins of the Caroni River, Apr 1964 (fl, fr), *Aristeguieta 5317* (VEN); 3 km SE of Hato, El Cuajo betwen Los Castillos de Guyana and Piacoa, 5 Jun 1960 (fl), *Steyermark 86275* (US, VEN); Salto de Para, Medio Caura, alt 250 m, 10 Mar 1939 (fl), *Williams 11463* (F, US, VEN); medio Orinoco Caicara, alt 90 m, 12 Jun 1940 (fr), *Williams 13293* (F, VEN). Amazonas: Río Casiquiare, milla 204, 20 Apr 1968 (fr), *Medina 329* (VEN); Río Orinoco, Río Cuao, above Caño Grande, 21 Jan 1949 (fl), *Maguire & Politi 28531* (NY, WIS). TRINIDAD. Port of Spain Botanical Graden, 13 Feb 1932 (fl), *Fairchild 2852, 2853* (US). GUYANA. Northwest District, Doriabo River, 20-22 Jul 1934 (fr), *Archer 2399* (BRG, US); Georgetown Botanical Garden, 27 Sep 1934 (fl, fr), *Archer 2551* (US); Sand Creek, Rupununi River, Sep 1948 (fl), *Forest Dept. Br. Guiana WB148* (NY); Corentyne River, 1849 (fl), *Jenman 469* (P); Essequibo River, Jun 1899 (fl), *Jenman 7567* (NY); NW slopes of Kanuku Mountains, drainage of Moku-Moku Creek, alt 150-400 m, 31 Mar-16 Apr 1938 (fl), *A. C. Smith 3510* (A, F, IAN, MO, NY, US). SURINAM. Carolina and vicinity, 13-17 Dec 1934 (fl), *Archer 2890* (US); Sectie 0, 14 Jan 1920 (fr), *Boschwezen 4534* (IAN, US); Moengo Tapoe, at Coermotibo Creek, 9 Aug 1949 (fl), *Lanjouw & Lindeman 452* (NY); near Kabelstation, 9 Nov 1933 (st), *Lanjouw 1193* (NY); Tibiti Savanne, 5 Jan 1949 (fr), *Lanjouw & Lindeman 1571* (NY); Saramacca River, riverbanks above Kwatta Hede, 22 Jun 1944 (fr), *Maguire 23930* (US); Fallawatra, 23 Nov 1971 (fl), *Jiménez-Saa 1654* (NY, WIS). GUYANE FRANÇAISE. Montagne du Rorota, 12 Dec 1949 (fl), *BAFOG 3221* (P); St. Laurent-du-Maroni, Crique Sendu, 15 Feb 1949 (fr), *BAFOG 4471* (P); Cayenne, 25 Dec 1913 (fl), *Benoist 17* (P); Môrro do Pariacabo, 23 Oct 1954 (fl), *Black & Klein 54-17189* (IAN); Montagne de Kaw, 12 Dec 1954 (fl), *Cowan 38766* (NY); Territoire contesté Franco-Bresilien, 1897-98 (fl), *Geay sn* (P); Rivière Camopi, saut Tampec, 6 Dec 1967 (fl), *Oldeman 2560* (INPA). BRAZIL. Roraima: Rio Branco, fazendas São Bento, Capela e Bom Intento, 3 Sep 1951 (fl), *Black 51-13288* (IAN); 85 km N of Boa Vista, Fazenda União, 1 Feb 1969 (fl), *Prance et al 9568* (A, FHO, K, M, MO, P, S, U, US); Posto Mucajaí, Rio Mucajaí, 18 Mar 1971 (fr), *Prance et al 11101* (FHO, INPA, K, MO, NY, S, U, US, WIS); Serra do Mel, Feb 1910 (fl), *Ule 8237* (MG). Amapá: Igarapé Ponta-Narri, cachoeira Limão, beira do Rio Muzeze, 8 Oct 1949 (fl), *Black 49-8485* (IAN); Serra do Navio, Rio Amapari, 23 Nov 1954 (fl), *Cowan 38522* (NY); Rio Jari, Santo Antonio da Cachoeira, 30 Jul 1961 (fl), *Egler & Irwin 46041* (NY); Rio Oiapoque, Igarapé Nataia, 6 Feb 1950 (fl, fr), *Fróes 25899* (IAN); Rio Araguari, between 1° 26' N - 51° 58' W and 1° 9' N - 51° 52' W, 11 Sep 1961 (fl), *Pires et al 50833* (NY). Amazonas: Codajás, Igarapé da Oncinha, 24 Apr 1958 (fl, fr), *Ferreira 58-280* (IAN); Basin of Rio Demeni, vicinity of Tototobi, 1 Mar 1969 (fr), *Prance et al 10360* (FHO, INPA, K, M, MO, NY, P, S, U, US); Rio Purus, Rio Ituxi, between Santa Maria and Mari, N of Lábrea, 22 Jun 1971 (fr), *Prance et al 13448* (FHO, NY, US, WIS); Rio Negro betwen Ilha Jacaré and Airão, 11 Oct 1971 (fr), *Prance et al 15097* (FHO, INPA, NY, WIS); Maués, Limão-Limoeiro, 18 Apr 1966 (fl), *Rodrigues & Coêlho 7710* (NY); Solimões, Manacapurú, lago do Jacaré, 1 Apr 1967 (fl), *Silva 746* (NY). Pará: Belém, Jardim Botánico do Museu Goeldi, 29 Oct 1942 (fr), *Archer 7724* (NY); Soure, Ilha do Marajó, 12 Nov 1948 (fl), *Black 48-3438* (IAN); estrada planejada de São Miguel do Guamá a Imperatriz, Km 7, 9 Nov 1956 (st), *Black 56-18861* (IAN); Rio Tocantins, Remansão, 7 Sep 1948 (fl), *Fróes 23409* (IAN); Planalto de Santarém, localidade Sertão, Oct 1954 (fl), *Fróes 31441* (IAN); Rio Xingu, municipio de Moz em frente Souzel, 17 Nov 1955 (fl, fr), *Fróes 32317* (IAN); upper Cupary River, plateau between the Xingu and Tapajós Rivers, 10 Sep 1931 (fl), *Krukoff 1072* (BM, NY); vicinity of Paragominas, Belém-Brasilia, km 161, 13 Aug 1964 (fl, fr), *Prance & Silva 58696* (K, NY). Maranhão: Maracassume River region, 10 Sep 1932 (fl), *Fróes 1890* (A, BM, F, MO, NY, US); Island of São Luiz, Jan 1940 (fl), *Fróes 11723* (A, F, MO, NY). Ceará: Without date (fl), *Allemão & Cysneiros 718* (P, R); Serra de Maranguapa in Pirapora Valley, 21 Oct 1958 (fr), *Ducke 2633* (IAN). Goiás: Região de Araguatins, Igarapé Ucuricaca, 25 Aug 1961 (fl), *Oliveira 1831* (IAN). Acre: Municipio of Sena Madureira, 5 km E of Sena Madureira, 3 Oct 1968 (fl), *Prance et al 7783* (FHO, INPA, K, S, U, US). Pernambuco: Dois Irmãos, Recife, Feb 1940 (fl), *Deslandes 109* (SP); near Pernambuco (Recife), without date (fl), *Gardner 1022* (BM, GH, K, OXF, W), 30 Dec 1929 (fl), *Pickel 2234* (US), 1887 (fl), *Lea & Ramage sn* (BM); Pernambuco, Olinda, 21 Sep 1961 (fl), *Tavares 825* (US). Bahia: Without date (fl), *Bondar 1760* (SP). Mato Grosso: Source of Jatuarana River, Machado River region, Dec 1931 (st), *Krukoff 1525* (A, BM, NY, P). Minas Gerais: Belo Horizonte, cultivated, 1915 (st), *Silveira sn* (R). Guanabara: Rio de Janeiro, cultivated, without date (fl), *Glaziou 139b* (P), 15 Sep 1883 (fl), *Glaziou 14889a* (R). PERU. Loreto: Río Itaya, above Iquitos, 16 Aug 1972 (fr), *Croat 19228* (MO); Middle Ucayali, Yarina Cocha, Dec 1932 (fr), *Tessman 3410* (GH, NY); Juan Juim alto Río Huallaga, alt ca 400 m, Oct 1934 (fl), *Klug 3900* (BM, F, GH, MO, NY, US); Tarapoto, 26 Feb 1947 (fl), *Woytkowski 35191* (F, MO). BOLIVIA. Pando: W bank of Río Madeira, 3 km above Abuña, 13 Nov 1968 (fl), *Prance et al 8351* (FHO, INPA, K, M, MO, NY, P, S, U, US).

Ecology. *Gustavia augusta* is most commonly found along river margins but may also be encountered away from rivers, especially in habitats that have waterlogged soil for part of the year.

As with most widespread species, *G. augusta* exhibits considerable variability. Nevertheless, there are no clear discontinuities which permit the recognition of more than one species. The riverine habitat of *G. augusta* and possible dispersal by water favors distribution over a large area and lessens geographic isolation.

Local names. COLOMBIA. Matamatá *(Schultes 6818, 7126; Duque-Jaramillo 2051);* Matamatá Pequeña *(Duque-Jaramillo 2049, 2050).* VENEZUELA. Coco de Mono *(Williams 13293);* Guatero *(Williams 11992);* Guatoso *(Williams 11992);* Rosa de Muerto *(Williams 13293).* SURINAM. Arepawana (Carib language, *Lanjouw & Lindeman 1571);* Lanaballi (Arawak language, *Archer 2864, Stahel 292);* Oran Tapoeripa *(Lanjouw 1215);* Wanaballie (Arawak language, *Lanjouw & Lindeman 1571);* Watramammabobbie (Surinam Dutch, *Lanjouw & Lindeman 1571).* GUYANE FRANÇAISE. Camaca *(BAFOG 4471);* Cona-da-cona-dou *(BAFOG 3221);* Mau Tapouhoupa *(BAFOG 4471).* BRAZIL. Genipaparana *(Capucho 502, Krukoff*

1072); Geniparana *(Archer 7931, Cavalcante 297, Egler, 667, Ferreira 58-280, Huber 324, Oliveira 2394, 3159, 3388, 4310, Pessoal do Museu 9779, Pires & Black 491, Pires 51852, Prance & Pennington 1670, Rodrigues & Mello 2369, Silva 545);* Japuaranduba *(Glaziou 139a, 14889b);* Janipara *(Cavalcante 1904);* Jeniparana *(Black 828);* Matamatá do Igapó *(Byron & Lima 283);* Pão Fedorento *(Sampaio 8409);* Rikodim (Uaicá-Mucajaí language, *Prance et al 11101);* Taminromre (Uaicá-Mucajaí language, *Prance et al 11138).* PERU. Chopé *(Mexia 6517, Tessman 3410, Woytkowski 7177);* Sacha Chopé *(Klug 1021).*

14. Gustavia dodsonii Mori, Selbyana **2**(1): 37-38, *pl 11.* 1977. Fig 48.

Trees, to 18 m tall. Leaf blades sessile, oblanceolate, 78-90 × 20-27 cm, glabrous, coriaceous, with 36-37 pairs of lateral veins; apex acuminate; margins entire. Inforescences suprafoliar, racemose, with ca 8 flowers, the rachis 60 mm; pedicels 140-170 mm, subtended by a single caducous bract and bearing above the middle 2 oblong bracteoles 12 × 5 mm. Flowers 14 cm in diameter; calyx lobes 4(-5), broadly triangular, 14-18 × 8-9 mm; petals (7-)8, broadly to narrowly obovate, 80-90 × 40-52 mm, pink; connate androecium base 13 mm high; outermost filaments 27 mm; anthers 4 mm long; ovary 5-locular, with 16-20 ovules in each locule, puberulous, obscurely 4-costate, white-pubescent at the summit; style conical, 4 mm. Fruit turbinate, dark brown, 13 × 9-10 cm, the pericarp 9-13 mm thick. Seeds 4 per fruit, 48-74 × 45-58 mm, with distinctive funicles.

Type. *Gentry & Dodson 12048* (holotype, MO 2272186; isotypes, NY QCA). Ecuador. Los Ríos: Río Palenque Science Center, km 56 between Quevedo and Santo Domingo de Los Colorados, tropical wet forest, alt ca 200 m, 25 Oct 1974 (young fr).

Distribution. Known only from northwestern Ecuador.

ECUADOR. Esmeraldas: Alto Tambo, alt 650 m, 23 Sep 1965 (fr), *Little & Dixon 21139* (NY). Los Ríos, Río Palenque Biological Station, km 56 Quevedo-Santo Domingo, 150-200 m, 4 Sep 1972 (fl), *Dodson & McMahon 5070* (SEL, UCQ); Km 12, road from Patricia Pilar to 24 de Mayo, alt 540 m, 7 Oct 1974 (fr), *Dodson & Gentry 6596* (NY).

Ecology. *Gustavia dodsonii* is uncommon in the middle story of wet, mature forest. The trunks of this species have very great tensile strength and are therefore used by natives as levers to lift heavy objects. This reduces the number of trees in the woods and probably accounts for the fact that it is uncommon (Dodson, pers. comm.).

15. Gustavia terminaliflora Mori, sp nov Fig 48.

Arbores 7 m alta, folia arcte aggregata ad apicem ramorum, rami 8 mm in diametro sub folia. Laminae oblanceolatae vel spathulatae, 29-35 × 10-12 cm, glabrae, paribus venarum lateralium 16-20; apice laesae; basi acutae; marginibus integris. Petioli carentes vel usque ad 5 mm longi. Inflorescentiae racemosae, terminales; pedicelli 35-40 mm, bracteolis 2, sub hypanthium insertis. Flores ignoti. Fructus globosus, planatus ad summum, seminibus 1-4 per fructum, sine carunculis contortis.

Type. *Kayap 669* (holotype, MO 2272930). Peru. Amazonas: Lugar Isla de Chigkan Entsa, alt 1100 ft, 28 Apr 1973 (fr).

Distribution. Known only from the type locality.

The only other species of *Gustavia* with terminal inflorescences and sessile or nearly sessile leaves are *G. pubescens, G. sessilis, G. monocaulis, G. angustifolia,* and *G. dodsonii.* The first three species belong to section *Grandibracteata* and therefore differ from the new species, a member of section *Gustavia,* in the characters given in the key to sections of *Gustavia.* The glabrous abaxial leaf surface of *G. terminaliflora* separates it from *G. angustifolia* and its smaller leaves (29-35 x 10-12 cm versus 78-90 x 20-27 cm) with fewer pairs of lateral veins (16-20 versus 36-37) distinguish it from *G. dodsonii.*

The specific epithet refers to the terminal position of the flowers.

16. Gustavia verticillata Miers, Trans. Linn. Soc. London **30**(2): 181. 1874. Fig 48.

Trees, to 10 m tall; leaf-bearing branches 4-6 mm in diameter, the leaves in tightly congested clusters at their ends; petiole scars touching to several mm apart. Leaf blades narrowly elliptic to oblanceolate, 16-30 x 3-6(-9.5) cm, glabrous, chartaceous, with 13-21 pairs of lateral veins; apices acuminate to long acuminate; bases acute, cuneate or obtuse, very narrowly decurrent; margins entire to minutely and sparsely serrulate. Petioles 10-55 x 2-3 mm, subterete in cross section. Inflorescences suprafoliar, racemose, with 2-5 flowers, the rachis ca 10 mm; pedicels 15-17 mm, subtended by a single narrowly ovate to ovate bract 2-3 x 2-3 mm and bearing slightly above the middle of the pedicel 2 ovate pedicellary bracteoles 2-3 x 3-4 mm wide. Flowers ca 7 cm in diameter; calyx entire, the rim 1-1.5 mm wide; petals 8, narrowly oblong to oblanceolate, 40 x 14-17 mm, puberulous at anthesis; connate androecial base 12 mm high; outermost filaments 14-16 mm; anthers 2.5-3 mm; ovary smooth, rusty-pubescent, 4-locular, the summit white-tomentose; style 1-1.5 mm long; stigma with 4 lobes. Fruits known only from a single imperfect specimen, 32 x 30 mm, without persistent calyx lobes. Seeds more or less rounded in cross section, 15 x 10 mm, with a well developed caruncle; funicles not in evidence.

Type. *Triana 4167* (lectotype, BM, here designated; isolectotypes, BM, F, K, P, W). Colombia. Tolima: Magdalena Valley, 450 m alt, 1851-1857 (fl).

Distribution. *Gustavia verticillata* is known from the middle of the Magdalena Valley of Colombia into the Province of Darién, Panama.

PANAMA. Darién: Near Estero Grande of Río Marea, 13 Mar 1967 (fl), *Duke 10964* (MO). COLOMBIA. Cundinamarca: Viotá-Tocaima (quebrada "Cachinibulo"), 380 m alt, 19 Feb 1876 (fl), *André 1772* (K); de Villeta a Honda, Jan 1844 (fr), *Goudot sn* (P). Tolima: Cunday, 700 m, Feb 1883 (fl), *Lehmann 2591* (BM).

Local name. PANAMA. Membrillo (Duke 10964).

17. Gustavia parviflora Mori, nom nov Fig 51.

Lecythis longifolia Humb., Bonpl. and Kunth, Nov. Gen. et Sp. 7: 260. 1825. Type. (same as for *Gustavia parviflora).*

Trees to 15 m tall; leaf-bearing branches 6-7 mm in diameter, light brown, lenticellate, the leaves loosely grouped at their ends. Leaf blades narrowly oblong to narrowly elliptic, 29-36 x 6-9 cm, glabrous, chartaceous, with 25-27 pairs of lateral veins; apices acuminate; bases acute; margins nearly entire to finely serrulate. Petioles 8-13 x 3-4 mm, semi-circular in cross section. Inflorescences suprafoliar, racemose, pubescent, subtended by persistent ovate, apiculate bud scales, 5 x 5 mm, the rachis 45-60 mm; pedicels 34-40 mm, subtended by a single caducous bract, bearing 2 bracteoles near the middle, and becoming woody below the bracteoles. Flowers 5-8 cm in diameter; calyx with 4 broadly rounded to triangular lobes, 4 x 7.5 mm wide; petals 8, narrowly oblong to obovate, 20-40 x 10-15 mm, puberulous at anthesis, white or white suffused with pink; connate androecial base 6-11 mm high; ovary with 4 obscure costae, 4-locular, puberulous at summit; style conical, 2-3 mm; stigma with 4 lobes.

Type. *Humboldt & Bonpland 1245* (holotype, P; isotypes, BM, P). Venezuela. "Crescit ad ripam fluminis Orinoci, in convallibus Araguensium, alt 260 hex, Provincia Caracasana" (locality taken from protologue collection), without date (st).

Distribution. A poorly collected species known only from the Venezuelan states of Sucre and Monagas (see comments below).

VENEZUELA. Sucre: Provincia de Cumaná, Cumanacoa, Mar 1846 (fl), *Funck & Schlim 698* (P). Monagas: Between Caripe and summit of Cerro de la Cueva de Doña Anita, alt 900-1200 m, 7 Apr 1945 (fl), *Steyermark 61934* (F, NY, VEN).

Ecology. The only ecological information for this species is given on Steyermark's label. He reports it to be a "common tree, 30-50' tall; understory or substory in virgin forest, at base of bluff and in cafetal."

My examination of a sterile isotype (P) of *Lecythis longifolia* clearly indicates that it is the same species of *Gustavia* collected by Funck & Schlim and Steyermark at Cumanacoa and near Caripe respectively. Humboldt & Bonpland visited both of these localities in 1799 (Sandwith, in Stearn 1968) and probably made their collection at one of them. Consequently Kunth's statement that it grows as far south as the Orinoco is probably based on misidentification by Humboldt & Bonpland, there being no extant collections documenting its existence there.

Transference of *Lecythis longifolia* Kunth to *Gustavia* results in a later homonym of *Gustavia longifolia* Poeppig ex Berg published in 1858 for a completely different taxon. Hence, under articles 55 and 64 of the Code, a *nomen novum* must be coined. I have chosen the epithet *parviflora* (= small-flowered) because the flowers are about one-half the diameter of those of most other species of *Gustavia.*

This species is very closely related to *G. speciosa* and *G. macarenensis.* It differs by having flowers only 5-8 cm in diameter and by its obscurely 4-costate ovary. The flowers of the above mentioned species are always 13 or more cm in diameter and have smooth ovaries.

Local names. VENEZUELA. Coco de Mono *(Humboldt & Bonpland 1245)*.

18. Gustavia fosteri Mori, Brittonia **30:** 340-341. 1978. Fig 48.

Trees to 5 m tall; the leaves arranged in densely crowded verticils of 10-11 leaves, leaf-bearing branches 9 mm in diameter. Leaf blades oblanceolate to spathulate, glabrous, 26-72 × 5-10 cm, with 21-31 pairs of lateral veins; apices acuminate to acute; bases acute; margins serrate towards the apex. Petioles 5-23 mm. Inflorescences terminal or rarely cauline, racemose, with up to 13 flowers, the rachis 55-65 mm; pedicels 60-80 mm, puberulous, subtended by a caducous bract 8-12 × 5-7 mm and bearing above the middle 2 ovate bracteoles 7-11 × 5-8 mm. Flowers 13-17 cm in diameter; calyx of 4 broadly triangular lobes 4 × 14 mm; petals 8, pale pink, obovate to oblanceolate, 55-65 × 20-25 mm; connate androecial base 11-12 mm high; outermost filaments 18-19 mm, white at bases and dark pink towards apices; anthers 2.5-3 mm, yellow; ovary puberulous on exterior, white-pubescent on the summit, 5-6-locular, with 20-30 ovules in each loculus; style conical, 3 mm; stigma with 6 lobes. Fruits globose, 45 × 45 mm, the mesocarp white. Seeds white, 30-35 × 22-24 mm, 5 per fruit, with short funicles 5 × 4-5 mm.

Type. *Foster 2790* (holotype, MO; isotype, F). Panama. Canal Zone: Barro Colorado Island, 18 Jun 1974 (fl).

Distribution. Known only from the type locality.

PANAMA. Canal Zone: Barro Colorado Island, 30 Sep 1974 (fr), *Mori & Kallunki 2219* (MO, NY).

This species is known only from several individuals on Barro Colorado Island near the junction of the Synder-Molino and Wheeler Trails. It can be easily confused with the much more abundant *G. superba* from which it is distinguished by 1) leaves grouped in several verticels at the branch ends instead of scattered along the ends of the branches, 2) mostly terminal instead of cauline inflorescences, 3) calyces with 4 broadly triangular lobes instead of without lobes, i e, entire, 4) petals light pink throughout instead of white with flushes of pink, 5) the opercular region nearly as wide as the fruit diameter instead of much constricted, and 6) white instead of orange mesocarp at maturity. The leaves of *G. fosteri* also tend to be smaller than those of *G. superba* but there is much overlap. The phenologies of the two species are also different. *Gustavia superba* flowers during the dry season into the early wet season and fruits at the beginning of the wet season, whereas *G. fosteri* starts to flower well into the wet season and its fruits reach maturity from the middle towards the end of the wet season.

The closest relative of *G. fosteri* is *G. angustifolia* of the dry coastal forests of Ecuador. The principal difference between these two species is the glabrous abaxial leaf surface of *G. fosteri* in contrast to the pubescent one of *G. angustifolia*.

19. Gustavia macarenensis Philipson, Mutisia **24:** 3. 1956. Figs 1C, 6, 49, 51.

Trees to 25 m tall, with a dense, globose to obovate crown; leaf bearing branches 5-10 mm in diameter; sylleptic branches often present. Bark nearly smooth, light gray. Leaf blades elliptic or oblanceolate, glabrous, coriaceous, 15-61 × 6-19 cm, with 10-25 pairs of lateral veins; apices acuminate to long acuminate; bases acute, obtuse, or rounded; margins entire to serrulate. Petioles 10-70 × 2-4 mm thick. Inflorescences suprafoliar, sometimes at the end of sylleptic branches, racemose, tan-to-rusty-tomentose, with 3-6 flowers, the rachis 30-95 mm; pedicels (20-)50-70 mm, with a single caducous basal bract and 2 bracteoles inserted near the middle. Flowers to 18 cm in diameter; calyx of 4 rounded or broadly triangular lobes, 3-5 × 5-11 mm wide, tan- to rusty-tomentose; petals 8, oblong to obovate, 50-70 × 25-50 mm, densely tomentose-papillose in bud, glabrous to puberulous at maturity, white; connate androecial base 15 mm high; outermost filaments 20-22 mm; anthers 3-5 mm, yellow; ovary without costae, tan- to rusty-tomentose, the indumentum of simple, multicellular pointed hairs, (4-)5-locular, glabrous at summit; style conical, 4-5 mm; stigma with 4-5 lobes. Fruits in clusters at the branch ends, globose, truncate at apex, 55 × 55 mm, with a small umbo; pericarp 10-15 mm thick. Seeds round in cross section, 40 × 40 mm, 1 or 2 per fruit, with a non-expanded funicle 4 mm long.

Type. *Philipson et al 1987* (holotype, BM; isotypes, COL, MEDEL, NY, S, US). Colombia. Meta: Sierra de la Macarena, Central Mountains, N ridge, 29 Dec 1949 (fl).

Key to the Subspecies of *Gustavia macarenensis*

1. Leaf blades elliptic to narrowly elliptic, 15-30 × 5-13 cm, with 10-18(-24) pairs of lateral veins; petioles 17-40 mm long. Known from east of the Andes in Colombia, Ecuador and Peru. a. subsp *macarenensis.*
1. Leaf blades oblanceolate, 28-61 × 7-19 cm, with 15-25 pairs of lateral veins; petioles 15-70 mm long. Known from the State of Merida, Venezuela. b. subsp *paucisperma.*

19a. Gustavia macarenensis Philipson subsp **macarenensis** Fig 51.

Trees to 25 m tall, the leaves loosely congested at the apices of the branches. Leaf blades elliptic to narrowly elliptic, 15-30 × 5-13 cm, glabrous, with 10-18(-24) pairs of lateral veins, these prominent beneath; apices acute to acuminate; bases acute to obtuse; margins entire to irregularly crenate. Petioles 17-40 × 2 mm. Inflorescences suprafoliar, racemose, with 4-6 flowers; pedicels pubescent, 25-30 mm, with 2 bracteoles 3 mm long inserted at or above the middle. Calyx with 4 puberulous, broadly triangular lobes, 3 × 5 mm; petals ovate, 50 × 25 mm; androecium 30 mm in diameter; anthers 4 mm. Fruits unknown.

Distribution. This subspecies ranges from the Sierra de la Macarena, Colombia south through lowland Ecuador into Amazonian Peru.

ECUADOR. Napo-Pastaza: Between Tena and Archidona, 6 Jan 1940 (fl), *Asplund 10282* (S); Tena, island in river, 7 Jan 1940 (fl), *Asplund 10298* (S); Puerto Napo, 4 Apr 1969 (fl), *Lugo 1036* (S). PERU. Loreto: Mishuyacu, near Iquitos, alt 100 m, Dec 1929 (fl), *Klug 675* (NY, US).

The fruits of *G. macarenensis* subsp *macarenensis* are said to be edible by several collectors *(Asplund 10282, 10298; Klug 675).* In this respect, and in many morphological features, *G. macarenensis* resembles *G. speciosa.* In fact, the relationship between these two taxa is so close that field study may prove them to be conspecific.

Local name. PERU. Chope *(Klug 675)*

19b. Gustavia macarenensis Philipson subsp **paucisperma** Mori, subsp nov
Figs 1C, 6, 49, 51.

Arbores usque ad 12 m altae × 16 cm diametro; corona globosa vel obovata, densa; rami sub folia 6-10 mm diametro; folia ad apicem ramorum laxe aggregata. Cortex fere laevis, laete griseus. Laminae oblanceolatae, 28-61 × 7-19 cm, glabrae, apice acuminatae, basi acutae vel obtusae, marginibus integris vel serrulatis, paribus venarum lateralium 15-25. Petioli 15-70 × 2-4 mm, semicirculares in sectione transversali. Inflorescentiae suprafoliares, fulvo- vel ferrugineo-tomentosae, floribus 3-6, rhachidi 30-95 mm; pedicelli (20-)50-70 mm, singula caduca bractea ad basim, bracteolis cucullatis caducis 2, ad medium insertis. Flores usque ad 18 cm diametro; lobi calycis rotundati, 4-5 × 7-11 mm, fulvo-vel ferrugineo-tomentosi; petala 8, oblonga vel obovata, 55-70 × 35-50 mm, dense tomentosa in gemma, puberula sub anthesi, alba; basis connata androecii 15 mm alta; filamenta externa 20-22 mm, minute puberula; antherae 3-5 mm, luteae; ovarium sine costis, fulvo- vel ferrugineo-tomentosum, glabrum ad summum; stylus 4-5 mm, conicus; stigma (4-)5 lobis ornatum. Fructus globosi, brunnei, 55 × 55 mm, pericarpio 10-15 mm crasso. Semina rotunda in sectione transversali, 40 × 40 mm, funiculo recto, 4 mm longo.

Type. *Breteler 4615* (holotype, U; isotypes, US, VEN). Venezuela. Mérida: 5 kms from La Azulita, along road to Mérida, in pasture, 24 Sep 1965 (fl).

Distribution. This subspecies is relatively common in the mountains west of the city of Mérida, Venezuela.

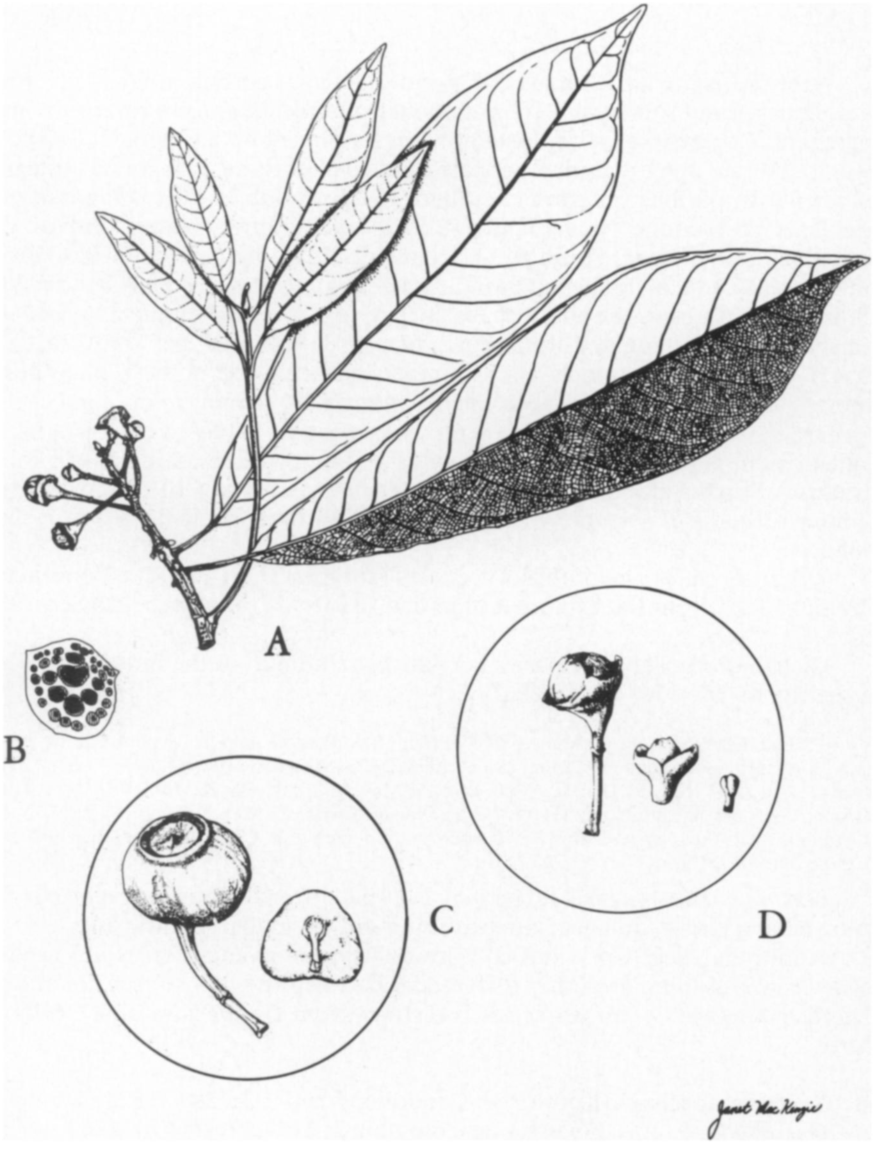
VENEZUELA. Mérida: La Azulita, 24 Oct 1953 (fl), *Bernardi 1030* (NY); plus or minus 5 km from La Azulita, along road to Mérida, 23 Feb 1966 (fr), *Breteler 4936* (U), 4 May 1971 (fl), *Nee & Mori 4159* (K, MO, NY, P, U, US, VEN, WIS), 4 May 1971 (st), *Nee & Mori 4161* (NY, VEN, WIS); ca 7 km past La Azulita, 4 May 1971 (fr), *Nee & Mori 4156* (MO, NY, P, US, VEN, WIS); El Molinillo-San Luis, entre la aldea El Dalado y la población de La Azulita, 18 Mar 1963 (fl), *Ruiz-Terán 1426* (MO).

Gustavia macarenensis subsp *paucisperma* differs from supsp *macarenensis* by having larger, oblanceolate leaves instead of smaller, elliptic ones.

Additional field work and collections from intervening areas are needed to determine if there are other differences between the two subspecies and to establish whether *G. macarenensis* is distinct from *G. speciosa* and *G. parviflora.*

20. Gustavia speciosa (Kunth) de Candolle, Prodr. **3:** 289. 1828; Romero-Castañeda, Frutas Silvestres de Colombia **2:** 215-217, *fig 57a.* 1969.
Figs 6, 50, 51.

GUSTAVIA MACARENENSIS subsp. PAUCISPERMA



Pirigara speciosa Kunth, Synops. Plant. Aeq. 3: 426. 1824; H.B.K., Nov. Gen. Sp. 7: 262. 1825. Type. Same as for *Gustavia speciosa* (Kunth) de Candolle.
Japarandiba speciosa (Kunth) O. Kuntze, Rev. Gen. 1: 240. 1891.

Trees, medium sized, to 20 m tall, 40 cm in diameter, with a dense ovate crown; leaf-bearing branches 3-8 mm in diameter, the leaves loosely grouped at their ends; petiole scars to 10 mm apart. Bark nearly smooth, gray to brownish-gray. Leaf blades narrowly elliptic, oblanceolate or narrowly ovate, 13-44 × 4-18 cm, glabrous, chartaceous, with 15-22 pairs of lateral veins; apices acuminate; bases acute, cuneate or obtuse, sometimes unequal; margins entire to remotely serrulate. Petioles 20-80 × 2-3 mm, subterete in cross section. Inflorescences usually suprafoliar, racemose, glabrous to white-rusty-tomentose, with 3-10 fls; rachis 20-70 mm; pedicels 40-90 mm, subtended by a single, early-caducous, oblong to oblanceolate, cucullate bract 30 × 12 mm and bearing at some point from the middle to directly below ovary 2 ovate to narrowly ovate bracteoles, 2-7 × 3-4 mm. Flowers 13-14(-18) cm in diameter; calyx an entire or undulate rim or with 4 triangular, rounded or irregularly incised lobes; petals 6 or 8, narrowly oblong, narrowly obovate or lanceolate, 45-60(-88) × 15-30 mm, tawny-tomentose in bud, puberulous at anthesis, usually white, occasionally tinged with rose on the outside; connate androecial base 9-17 mm high, light yellow; outermost filaments 12-20(-25) mm, yellow at the apex; anthers 2-3.5(-4) mm, yellow; ovary smooth, glabrous or buff-rusty-tomentose, (4-)6-locular, the summit with a white-puberulous to white-tomentose indumentum tending to be arranged in irregular lines radiating from the style, style 1.5-3(-4) mm; stigma with 4-6 lobes. Fruits globose, with the opercular region bulging upwards, umbonate, 40-60 × 50-80 mm, with the calyx persisting only as an irregular rim without distinguishable lobes. Seeds trigonous in cross section, surrounded by a yellow-orange pulp, 30-35 × 20-25 mm, 1-4 per fruit, without distinctive funicles.

Type. *Humboldt & Bonpland 1881* (holotype, P; isotypes, F neg. no. 38306, GH, photo, P). Colombia. Tolima: Near Mariquita, alt 450 ft, without date (fl).

Key to the Subspecies of *Gustavia speciosa*

1. Medium sized trees, to 10 m tall; leaf blade length to width ratio greater than 3; ovary walls pubescent; central valleys of Colombia, infrequently Amazonia; often cultivated. a. subsp *speciosa*.
1. Large trees, to 20 m tall; leaf blade length to width ratio less than 3; ovary walls glabrous; Pacific Coast of Colombia; not cultivated. b. subsp *occidentalis*.

20a. Gustavia speciosa (Kunth) de Candolle, subsp speciosa Figs 6, 50, 51.

FIG 49. *Gustavia macarenensis* subsp *paucisperma:* A, Habit, note the smaller sylleptic branch *(Breteler 4615);* B, Petiole cross section made at petiole-blade juncture *(Nee & Mori 4156);* C, Mature fruit and seed with attached funicle *(Nee & Mori 4156);* D, Different stages of bud development, note that the youngest bud is completely covered by the pedicellary bracteoles *(Nee & Mori 4159).*

Trees, medium sized, to 10 m tall (fide Romero-Castañeda). Leaf blades narrowly elliptic to lanceolate, 21-44 × 6-10(-14) cm, with a length to width ratio of 3.2-4.8, with 16-21 pairs of lateral veins. Petioles (20-)40-80 mm. Flowers usually with a calyx of 4 rounded, triangular or irregularly incised lobes, 2-10 × 2-13 mm wide; ovary walls puberulous to rusty-tomentose.

Distribution. This subspecies is native to the Interandean Valleys of Colombia and Ecuador and is cultivated in several lowland localities for its edible fruit.

COLOMBIA. Bolívar: Alrededores de San Andrés, alt 100-1300 m, 24 Mar 1959 (fl, young fr), *Romero-Castañeda 7603* (COL). Antioquia: Planta Providencia, 26 km S and 23 km W (by air) of Zaragoza (7° 13' N, 75° 03' W), in valley of Río Anorí between Dos Bocas and Anorí, alt 400-700 m, 11 Jul 1972 (fl), *Denslow 503* (WIS), 12 Jul 1972 (fl), *Denslow 504* (WIS). Cundinamarca: Guaduas, 8 Dec 1952 (fl), *Uribe-Uribe 2393* (COL). Tolima: Within city limits of Mariquita, 29 Jun 1971 (fl), *Nee & Mori 4239* (WIS). ECUADOR. Esmeraldas: San Lorenzo, "Proyecto NO" at the end of new road (km 14), 18 Aug 1967 (young fr), *Sparre 18140* (S). PERU. Loreto: Iquitos, cultivated, 19 Nov 1945 (fl), *Ducke 1841* (A, F, IAN, MG, NY, US).

Gustavia speciosa subsp *speciosa* is cultivated for its edible fruits. The edible portion of the fruit is the yellowish pulp that surrounds the seeds. This is sucked from the fruit raw or is cooked with meat and rice (Romero-Castañeda, 1969). Sucking the pulp gave rise to the common name *"chupo"* which comes from the Spanish verb *chupar* (to suck).

Humboldt, Bonpland and Kunth (1825) reported the fruits to be eagerly sought after by youngsters who, after consuming too many, took on a yellowish cast. The yellow color disappeared 24-48 hours later without requiring medical attention.

On a visit to Mariquita, Colombia vendors at fruit stands informed me that the fruits of this variety are sold at two different times of the year. The initial harvest is in January and another follows in July and August.

Local names. COLOMBIA. Chupo *(Humboldt & Bonpland 1881, Nee & Mori 4239, Romero-Castañeda 7603).* PERU. Chopé *(Ducke 1841).*

20b. **Gustavia speciosa** (Kunth) de Candolle subsp **occidentalis** (Cuatrecasas) Mori, stat nov Fig 51.

Gustavia occidentalis Cuatrecasas, Fieldiana, Bot. 27(2): 94, *fig 5.* 1951. Type. Same as for *Gustavia speciosa* (Kunth) de Candolle subsp *occidentalis* (Cuatr.) Mori.

Eschweilera cincta Cuatrecasas, Fieldiana, Bot. 27(2): 83-85, *fig 1.* 1951. Type. *Cuatrecasas 15531* (lectotype, F 1358490, here designated; isolectotype, F). COLOMBIA. Valle: Hoya de Río Sanquinini, lado izquierda, La Laguna, bosques, 1250-1400 m alt, 14 Dec 1943 (young fr).

Gustavia cincta (Cuatrecasas) Williams & Kukachka, Fieldiana, Bot. 31(10): 257. 1967.

Trees, large sized, to 20 m tall. Leaf blades narrowly obovate or elliptic, 13-41 × 4-18 cm, with a length to width ratio of 1.9-2.7, with 15-19 pairs of lateral veins. Petioles 4-55 mm. Flowers with an entire calyx, 1-5 mm wide; ovary walls glabrous.

Type. *Cuatrecasas 16639* (lectotype, F 1358513, here designated; isolectotype, F). Colombia. Valle: Río Calima, La Trojita, 50 m alt, 2 Mar 1944 (fl).

GUSTAVIA SPECIOSA

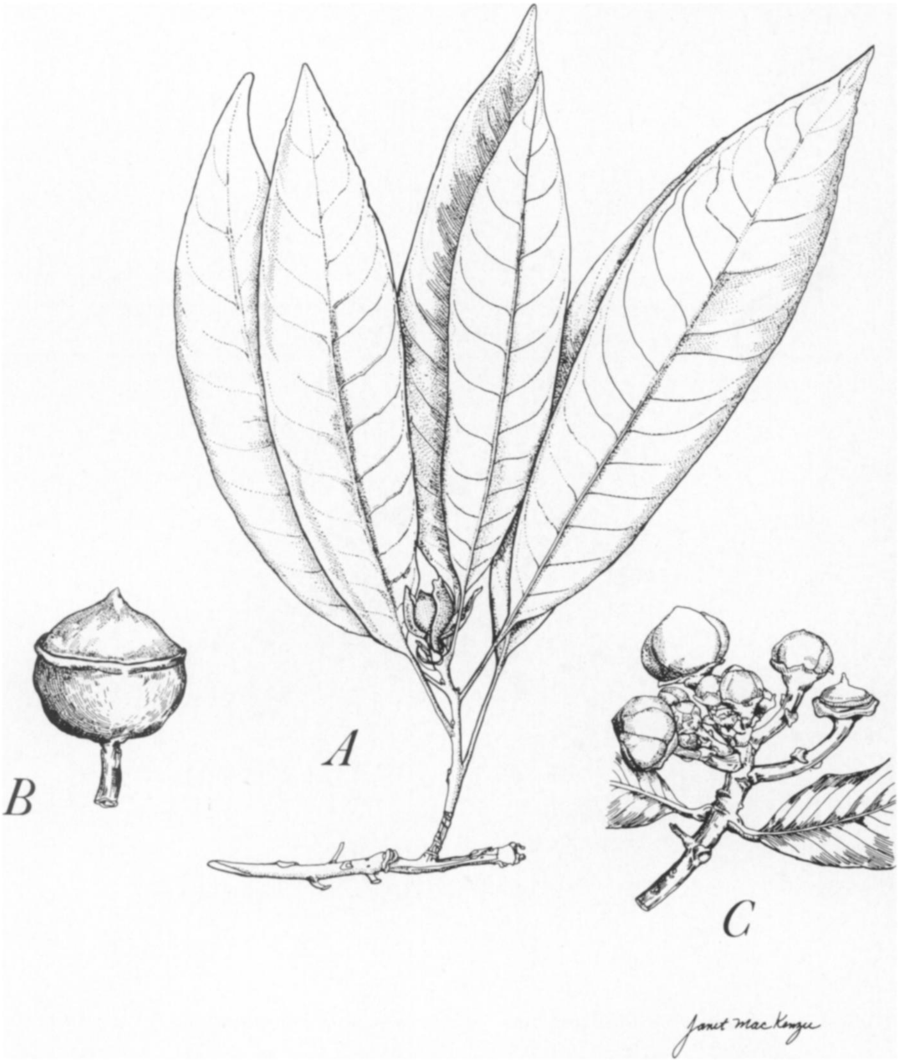


FIG 50. Leaves, inflorescences, and fruit of *Gustavia speciosa* subsp *speciosa:* A, Branch with immature inflorescence at apex *(Nee & Mori 4239);* B, Mature fruit, note upward bulging opercular region (after Romero-Castañeda 1969, p 216); C, Inflorescence (after Romero-Castañeda 1969, p 216).

Distribution. This subspecies is known only from the Pacific slopes of Valle, Colombia from the two type collections cited above.

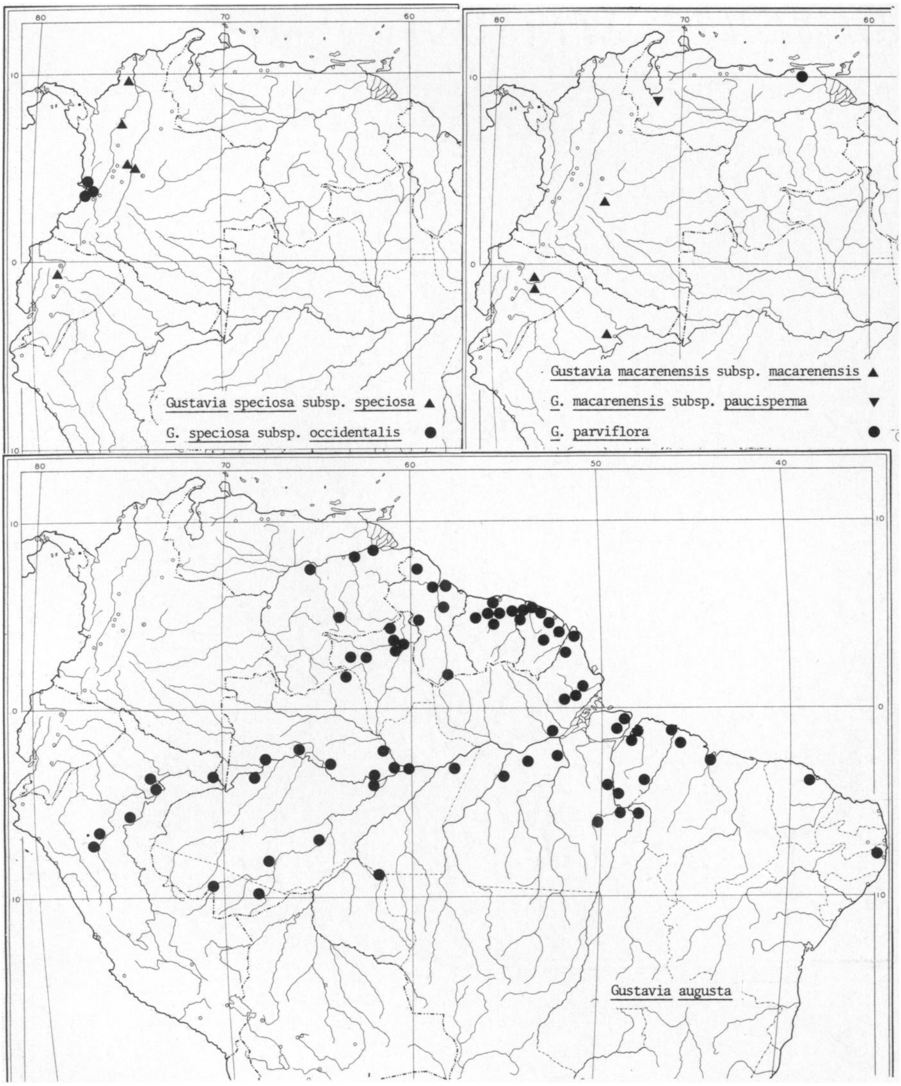


FIG 51. Distributions of *Gustavia speciosa, G. macarenensis, G. parviflora,* and *G. augusta.*

21. Gustavia romeroi Mori & García-Barriga, Caldasia **11**(3): 51-53, *fig 1.* 1975. Fig 52.

Trees, medium sized, to 18 m × 40 cm, the leaf-bearing branches 3-5 mm in diameter, arching upwards. Bark brown, lightly fissured. Leaf blades elliptic, 17.5-21 × 6-7 cm, glabrous, coriaceous, with 12-14 pairs of lateral veins; apices acuminate; bases acute; margins entire. Petioles 15-35 × 1-2 mm, subterete in cross section. Inflorescences cauline, contracted, racemose, with 4-5 flowers, the rachis 7-15 mm; pedicels 25-45 mm, with a single caducous bract at the base and two ovate, persistent bracteoles 2-4 × 4-5 mm, inserted just below the hypanthium. Flowers 8-12 cm in diameter; calyx with 4, more or less cucullate lobes, 2-4 × 7-10 mm, greenish-yellow; petals (11-)12(-18), oblong to oblanceolate, 35-70 × 20-25 mm, puberulous, mostly white but slightly pink at apex; androecium 15-30 mm in diameter, the connate base 7-14 mm high, the outermost filaments 12-20 mm, yellow at the base, rose at the apex; anthers 2-2.5 mm, yellow; ovary without wings, with a white tomentum of simple, 2 to 5-celled hairs and reddish-brown lenticels on the outside, 4-locular, white-tomentose at the summit; style 1-2 mm; stigma 4-lobed. Fruits unknown.

Type. *Nee & Mori 4303* (holotype, COL; isotypes, BM, COL, F, MO, NY, US, VEN, WIS). Colombia. Santander: Camp Capote (6° 38' N, 73° 55' W) and vicinity, compartment 82, alt 100-200 m, 9 Jul 1971 (fl).

Distribution. Apparently confined to the central Magdalena Valley of Colombia.

COLOMBIA. Santander: vicinity of Barrancabermeja, Magdalena Valley, between Sogamoso and Carare Rivers, alt 100-500 m, 28 Oct 1936 (fl), *Haught 2042* (NY, US); Magdalena Valley, Cimitarra, 1 Sep 1954 (fl), *Lamb 186* (US); Camp Capote and vicinity, Compartment no. 23, ca 1 km S of the main camp, 8 Jul 1971 (st), *Nee & Mori 4288* (COL, MO, NY, US, WIS); 10 leguas al SE de Barrancabermeja, a 8 kms de la margen izquierda del Río Opón, alt mas o menos 200 m, 26 Aug 1954 (fl), *Romero-Castañeda 4708* (COL, US), 3 Sep 1954 (fl), *Romero-Castañeda 4819* (COL, US); 12 leguas al SE de Barrancabermeja, a 5 km de la margen derecha del Río Opón, alt 200 m, 29 Sep 1954 (fl), *Romero-Castañeda 4960* (COL, US).

Ecology. This species, a medium sized forest tree, is usually found at elevations of 200 or fewer meters but may be found up to 500 meters. The 6 flowering collections were made between July and October with 3 of these collected in September. Fruits of the species are not known.

This species differs from all other species of *Gustavia* by having 12 or 18 petals. The usual petal number in the genus is 6 or 8. The cauline inflorescences, upward curving pedicels, and the reddish brown lenticels on the hypanthium are also diagnostic.

A short time after being cut the wood emits a fetid odor. This smell is alluded to in the common names (Coco hediondo = evil smelling coco, Mula muerta = dead mule).

Local names. COLOMBIA. Coco hediondo *(Lamb 186)*, Mula muerta *(Romero-Castañeda 4708, 4960)*.

22. Gustavia nana Pittier, Contr. U.S. Natl. Herb. **26**(1): 5-6, *pl* 3-4. 1927; Woodson, Ann. Missouri Bot. Gard. **45**(2): 120. 1958. Figs 6, 52.

Trees, small, to 10 m × 25 cm, known to flower at 1.5 m; leaf-bearing branches (4-)5-8(-12) mm in diameter, the leaves tightly grouped at their ends. Leaf blades elliptic, narrowly ovate, or lanceolate, (11-)18-27(-43) × 5-13(-15) cm, glabrous, chartaceous, with 10-21 pairs of lateral veins; apices acuminate; bases acute, cuneate, obtuse or rounded; margins serrulate. Petioles (20-)60-150(-250) × 1.5-3 mm, subterete in cross section. Inflorescences cauline, contracted, racemose, glabrous, puberulous, or occasionally rusty-tomentose, with 3-7 flowers, the rachis 8-50 mm; pedicels 15-40 mm, subtended by a single caducous bract, and bearing near the middle 2 ovate bracteoles usually fused at their bases, 2-6 × 3-8 mm. Flowers 13-18 cm in diameter; calyx with 4 broadly triangular lobes, 2-5 × 8-13 mm; petals 8, narrowly obovate or oblanceolate, 60-85 × 30-42 mm, usually pinkish; connate androecial base (11-)17-20 mm high, the outermost filaments 13-20 mm; anthers 2.5-3.5 mm; ovary without costae, glabrous to puberulous, 4(-5)-locular, the summit usually puberulous with glabrous spots but sometimes tomentulose; style conical, 2-4 mm; stigma with 4 lobes. Fruits globose, truncate at the apex, the opercular region nearly as great in diameter as the fruit diameter, 30-70 × 40-70 mm, without persistent calyx lobes, first green then yellow-orange; pericarp coriaceous, ca 0.5 mm thick, with a yellow inner pulp; opercular region slightly convex, apiculate or umbonate. Seeds brown, angular in cross section, 20-30 × 20-30 mm, 1-3 per loculus, without distinctive funicles.

Type. *Pittier 4093* (holotype, US 679189; isotype, GH). Panama. Colón: Loma de la Gloria, near Fató (Nombre de Dios), alt 10-14 m, Aug 1911 (fr).

Key to the Subspecies of *Gustavia nana*

1. Leaf blades narrowly elliptic, the length to width ratio greater than 4; plants of *Raphia* and *Prioria* swamps. a. subsp *nana*.
1. Leaf blades narrowly ovate or lanceolate, the length to width ratio less than 4; plants of woods, riverbanks and lake shores but not of swamps. b. subsp *rhodantha*.

22a. **Gustavia nana** Pittier subsp **nana**. Fig 52.

Shrub, small, ca 1.5 m tall, not over 6 cm dbh, with a single stem (fide Pittier); leaf-bearing branches 5-8 mm in diameter; leaves alternate or subverticillate, densely grouped at branch ends (fide Pittier). Leaf blades narrowly elliptic, 22-42 × 5-9 cm wide, glabrous, chartaceous, with 18-21 pairs of lateral veins; apices acuminate; bases acute to cuneate; margins serrulate. Petioles 30-150 × 2-3 mm. Inflorescences appearing near base of trunk (fide Pittier), racemose, glabrous or puberulous. Flowers incompletely known; calyx with 4 broadly triangular lobes. "Pyxis rather large, borne on a pedicel 3 cm long, globose-subpyriform, the body 7 cm long and 7 cm in diameter, 5-celled, obsoletely costate; calycinal zone prominent and bearing the remnants of the calyx; interzonal band flat, 2.5 mm broad; operculum slightly convex; apiculate-umbonate, smooth and lustrous, bright yellow; pericarp coriaceous, about 5 mm thick, smooth and light brown outside; inner pulp yellow. Seeds 1 to 3 in each cell, angulose, irregularly shaped and compressed, 2 to 3 cm long and broad; testa membranous, brownish" (fide Pittier, 1927).

Distribution. This subspecies is known from eastern Colón, Panama and the Chocó region of Panamá and Colombia.

PANAMA. Darién: Ca 6 miles NW of El Real, 15 Jun 1962 (fr), *Duke 4825* (GH, MO, US). COLOMBIA. Chocó: near helipad in *Raphia* swamp, Río Truando at junction with Quebrada Buche, alt ca 40 m, 1 Apr 1968 (fl), *Duke 15739* (MO).

22b. **Gustavia nana** Pittier subsp **rhodantha** (Standley) Mori, stat nov

Fig 6, 52.

Gustavia rhodantha Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 4: 239. 1929. Type. Same as for *Gustavia nana* Pittier subsp *rhodantha* (Standley) Mori.

Small trees, to 10 m × 10(-25) cm; leaf-bearing branches 4-10 mm in diameter, the leaves tightly grouped at their ends. Leaf blades narrowly ovate or lanceolate, (11-)18-27(-43) × (4-)5-13(-15) cm, glabrous, chartaceous, with 10-18 pairs of lateral veins; apices acuminate; bases acute; margins serrulate. Petioles (20-)60-150(-250) × 1.5-3 mm, subterete in cross section. Inflorescences cauline, contracted, racemose, puberulous or occasionally rusty-tomentose, with 3-7 flowers, the rachis 8-50 mm; pedicels 15-40 mm, subtended by a single caducous bract and bearing near the middle 2 ovate bracteoles usually fused at their bases, 2-6 × 3-8 mm wide. Flowers 13-18 cm in diameter; calyx with 4 broadly triangular lobes, 2-5 × 8-13 mm; petals 8, narrowly obovate or oblanceolate, 60-85 × 30-42 mm, usually pinkish; connate androecial base (11-)17-20 mm high, the outermost filaments 13-20 mm; anthers 2.5-3.5 mm; ovary smooth, glabrous to puberulous, 4(-5)-locular, usually with glabrous spots but sometimes tomentulose at the summit; style conical, 2-4 mm; stigma with 4 lobes. Fruits globose, truncate at the apex, the opercular region nearly as great in diameter as the fruit diameter, 30-50 × 40-50 mm, without persistent calyx lobes, first green then yellow-orange. Seeds angular in cross section, 17-22 × 15-17 mm, without a distinctive funicle.

Type. *Cooper 633* (holotype, F 579238; isotype, NY). Panama. San Blas: 3-10 Apr 1928 (fl).

Distribution. This subspecies ranges from eastern Panamá into the Chocó and the Magdalena Valley of Colombia.

PANAMA. San Blas: Caledonia Harbor, Mt. Vernon, 3 Apr 1939 (fl), *Elmore L23* (F); trail to Colombian border from Puerto Obaldia, 19 Aug 1971 (fr), *Gentry 1531* (MO). Darién: 12 Jun 1961 (st), *Sexton 101* (MO); near mouth of Río Yapé ca 20 m alt, 12-14 Jul 1937 (fr), *Allen 349* (F, MO); Rió Chucanaque, between Río Membrillo and Rió Subcuti, 21 Aug 1966 (fr), *Duke 8612* (MO, WIS); between upper Río Membrillo and Camp 7 on the construction road to San Blas 100-800 m, 26-28 Apr 1967 (fl), *Duke 10930* (MO, WIS); Cerro Pirre, alt 2500-4500 ft, 9-10 Aug 1967 (fl), *Duke & Elias 13760* (MO); on tributary of Río Canglones, without date (fl), *Sexton 212* (GH, MO); shores of Bahia de Piñas, 26 Jun 1957 (st), *Stern & Chambers 189* (MO, NY, US); vicinity of Campamento Buena Vista, Río Chucunaque above the confluence with Río Tuquesa, 5 Jul 1959 (fr), *Stern et al 928* (MO); Marraganti and vicinity, 10-200 ft alt, 3-9 Apr 1908 (fl), *Williams 655* (NY). COLOMBIA. Chocó: Orillas de Río Truandó, 20 km al oeste de Riosucio, 25 Mar 1958 (fl), *Bernal 99* (COL); logging road ca 2-4 km NW of Teresita, 100 m alt, 18 May 1967 (fl), *Duke 11028* (NY, WIS); trail between Alto Curiche and Camp Curiche, E of Boca Curiche, alt 10-400 ft, 20 May 1967 (fl), *Duke & Idrobo 11285* (NY, WIS); between Camp Curiche and Q. Changame, 3.7 miles S of Camp Curiche, 24 May 1967 (fl), *Duke & Idrobo 11532, 11534* (NY, WIS); behind logging camp below first rapids on Río Truandó, alt 4-200 m, 15 Jun 1967 (fr), *Duke 12259* (NY); costa del Pacifico, Coredó, 16 Jun 1950 (fl), *Fernández 362* (COL, US). Antioquia: In the rain forest near Río León approximately 20-30 km upstream and south of the river mouth and approximately 15 km W of Chigrodó (probable lat ca 7° 45' N, long ca 76° 50' W) less than 100 m alt, 12 Mar 1962 (fl), *Feddema 1834* (US). Córdoba: On Río Sinú, 50-100 m alt, 7-10 Mar 1918 (fl), *Fennell 4629* (NY). Boyacá: El Humbo, 130 mi N of Bogotá, 3,500 ft above sea level, 23 Feb 1933 (fl), *Lawrance 633* (F).

Ecology. This subspecies is found as scattered individuals in tropical moist and tropical wet forests. It flowers from February through May (middle dry through early wet season) and bears fruit from June through August (middle wet season).

Standley (1929) recognized *G. rhodantha* as separate from *G. nana* because of its smaller leaves and fewer lateral veins. However, Woodson (1958) did not accept *G. rhodantha* as a distinct entity, merging it with *G. nana*. Although *G. nana* subsp *nana* is represented by only 3 collections their differences in leaf shape and habitat support their recognition at least at the subspecific level. A final solution to the problem awaits better collections of *G. nana* subsp *nana*.

Local names. Panama: Achucalo *(Sexton 101)*, Membrillo *(Duke 8612, Sexton 101, Stern & Chambers 189)*, Paco *(Duke 11028, 11534)*.

23. Gustavia tejerae R. Knuth, Pflanzenreich IV. **219a:** 23-24. 1939. char. emend. Fig 52.

Tree, leaves loosely aggregated at the apex of the branches, the branches 5 mm in diameter below the leaves. Leaf blades elliptic to narrowly obovate, 20-22 × 8-9 cm, glabrous, with 13-15 pairs of lateral veins; apices acuminate; bases acute to obtuse; margins serrate. Petioles 35-45 mm. Inflorescences cauline, racemose. Flowers not studied. Fruits unknown.

Type. Venezuela. *Tejera 4* (holotype, US 105686; isotype, GH). Zulia: Vicinity of Perijá, 1919-1920 (young fr).

Distribution. Known only from the type locality.

VENEZUELA. Zulia: Vicinity of Perijá, without date (fl), *Tejera 204* (GH).

The original description of this species by Knuth included characters from two Schultze-Rhonhof Ecuadorian collections *(2027, 2075)*, which were apparently destroyed at Berlin. Although I have not seen these collections I feel that their collection so far from the type locality argues against their treatment as *G. tejerae*. Consequently, I have emended Knuth's description to include only the scanty material of the type, *Tejera 4*. Another collection, *Tejera 204*, cited by Knuth, also has not been seen.

24. Gustavia gentryi Mori, sp nov Fig 53.

Arbores parvae, usque ad 8 m altae; folia ad apicem ramorum in 1 vel 2 verticillis congesta; rami sub folia 3-6 mm in diametro. Laminae anguste ellipticae vel oblanceolatae, glabrae, chartaceae, apice acuminatae, basi acutae, marginibus serrulatis vel serratis, 18-31 × 6-8.5 cm, paribus venarum lateralium 13-20. Petioli subsessiles usque ad 10 mm longi, 2-3 mm crassi, semicirculares in sectione transversali. Inflorescentiae caulinae vel axillares, contractae, racemosae, floribus 2-7, rhachidi 11-20 mm; pedicelli 25-30 mm, singula bractea caduca ad basim et bracteolis 2, lanceolatis, 2-3.5 × 2 mm, ad vel infra medium orientibus. Flores 8-10 cm in diametro; calyx glabrus, lobis 4, rotundatibus vel triangularibus, 2.5-3.5 × 6-7 mm; petala 8, anguste obo-

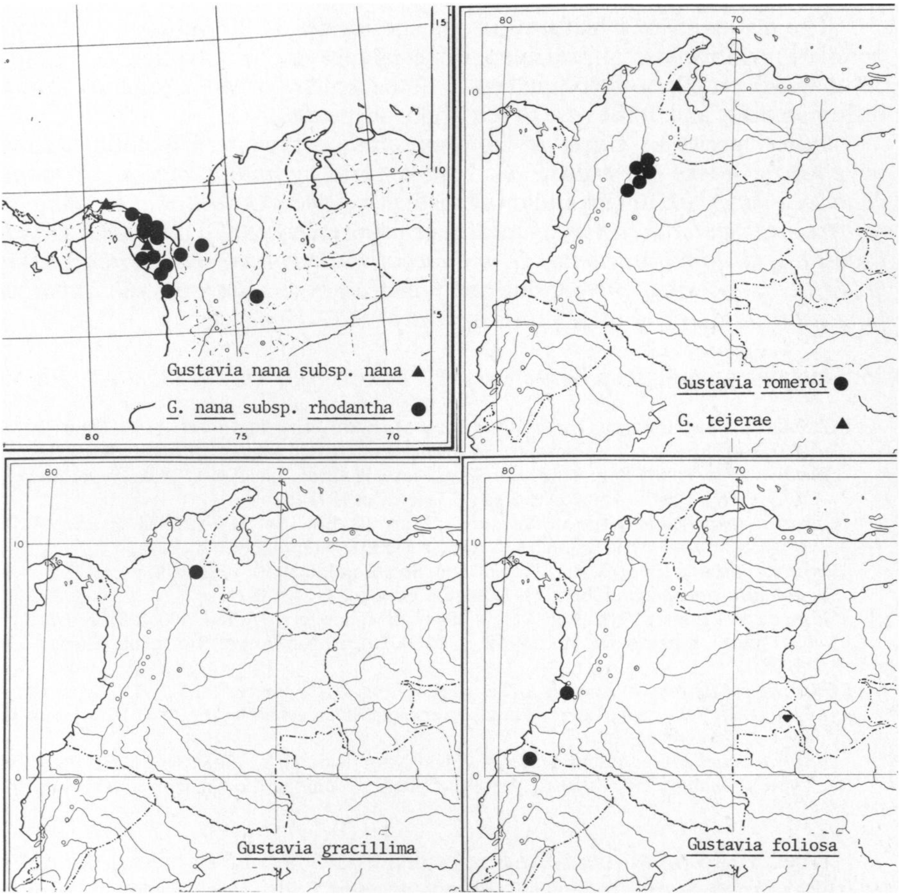


FIG 52. Distributions of *Gustavia nana, G. romeroi, G. tejerae, G. gracillima,* and *G. foliosa.*

vata, 44 × 20 mm, puberula sub anthesi, rosea vel roseo-purpurata; basis connata androecii 10-11 mm alta, filamenta extima 12-16 mm; antherae 2-2.7 mm; ovarium extus laevis, puberulum, 4-loculare, ad summum albo-tomentosum. Fructus imperfecte cognitus, probabiliter globosus, 55 × 60 mm, sine lobis calycis persistentibus. Semina trigona in sectione transversali, 22 × 21 mm, sine caruncula vel funiculo.

Type. *Gentry 9318* (holotype, MO 2272189; isotypes, NY, others to be distributed). Colombia. Chocó: Upper Río Truandó, La Teresita (INDERENA camp), alt ca 100 m, 18 Jan 1974 (fl).

Distribution. Known only from the departments of Antioquia and Chocó, Colombia.

COLOMBIA. Antioquia: Between Villa Arteaga and Chigorodó, El Tigre, 100 m alt, 1 Oct 1961 (fl), *Cuatrecasas & Willard 26134* (COL); carretera al mar cerca de Villa Arteaga, 150 m alt, *Hodge 6971* (US), 6 Dec 1948 (fl), *López & Sánchez sn* (US).

The distinguishing features of this species are 1) the subsessile to short-petiolate, relatively small, serrulate or serrate leaves grouped in 1 or 2 tightly compacted verticils at the branch ends, 2) the axillary or less frequently cauline inflorescences, and 3) the rose to red or purple petals.

Other species of *Gustavia* from extreme northwestern Colombia either have longer leaves *(G. excelsa, G. gracillima, G. grandibracteata, G. monocaulis, G. superba),* longer and more distinct petioles *(G. latifolia, G. nana, G. romeroi, G. santanderiensis),* suprafoliar inflorescences *(G. dubia, G. grandibracteata, G. longifuniculata, G. monocaulis, G. santanderiensis, G. sessilis, G. verticillata),* winged hypanthia and 6 instead of 4 calyx lobes *(G. dubia, G. longifuniculata),* or 12 or 18 petals instead of 8 *(G. romeroi).*

25. Gustavia poeppigiana Berg, Mart. Fl. Bras. **14**(1): 471. 1858. Fig 53.

Gustavia augusta Linnaeus var *conferta* Berg, Mart. Fl. Bras. **14**(1): 471. 1858. Type. *Spruce 1165* (BM, M). Brazil. Amazonas: Between Santarém and Manaus, without date (fl).

Gustavia poeppigiana Berg var *opaca* Berg, Mart. Fl. Bras. **14**(1): 471. 1858. Type. *Poeppig 2658* (F, W). Brazil. Amazonas: Ega (= Tefé), Oct 1831 (fl).

Gustavia poeppigiana Berg var *nitens* Berg, Mart. Fl. Bras. **14**(1): 471. 1858. *ex char.* Type. Brazil. Amazonas: Rio Solimões, Oct, no other information given by Berg.

Gustavia conferta (Berg) Miers, Trans. Linn. Soc. London **30**(2): 178. 1874.

Japarandiba poeppigiana (Berg) O. Kuntze, Rev. Gen. **1**: 240. 1891.

Gustavia ulei Pilger, Verh. Bot. Vereins Prov. Brandenburg **47**: 164. 1905. Type. *Ule 5072* (GH photo, F photo neg. no. 29169, K, MG). Brazil. Amazonas: Rio Juruá, Marary, Oct 1900 (fl).

Gustavia yaracuyensis Pittier, Bol. Ci. y Tecn. Mus. Com. Venez. **1**: 63. 1925. Type. *Pittier 6370* (US). Venezuela. Lara: Around Palmasola, in forest along the Aroa River, near sea level, 26-28 Jun 1913 (fl).

Gustavia caballoensis Macbride, Publ. Field Mus. Nat. Hist., Bot. Ser. **11**(3): 28. 1931. Type. *Williams 2240* (F). Peru. Loreto: Caballo-Cocha on the Amazon River, Aug 1929 (fl).

Trees, to 15 m tall, leaf-bearing branches 3-7 mm in diameter, the leaves tightly grouped in one to several whorls at their ends. Bark fissured, brown. Leaf blades narrowly obovate or oblanceolate, 15.5-41 × 4.5-11.5 cm, glabrous, chartaceous, with (11-)13-18(-22) pairs of lateral veins; apices short to long acuminate; bases auriculate, rounded or truncate; margins serrate to serrulate on the upper 1/2, sometimes concave towards the base. Petioles 1-12 × 2-4 mm, semi-circular in cross section. Inflorescences in axils of leaves, reduced racemes of usually 1(-3) flowers, glabrous or puberulous, the rachis very short, 1-7 mm, with persistent bracts at the base; pedicels 10-48 mm, subtended by a single ovate, oblong or lanceolate bract 2-5 × 2-4 mm and bearing at some point along the length 2 ovate or oblong bracteoles, 2-7 × 2-6 mm. Flowers 12-18 cm in diameter; calyx of 4 broadly triangular or rounded lobes, sometimes appearing as an undulate rim in older flowers, the lobes 1-5 × 6-11 mm; petals 8, widely obovate or oblanceolate, (20-)40-70(-80) × (10-)20-50 (-60) mm, rusty- or gray-pubescent in bud, puberulous at anthesis, mostly white with tinges of rose or pink outside; connate androecial base 14-20 mm in diameter, white outside, yellow inside, 10-15(-20) mm high, the outermost filaments (12-)16-22(-25) mm, all white or white at the base with pink, rose, or red at the apex; anthers 2-5 mm, yellow or cream; ovary without costae, glab-

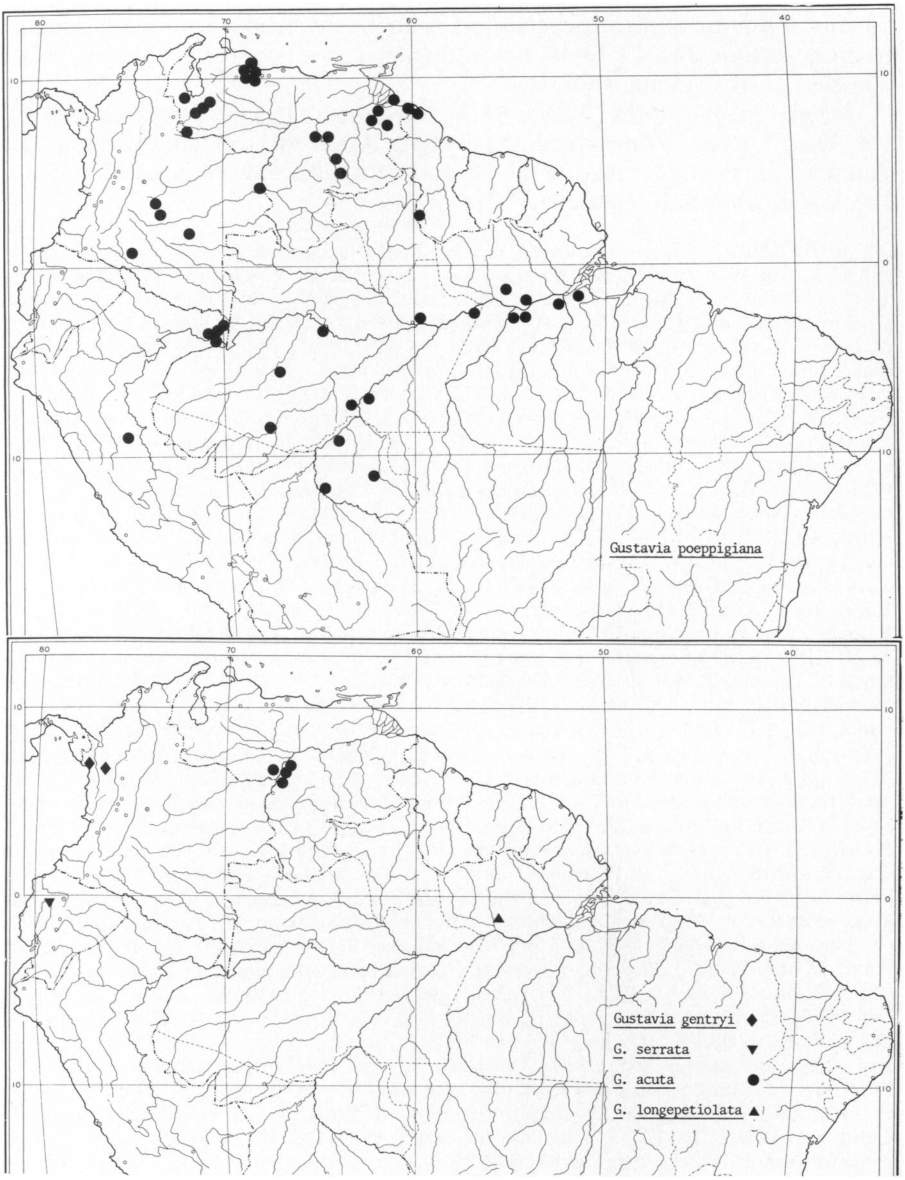


FIG 53. Distributions of *Gustavia poeppigiana, G. gentryi, G. serrata, G. acuta,* and *G. longepetiolata.*

rous to rusty-white-pubescent outside, 4-6(-10)-locular, the summit pubescent with glabrous spots to densely white-woolly throughout; style 1-3 mm; stigma with 4-6 lobes. Fruits depressed globose, 30-60×40-70 mm, with the calyx usually absent or sometimes persistent as an inconspicuous rim. Seeds rounded in cross section, 13-24×13-15 mm in diameter; with contorted, fleshy, yellow funicles 10-20×3-5 mm wide.

Type. *Poeppig 2658* (F, W). Brazil. Amazonas: Ega (=Tefé) Oct 1831 (fl).

Distribution. Widespread in western Amazonia, extending along the Amazon River east to near its mouth and with a disjunct population north of the Andes in coastal Venezuela.

COLOMBIA. Vichada: A orillas del Río Guaviare en la región de Amanabel (a bocas del río), 250 m, 23 Nov 1948 (fl), *Molina & Barkley 18 vi 112* (US). Meta: Villavicencio, alt 500 m, 19 Mar 1939 (fl), *Alston 7615* (BM); Cordillera La Macarena, trocha entre el Río Güejar y el Caño Guayapita, alt ca 500-600 m, 20-28 Dec 1950 (fl), *Idrobo & Schultes 814* (NY, US); Reserva Nacional de La Macarena, Río Guapaya, alt 400-500 m, 17 Mar 1947 (fl), *Idrobo 2441* (NY); Sierra de La Macarena, Caño Entrada, 500-600 m, 4 Jan 1950 (fl), *Philipson et al 2019* (BM, F, US). Caquetá: Cartagena, 20 Apr 1953 (fr), *Romero-Castañeda 4032* (COL). Vaupés: Forest between Itilla and Macaya rivers, alt 300 m, 1-7 Apr 1943 (fl), *Schultes 5350* (F, US). Amazonas: Entre los ríos Loretoyacu y Hamacayacu, orilla del Loretoyacu, 260 m alt Nov 1945 (fl), *Duque-Jaramillo 2071* (COL); trapecio Amazónico, 2 kms downriver from Puerto Nariño, 28 Jan-7 Feb 1969 (fr), *Plowman et al 2331* (GH); Loreto-Yacu, 2 Nov 1946 (fl), *Schultes & Black 46-296* (IAN, US); interior regions of trapecio betwen Amazon and Putumayo watersheds, alt above 100 m, without date (fr), *Schultes 6744* (COL). VENEZUELA. Falcón: Between Sanare and Mirimire, near El Alto, 1 km NW of bridge crossing the Río Tocuyo, 18 Apr 1971 (fr), *Nee & Mori 3964* (US, VEN, WIS); lado sur del Río Tocuyo, cerca de Tocuyo de la Costa, alt 100 m, 22 Jan 1966 (fl), *Steyermark 94496* (NY, US, VEN). Lara: Around Palmasola, along Aroa River, 26-28 Jun 1913 (fl), *Pittier 6370* (US). Yaracuy: Selva El Diamante-El Chorro, cerca de Sabana de Parra, 14 Dec 1953 (st), *Aristeguieta 1268* (VEN); Reserva Forestal Yaracuy, on Carretera 18 at the entrance to the forest preserve, 15 km N of Yumare, 21 Apr 1971 (fl), *Nee & Mori 3986* (US, VEN, WIS); Los Guaremales, 3 Feb 1919 (fl), *Pittier 8407* (US); between Marin and Carbonero, 11 Apr 1925 (fl), *Pittier 11772* (GH photo, NY, US, VEN). Carabobo: Guaremales, cerca de Urama, 12 Nov 1920 (fl), *Pittier 9096a* (VEN). Sucre: Península de Paría, Macuro (Cristóbal Colón), alt 100 m, 6 Apr 1964 (fl), *Beard 258* (A, MO); Península de Paría, Cerro de Humo, entre la Laguna y Roma, NW de Irapa, 5 Mar 1966 (fl), *Steyermark 95651* (NY, US). Delta Amacuro: Near the border (=Río Grande o Toro) between Estado Bolívar and Territorio Delta Amacuro (ca 61° 44’ W, 8° 44’ N), 18 Apr 1954 (fl), *Breteler 3855* (NY, US, VEN); Villa de Repata, 1864 (fl), *Grosourdy sn* (P); from region of Moron and Temiche to mouth of Río Cuyubini, alt 90 m, 21 Nov 1960 (fl), *Steyermark 87703* (NY, US, VEN); along Río Grande del Orinoco between Curiapo and Pta. Cangrejo, 10 Apr 1955 (fl), *Wurdack 313* (NY, US, VEN); Serrania Imataca, trail near Río Guanamo, 21 Nov 1955 (fl), *Wurdack & Monachino 39705* (NY). Mérida: Along Rio Onia near Bolero, north of Mesa Bolívar, alt 545-915 m, 23 May 1944 (fl), *Steyermark 56694* (F). Barinas: Reserva Forestal de Ticoporo, Feb 1969 (fl), *Aristeguieta & Zabala 6934* (VEN); along road Barinas-San Cristóbal, near village Bumbun (70° 45’ W, 80° 15’ N), 6 May 1964 (fl), *Breteler 3923* (VEN); a orillas del Río Socopo, Apr 1942 (fr), *Lasser 219* (US, VEN). Apure: Reserva Forestal San Camilo, vecindades del Chiricoa, 9-10 km al este del caserío San Camilo (El Nula), 1 Apr 1968 (fl), *Steyermark 101698* (NY, VEN). Bolívar: Río Paragua, between La Paragua and Salto de Auraima, alt 260-270 m, 9 Apr 1943 (fl), *Killip 37322* (A, NY, US, VEN); Altiplanicie de Nuria, on trail between El Cruzero and slightly beyond pica 101, ESE of Villa Lola, alt 1000 ft, 15 Jul 1960 (fr), *Steyermark 86360* (VEN); Cerro Cotorra (El Vigia), along south side of Río Paragua between La Paragua and San Pedro de Las Bocas, alt 600 m, 5 Aug 1960 (st), *Steyermark 86896* (VEN); Río Caura, below Salto de Para, 14 Mar 1939 (fr), *Williams 11516* (F, US, VEN). Amazonas: Mavaca: Alto Orinoco, Jan 1970 (fr), *Aristeguieta 7410* (NY, VEN). GUYANA. Hosororo: NW District, 18 Jul 1934 (fl), *Archer 2348* (US); upper Rupununi River, near Dadanawa, 29 May 1922 (fl), *De La Cruz 1393* (NY, US). PERU: Loreto: Pampas del Sacramento, Jun 1847 (fl), *Castelnau sn* (P); Caballo-Cacho on the Amazon River, 6 Aug 1929 (fl), *Williams 2152* (F). BRAZIL. Amazonas: Serra de Parintins, 15 Sep 1907 (fl), *Ducke 8731* (MG); Mun. Humaitá, near Tres Casas, 14 Sep-11 Oct 1934 (fl), *Krukoff 6153* (A, MO, NY, US); São Paulo de Olivença, near Palmares, 11 Sep-26 Oct 1936 (fl), *Krukoff 8367* (A, F, NY); Km 21 Rodovia Itacoatiara-Manaus, Rio Urubu, 7 Nov 1963 (fl), *Oliveira 2860* (IAN); Tefé, 20 Oct 1948 (fl), *Pires 1326* (IAN); Bôca do Acre, Rios Purus and Acre, 24 Sep

1966 (fl), *Prance et al 2523* (NY, VEN); Municipio de Silves, Praia de Mucajatuba, 30 Nov 1956 (st), *Rodrigues 275* (WIS); falls of the Madeira, Oct 1886 (fl), *Rusby 656* (F, GH, NY, PH, US); between Santarém and Manaus, without date (fl), *Spruce 2658* (BM, F, W); Paraná mirim do ramos, Rio Negro, without date (st), *Spruce 1101* (BM). Pará: Belterra, 15 Oct 1947 (fl), *Black 47-1684* (IAN); Rio Branco de Obidos, Rio Tucandeira, 16 Dec 1913 (fr), *Ducke 15154* (MG); Monte Alegre, Colônia Japonesa, Assaizal, 23 Sep 1953 (fl), *Fróes 30324* (IAN); Taperinha, Paraná do Ituqui, região do Planalto de Santarém, 5 Nov 1954 (fl), *Fróes 31151* (IAN); Rio Xingu, em frente Souzel, mun. Porto Moz, 18 Nov 1955 (fl), *Fróes 32341, 32375, 32383* (IAN); Gurupá, Rio Amazonas, 3 Nov 1929 (fl), *Killip & Smith 30620* (NY, US). Rondônia: Vida Nova, 20 Sep 1962 (fl), *Duarte 7209* (WIS); between Nova Vida and Rondonia along Porto Velho-Cuiabá highway, Sep 1963 (fl), *Maguire et al 56776* (NY); Guaporé, Rio Yata, 12 Aug 1952 (fr), *Silva 369* (IAN). BOLIVIA. Pando: W. bañk of Río Madeira, 12 km above Abunã, 20 Jul 1968 (fl), *Prance et al 6212* (NY); opposite Abunã, 19 Nov 1968 (fr), *Prance et al 8648* (INPA, NY).

Ecology. An understory tree found near sea level to 800 meters. It is most common at lower elevations in well drained forest *(terra firme)* but occasionally comes from forests that are periodically inundated *(várzea).*

This species is most closely related to *G. augusta* from which it differs by a somewhat auriculate instead of acute leaf base and an axillary inflorescence with a reduced rachis and usually one flower instead of a suprafoliar or cauline inflorescence with a developed rachis and more than one flower. In addition, the habitat preference of the two species is different; *G. augusta* prefers riverine habitats and is seldom found on *terra firme,* whereas *G. poeppigiana* prefers *terra firme* and is infrequently found in *várzea.*

Local names. COLOMBIA. Matamata *(Duque-Jaramillo 2071).* VENEZUELA. Guatoso *(Williams 11516, 11538);* Margo *(Breteler 3855).* PERU. Chopé *(Williams 2430).* BRAZIL. Geniparana *(Black 47-1684, Silva & Souza 2414, Krukoff 6192, Ule 5072).*

26. **Gustavia longepetiolata** Huber, Bull. Soc. Bot. Genève, ser. 2, 6: 191. 1915. Fig 53.

Tree, very small; leaf-bearing branches 4 mm in diameter, the leaves scattered at their ends; petiole scars widely separated. Leaf blades oblanceolate, 16-18 × 5-7 cm wide, glabrous, chartaceous, with 12-13 pairs of lateral veins; apices acuminate; bases attentuate, decurrent; margins minutely serrulate. Petioles 20-30 × 2.5 mm thick, semi-circular in cross section. Inflorescences cauline, arising low on trunk, racemose, puberulous, with 4 flowers, the rachis 14 mm; pedicels 15 mm, subtended by a single triangular basal bract 3 × 3 mm and bearing near the base of the ovary 2 triangular, acute bracteoles 4 mm long. Flowers 10 cm in diameter; calyx of 5 broadly triangular lobes, 2.5 × 5 mm; petals (5-)6, narrowly obovate or spathulate, 40 × 15-20 mm, puberulous at anthesis, white; outermost filaments 12 mm; anthers 2-2.5 mm; ovary gray-tomentose outside, tomentose at summit. Fruits unknown.

Type. *Ducke MG 7965* (holotype, R). Brazil. Pará: Rio Cuminá-mirim, ad locum "Padras," 14 Dec 1906 (fl).

Distribution. A poorly known species represented only by the type.

Gustavia longepetiolata is distinguished by its small stature and cauline inflorescences which arise a short distance from the ground. The pubescent androecial base and filaments also help to separate this from other small leaved Amazonian species, i e *G. acuta, G. elliptica, G. hexapetala,* and *G. serrata.*

27. Gustavia serrata Mori, sp nov Fig 53.

Arbor, folia ad apicem ramorum gracillum laxe aggregata; rami infra folia 5 mm diametro. Laminae angustae ellipticae vel oblanceolatae, apice acuminatae, basi acutae, 20-27 × 5-7.5 cm, marginibus serratae, glabrae, paribus venarum lateralium 19-20. Petioli 15-22 mm. Inflorescentiae caulinae, racemosae, floribus 3, rhachidi 10 mm, pubescenti; pedicelli 25-30 mm, dense tomentosi, bractea caduca et 2 bracteolis 2 × 2 mm supra medium insertis suffulti. Flores albi et rosei (fide *Dodson et Thien 1766);* calycis lobi 4, non profundi, late rotundati 1 × 9-11 mm, fere nulli; petala 8; androecii basis connata 8-10 mm alta; filamenta externa 18-20 mm; antherae 2.2 mm; ovarium indistincte 4-costatum, extus tomentosum, ad apicem sparse albo-tomentosum, 4-loculare, ovulis in quoque loculo 12-14; stylus 1.8 mm; stigma 4-lobatum. Fructus ignotus.

Type. *Dodson & Thien 1766* (holotype, WIS). Ecuador. Manabi: Road from Chone to Pichincha, km 82, alt 450 m, 29 Dec 1961 (fl).

Distribution and ecology. Known only from the type locality where it grows in tropical rain forest (fide *Dodson & Thien 1766).*

This is the only species of *Gustavia* with the combination of cauline inflorescences, medium sized leaves with serrate margins, and ovaries with 4 obscure costae. The specific epithet refers to the serrate leaf margins.

28. Gustavia acuta Mori, sp nov Fig 53.

Arbores usque ad 15 m altae; folia aggregata ad apicem ramorum; rami infra folia 5-9 mm diametro. Laminae ellipticae vel anguste ellipticae, apice acutae, basi acutae vel obtusae, 20-27 × 4-8.5 cm, marginibus integrae vel serrulatae, plerumque glabrae, paribus venarum lateralium 15-23. Petioli 5-20 mm, in sectione transversali semicirculares. Inflorescentiae caulinae, racemosae, floribus 1-5, rhachidi 10-45 mm; pedicelli 25-35 mm, pubescentes, bractea 3 × 2-4 mm et ad vel supra medium bracteolis 2 ovatis 2-3 × 2-4 mm insertis suffulti. Flores 12-16 cm diametro; calyx plerumque integer, infrequenter lobis 4 late rotundatis 4 × 8 mm constans; petala 8, anguste obovata vel oblonga, 55-78 × 30-35 mm, alba; androecii basis connata 15-20 mm alta; filamenta externa 15-20 mm; antherae 3-3.5 mm; ovarium plerumque ecostatum vel infrequenter indistincte 4-costatum, pubescens, 4-loculare, ad apicem albotomentosum; stylus (1.5-)3-3.5 mm; stigma 4-lobatum. Fructus ignotus.

Type. *Wurdack & Monachino 41336* (holotype, NY). Venezuela. Apure: Río Cinaruco between mouth and Las Galeras de Cinaruco, alt 60-90 m, 23 Jun 1956 (fl).

Distribution. Known only from the Río Orinoco especially between the mouths of the Ríos Apure and Meta.

VENEZUELA. Bolívar: Alrededores Laguna Los Francos, Ciudad Bolívar, Apr 1954 (fl), *Aristeguieta 2159* (NY); La Urbana, 27 Feb 1949 (fl), *Maguire & Maguire 28988* (NY); Río Parguaza between El Carmen and Raudal Maraca (50-100 km from river's mouth), alt 110-115 m, 1 Jan 1956 (fl), *Wurdack & Monachino 41053* (NY), *41068* (NY); northernmost slopes of Cerro Baraguan, 13 Jan 1956 (fl), *Wurdack & Monachino 41226* (NY); Río Suapure between mouth and Los Aceites (35 km upstream), 22 Jan 1956 (fl), *Wurdack & Monachino 41329* (NY).

This species appears to be most closely related to *G. augusta* from which it differs by having elliptic, mostly entire, acute leaves instead of oblanceolate, serrate to serrulate towards the apex, acuminate leaves and cauline inflorescences instead of mostly suprafoliar ones. Observations of the funicle of *G. acuta* are needed to confirm this species' relationship with *G. augusta* which has a distinctive, tortuous, yellow funicle.

The specific epithet refers to the acute leaf apices.

29. Gustavia gracillima Miers, Trans. Linn. Soc. London **30**(2): 180-181. 1874; Hooker, J. D., Bot. Mag. **101:** *t 6151.* 1875. Fig 52.

Japarandiba gracillima (Miers) Niedenzu in Engler & Prantl, Nat. Pflanzenfamilien 3(7): 37. 1892.

Trees, small, slender; leaf-bearing branches 5-7 mm in diameter, with the leaves densely congested at their ends. Leaf blades very narrowly elliptic to narrowly oblanceolate, 25-46 x 2-3.5 cm, glabrous, chartaceous, with 22-29 pairs of lateral veins; apices acuminate or attenuate; bases long and narrowly cuneate; margins distinctly serrulate. Petioles slender 20-50 x 2 mm, subterete in cross section. Inflorescences axillary or cauline, pubescent, the rachis short; pedicels 15-50 mm, subtended by a single oblong basal bract 5 x 2 mm and bearing near the middle 2 oblong to lanceolate bracteoles 5-6 x 2-3 mm. Flowers 10 cm in diameter; calyx with 4 rounded to broadly obtuse lobes, 2.5-8 mm; petals 8, narrowly obovate or oblanceolate, 45 x 23 mm, puberulous at anthesis, pink or purple; connate androecial base 15 mm in diameter, 12 mm high, yellow, the outermost filaments 18 mm, dark purple; anthers 2.5 mm, yellow; ovary without costae, pubescent, 4-locular, the summit densely white-woolly; style 1.5 mm; stigma with 4 lobes. Fruits and seeds unknown.

Type. *Purdie sn* (lectotype, K, here designated; isolectotype, BM). Colombia. Antioquia: Woods of Carmen, Jul 1845 (fl).

Distribution. This species is native to western Colombia but has been cultivated at the Singapore botanical garden and in a greenhouse at Chelsea, England.

SINGAPORE. Cultivated in the botanical garden, Jun 1929 (fl), *FHO sn* (OXF). COLOMBIA. Río Magdalena 28 May 1879 (fl), *Kalbreyer 1224* (K). Nariño: Province of Barbacoas, alt 1200 M, May 1853 (st), *Triana sn* (BM).

The very narrow leaves of this species are unique in *Gustavia.*

30. Gustavia foliosa Cuatrecasas, Fieldiana, Bot. **27**(2): 96. 1951. Fig 52.

Trees, to 20 m x 40 cm. Leaf blades obovate or oblanceolate, 15-57.5 x 18.5 cm, glabrous, with 18-24 pairs of lateral veins, the apices short acuminate, the bases acute or cuneate, the margins entire. Petioles 15-105 x 5 mm. Inflorescences axillary or in the axils of leaf scars just below the leaves, solitary, without a rachis; pedicels 75-95 mm, bearing above the middle 2 lanceolate bracteoles 6.5 x 2 mm. Flowers 10-16 cm in diameter; calyx subentire or with 4 shallow, rounded lobes; petals broadly obovate, rounded or subtruncate at the apex, 50-60 x 30-45 mm, whitish-pink to pale violet or red on the outside, white inside; androecium 35 mm in diameter, yellowish-white, the connate base 12-13 mm high, the outermost filaments 10-18 mm, puberulous, the anthers 2.5-4 mm, yellow. Fruits globose, unknown at maturity. Seeds without well developed arils.

Type. *Cuatrecasas 14394* (holotype, F; isotype, COL). Colombia. Valle: Cordillera occidental, hoya del Río Anchicayá, lado derecho, bosques entre Pavas y Miramar, 350-450 m alt, 16 Apr 1943 (fl).

ECUADOR. Esmeraldas: Río San Miguel, 28 Mar—6 Apr 1959 (fl & young fr), *Harling 4691* (S).

This species is characterized by its solitary flowers in the axils of the leaves or leaf scars.

31. Gustavia pulchra Miers, Trans. Linn. Soc. London **30**(2): 182-183. 1874. Fig 54.

Trees, to 18 m; leaf-bearing branches 5-12 mm in diameter, somewhat arching upwards, the leaves tightly grouped at their ends. Bark smooth, gray. Leaf blades narrowly oblanceolate or oblanceolate, 30-61 x 6-13 cm, glabrous, chartaceous to semi-coriaceous, with 21-29 pairs of lateral veins; apices acute or attentuate; bases acute; margins nearly entire to finely serrulate, slightly revolute. Petioles 2-40 x 3-5 mm, semi-circular in cross section, sometimes puberulous. Inflorescences cauline, racemose, rusty-tomentose, with 1-7 flowers, the rachis 15-100 mm; pedicels 25-55 mm, with small horizontal groove-like markings below the bracteoles, subtended by a single oblong or ovate bract 3-5 x 2-4.5 mm and bearing at or above the middle 2 ovate, cucullate bracteoles 2-4 x 2-4 mm. Flowers 12.5-14 cm in diameter; calyx with (5-)6 (-7) triangular lobes, 2-3.5 x 4-8 mm, rusty-pubescent; petals (7-)8(-10), narrowly obovate, 60-70 x 25-30 mm, densely rusty-pubescent in bud, puberulous at anthesis, white with flushes of pink on the outside; connate androecial base 18-26 mm high, the outermost filaments 13-18 mm, cream or yellow at base, pink apically; anthers 3-4 mm, yellow; ovary obscurely 4-6-costate, rusty-pubescent, 6-locular, white-woolly at summit; style conical, 2-3 mm; stigma with (5-)6 lobes. Fruits cylindrical, with a distinct constriction below the calycine rim, obscurely costate, 40-55 x 35-45 mm in diameter, without persistent calyx lobes. Seeds rounded in cross section, 20-22 x 10-15 mm in diameter, ca 4 per fruit, with a fleshy yellow funicle to 21 x 6 mm.

Type. *Spruce 1933* (lectotype, K, here designated; isolectotypes, BM, K, P). Brazil. Amazonas: Rio Uranacuá, Dec 1851 (fl).

Distribution. This species is confined to the upper Orinoco and middle to upper Rio Negro watersheds.

VENEZUELA. Amazonas: Serrania Parú, Río Ventuari, Caño Asisa below rapids to junct.

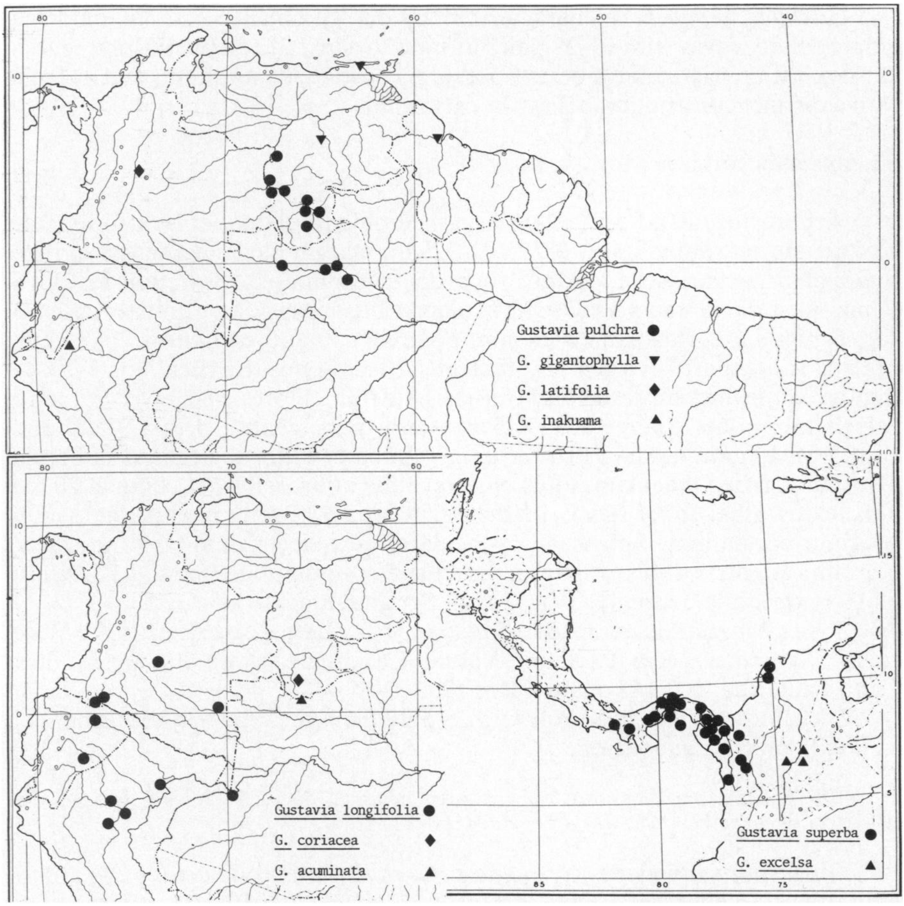


FIG 54. Distributions of *Gustavia pulchra, G. gigantophylla, G. latifolia, G. inakuama, G. longifolia, G. coriacea, G. acuminata, G. superba,* and *G. excelsa.*

with Río Parú, thence down Parú to mouth, 18 Feb 1951 (fl), *Cowan & Wurdack 31549* (NY); La Esmeralda, Jan-Feb 1969 (fl), *Fariñas & Velasquez 291* (VEN); Río Casiquiare between Piedra Lais and Caño Pamoni, 150 m alt, 1 Apr 1953 (fl), *Maguire & Wurdack 34769* (NY); Caño Cupueni at mouth of Río Atabapo, right bank of Río Orinoco, 16 Feb 1954 (fl), *Maguire et al 37681* (NY); Alto Río Negro, Vaupés, 14 Jan 1960 (fl), *Rodrigues & Coêlho 1464* (INPA); Puerto Ayacucho, alt 100 m, 18 May 1940 (fr), *Williams 12996* (F, US, VEN); San Carlos de Río Negro, alt 100 m, 28 Feb 1942 (fr), *Williams 14530* (F, US, VEN); Tamatama, Upper Orinoco, 9 May 1942 (fr), *Williams 15280* (F, US, VEN). BRAZIL. Amazonas: Providencia, Rio Negro, 12 Feb 1944 (fl), *Baldwin 3450* (IAN); Pôrto Cabray, Rio Negro, 4 Dec 1945 (fl), *Fróes 21489* (IAN, NY); Rio Negro between Ilha Uabetuba and Ilha da Silva, 14 Oct 1971 (fr), *Prance et al 15237* (INPA, NY, WIS); Rio Casiquiare, Jan 1853 (fl), *Spruce sn* (P); Rio Negro, Dec 1851 (fl), *Spruce 1934* (P); secus Rio Negro inter Barcellos et San Isabel, Dec 1851 (fl), *Spruce 1935* (BM).

Ecology. A common tree in the forests of periodically inundated river bottoms at elevations less than 200 meters. It flowers from December to April. Mature fruits have been collected in April, May and October.

Gustavia pulchra is characterized by its 1) oblanceolate to narrowly oblanceolate leaves with 21-29 pairs of lateral veins, 2) cauline inflorescences, 3) calyx with 6 triangular lobes, 4) obscurely costate hypanthium, and 4) fruits with a distinct constriction below the calyx rim.

32. **Gustavia coriacea** Mori, sp nov Fig 54.

Arbores usque ad 5 m altae. Laminae oblanceolatae, apice acuminatae, basi acutae vel rotundatae, 70-71 × 21-22 cm, marginibus integrae leviter revolutae, glabrae, coriaceae, paribus venarum lateralium 25-28. Petioli 15-21 × 8-9 mm, in sectione transversali semicirculares. Inflorescentiae caulinae, racemosae, floribus 2-3, rhachidi 20-25 mm; pedicelli sub anthesi lignosi, 65-75 mm, bractea triangulari 7 × 8 mm et bracteolis 2, suboppositis, cucullatis 3-7 × 4-7 mm ad vel leviter supra medium insertis suffulti. Flores 17-20 cm diametro; calycis lobi 4 late triangulares, 4-5 × 14 mm, pubescentes; petala 9 late obovata, 80 × 45 mm, in alabastro ferrugineo-pubescentia, sub anthesis puberula, extus alba, roseo-maculata, intus omnino alba; androecii basis connata 20 mm alta, extus alba, intus flava; filamenta externa 24-27 mm; antherae 3 mm; ovarium ecostatum, pubens, 4(-5)-loculare, ad apicem albo-lanatum; stylus 0.5 mm; stigma 4 lobis ornatum. Fructus e speciminibus immaturis cogniti, globosi, operculo depresso, 34 × 51 mm. Semina funiculo instructa.

Type. *Maguire et al 36505* (holotype, NY sheet 2; isotype, NY). Venezuela. Amazonas: Río Pacimoni-Yatua, Casiquiare along Río Yatua near Caño Tauavaca, 100-140 m alt, 4 Dec 1953 (fl).

Distribution. This species is known only from the type and one other collection from the same region.

VENEZUELA. Amazonas: Río Yatua between mouth of Río Yaciba and Piedra Arauicaua, 100-140 m alt, 1 Feb 1954 (fr), *Maguire et al 37421* (NY).

Gustavia poeppigiana, G. augusta, G. pulchra, and *G. acuminata* are the only other large-leafed species of *Gustavia* sympatric with *G. coriacea.* This new species is distinct from the first by its cauline instead of axillary inflorescences, from the second by its 25-28 instead of 14-22 pairs of lateral veins and its more robust flowers, from the third by its 4 instead of 6 calyx lobes, and from the fifth by its petiolate leaves.

The closest relative to *G. coriacea* is probably *G. longifolia* from which it differs by having fewer lateral veins. If additional collections show that the two are sympatric the former may have to be brought into synonymy with the latter.

32. **Gustavia inakuama** Mori, sp nov Figs 54, 55.

Arbores parvae, monocaules, usque ad 2 m altae; rami infra folia 15-25 mm diametro; folia in 1 ad 2 dense congestis verticillis 20-50 mm inter se distantibus, 14-20 in quoque verticillo. Laminae oblanceolatae, apice in speciminibus visis laesae, longe contractae versus basim, basi acutae, 63-80 × 13-18 cm, glabrae, marginibus integrae, paribus venarum lateralium 25-27. Petioli 40-60 mm, in sectione transversali semicirculares. Inflorescentiae caulinae, infra vel inter verticillos foliorum orientes, racemosae, floribus 2-3, rhachidi 15-

35 mm; pedicelli 50-65 mm, ± glabri, ad apicem curvi, singula bractea 2.5-4 mm longa et 2 bracteolis 2-3 × 2.5 mm ad vel infra medium insertis suffulti. Flores ca 12 cm diametro, verticaliter ordinati; calyx integer, 2.5 mm latus; petala dilute purpurea, albo-guttata, ungiculata, spathulata, 52 × 27 mm; androecii basis connata 10 mm alta; filamenta externa ca 15 mm; antherae 2.5 mm; ovarium ecostatum, extus glabrum, ad summum dense albo-tomentosum; stylus brevis vel subnullus; stigma 4-lobatum. Fructus globosus. Semina sine funiculis distinguibilibus.

Type. *Berlin 761* (holotype, MO 2272926). Peru. Amazonas: Above mouth of Quebrada Chigkán Entsa, N of Río Cenepa, alt 800-900 fr, 30 Dec 1972 (fl).

Distribution. This species is known only from the vicinity of the type locality in northeastern Peru.

PERU. Amazonas: Between Río Cenepa and Quebrada Kayamas, 7 Dec 1972 (fl), *Berlin 495* (MO); Río Cenepa, ridge above Quebrada chikisnuk throat, a tributary of Huampami, entering from S about 5 km from confluence with Cenepa, 21 Dec 1972 (fl), *Berlin 656* (MO); Quebrada Yutui Entsa, monte al lado de Cenepa, 22 Jan 1973 (fr), *Kayap 194* (MO); Quebrada Kayamas, monte al lado de Kayamas, 3 Mar 1973 (fr), *Kayap 443* (MO), alrededor de la comunidad Kusu, Río Numpatkin, 10 Mar 1973 (fr), *Kayap 513* (MO).

The closest relative of *G. inakuama* is *G. longifolia*. However, the new species differs from the latter by having the hypanthium smooth and glabrous instead of obscurely 4-costate and densely rusty tomentose and by having an entire calyx instead of one with 4 lobes. *Gustavia inakuama* produces several to many inflorescences directly below the verticils of leaves whereas those of *G. longifolia* are scattered on the stem and do not form a close association with the leaves.

Because the leaf verticils of *G. inakuama* are usually persistent through several growth flushes the flowers are often hidden among the leaves. In addition, the pedicels are curved in such a way that the flowers are vertically oriented (Fig 55) in contrast to the horizontal orientation of most species of *Gustavia.* The interfoliar flowers suggest that some group of non-flying insect, such as ants, may be the pollinator. The unusual vertical orientation of the flowers may provide more ready access to the flower by non-flying insects or may simply be a response to crowding by the leaves.

The specific epithet refers to the common name, inakuam, given to the plant by the Aguaruna Jivaro Indians of north central Peru. Their common name means "inak-like." Inak is an undescribed species of *Gustavia,* represented by an incomplete specimen *(Ancuash A139),* which is reputed to have edible fruits and, although not cultivated, is protected by the Aguaruna Jivaros (Berlin, pers. comm.). There are no known uses of *G. inakuama* (Berlin, pers. comm.).

34. **Gustavia acuminata** Mori, sp nov Figs 54, 56.

Arbor, 10 m alta × 10 cm diametro; folia ad apicem ramorum conferta, cicatricibus petiolorum inter se contiguis; rami infra folia 14 mm diametro. Laminae sessiles, oblanceolatae, apice longe acuminatae, 58-70 × 11-14 cm, marginibus minutae serrulatae, glabrae, chartaceae, paribus venarum laterali-

FIG 55. *Gustavia inakuama (Berlin 656).* Photo by Brent Berlin.

um 40. Inflorescentiae caulinae, racemosae, glabrae vel minute puberulae, floribus 5-7, rhachidi 15 mm; pedicelli 30 mm, bractea late triangulari 2×4 mm et bracteolis 2 anguste ovatis 2.5×2 mm paullo infra medium insertis suffulti. Flores ca 8 cm diametro; calycis lobi 4, late triangulares, 2×11 mm, puberuli, rosei; petala 8, 40×17 mm, in alabastro pubescentia, sub anthesi puberula, cremea; androecii basis connata 12 mm alta; filamenta externa 10 mm, pallide flava; antherae 2.5 mm, flavae; ovarium 4-loculare, extus puberulum, ad apicem albo-lanatum; stylus 1 mm; stigma 4-lobatum. Fructus ignotus.

Type. *Silva & Brazão 60944* ((holotype, NY). Brazil. Roraima: Serra Pirapucú, 1250-1300 m alt, 29 Jan 1966 (fl).

Distribution. This species is known only from the type.

Ecology. The type comes from "high forest" on *terra firme* at an elevation between 1250-1300 meters.

No other species of *Gustavia* in section *Gustavia* with cauline inflorescences has sessile leaves. This new species also has leaves with a longer acuminate apex than any other species of *Gustavia,* a feature alluded to in the specific epithet.

35. **Gustavia longifolia** Poeppig ex Berg, Mart. Fl. Bras. **14**(1): 472. 1858. Fig 54.

Japarandiba longifolia (Poeppig ex Berg) O. Kuntze, Rev. Gen. **1**: 240. 1891.

Japarandiba spruceana Ule in Karsten & Schenck, Vegetationsbilder Reihe 2, Heft 1, tafel 1. 1904. Type. *Ule 6302* (MG photo, F). Peru. Loreto: Yurimaguas, 2 Aug 1902 (fl).

Gustavia mangua Macbride, Publ. Field Mus. Nat. Hist., Bot. Ser. **11**: 29. 1931. Type. *Williams 281* (holotype, F). Peru. Loreto: Lower Río Nanay, May-Jun 1929 (fl).

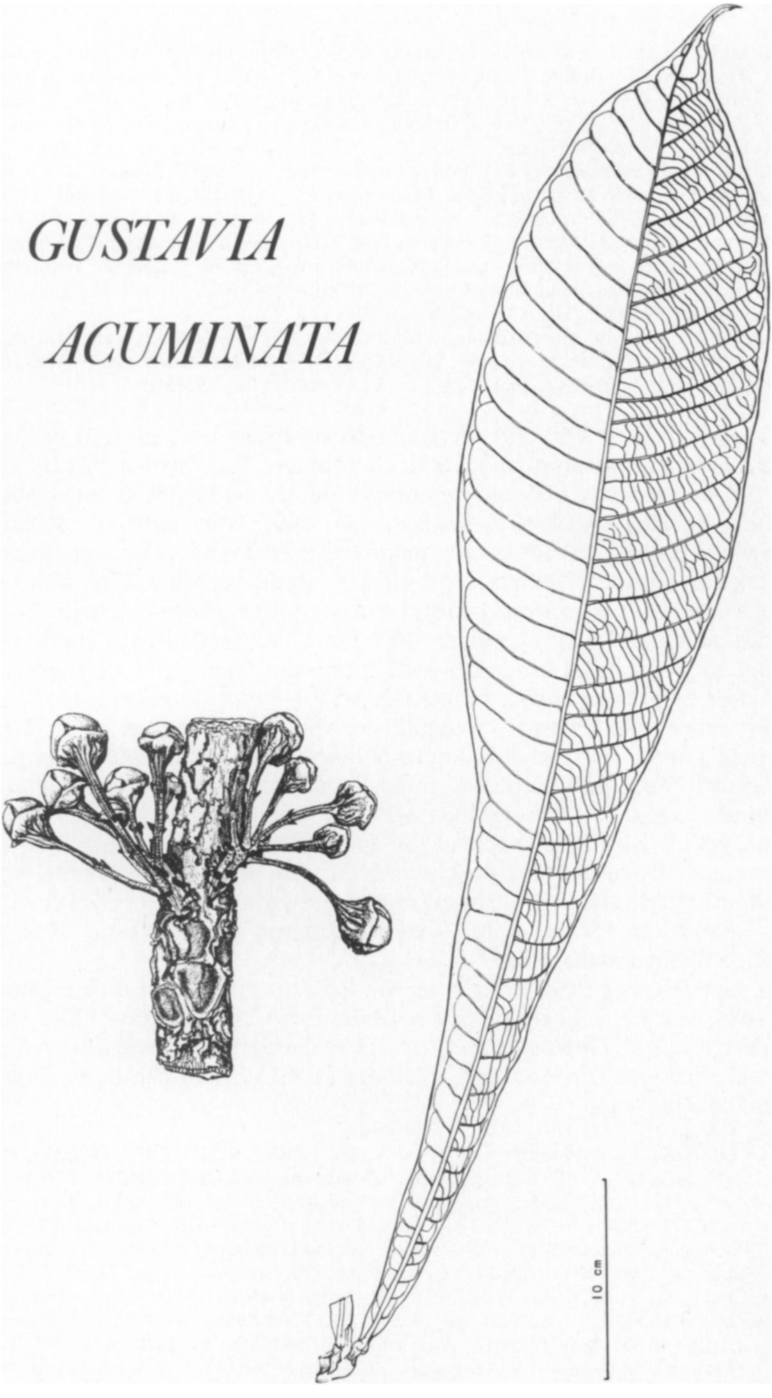


FIG 56. Leaf and inflorescence of *Gustavia acuminata (Silva & Brazão 60944).*

Gustavia iquitosensis R. Knuth, Repert. Spec. Nov. Regni Veg. **35:** 338. 1934. *ex char.* Type. *Tessmann 3645* (B fide Knuth, probably not extant). Peru. Loreto: Iquitos, Jun 1924 (fl).

Gustavia tessmannii R. Knuth, Repert. Spec. Nov. Regni Veg. **35:** 338. 1934. *ex char.* Type. *Tessmann 4574* (B fide Knuth, probably not extant). Peru. Loreto: At the mouth of the Santiago River, 1924 (fl).

Gustavia spruceana Berg ex R. Knuth in Engler, Pflanzenreich IV. **219a:** 27. 1939.

Gustavia duckei R. Knuth in Engler, Pflanzenreich IV. **219a:** 28. 1939. *ex char.* Type. *Ducke sn* (B fide Knuth, probably not extant). Brazil. Amazonas: On Rio Javari, 1939 (fl).

Gustavia magna Cuatrecasas, Fieldiana, Bot. **27**(2): 93-94. 1951. Type. *Cuatrecasas 11164* (lectotype, F 1358471, here designated; isolectotype, F, US). Colombia. Putumayo: Selva higrofila del Río Sucumbíos or San Miguel, entre la Quebrada de la Hormiga y San Antonio de Guamués, alt ± 330 m, 18 Dec 1940 (fl).

Gustavia dumitiana García-Barriga, Mutisia **12:** 4-7, *t 6-7.* 1952. Type. *García-Barriga 14000* (holotype, COL; isotypes, GH, NY, US). Colombia. Amazonas-Vaupés: Río Apaporis, entre los ríos Kananarí y Pacora, alt 450 m, 1-5 Dec 1951 (fl).

Trees, to 30 m × 50 cm, the leaf-bearing branches 7-20 mm in diameter, the leaves in one or more clusters at their ends. Bark brown, nearly smooth. Leaf blades narrowly obovate or oblanceolate, 40-120 × 8-38 cm, glabrous or minutely puberulous on the abaxial veins, with 27-49 pairs of lateral veins, narrowly tapered to an acute or cuneate base; apices acute or acuminate; margins entire, minutely serrulate or serrate. Petioles 5-90 × 4-15 mm, usually semicircular in cross section. Inflorescences cauline, racemose, with 5-16 flowers, the rachis 15-70 mm; pedicels 30-70 mm, subtended by a single ovate to oblong, rounded basal bract 2.5-6 × 2-5 mm and bearing at or slightly below the middle 2 ovate, cucullate bracteoles 2-5 × 2-8 mm. Flowers 6-16.5 cm in diameter; calyx with 4 broadly triangular or shallowly rounded lobes, 2-4 × 6-18 mm; petals 8(-9), narrowly oblong to oblanceolate, 30-80 × 10-45 mm, densely pubescent in bud, puberulous at anthesis, pale purple to dark red, sometimes rose-pink; connate androecial base 6-20 mm high, the outermost filaments 12-25 mm, yellow with pale purple at the apex; anthers 2-5 mm; ovary often with 4 costae, usually rusty-tomentose on the outside, 4(-6) locular, white-woolly at the summit; style short, 1-1.5 mm, conical; stigma with 4 lobes. Fruits imperfectly known, to 75 mm long. Seeds angular in cross section, 30 × 20 mm, without a distinctive funicle.

Type. *Poeppig 2094* (lectotype, W; isolectotypes, A photo, F photo neg. no. 31635, W). Peru. Loreto: "Sylvae obscuris ad Yurimaguas," Dec 1830 (fl).

Distribution. *Gustavia longifolia* is endemic to west central Amazonia. Several collections *(Fróes 22246, Loureiro et al INPA 37801)* come from as far east as the Rio Negro.

COLOMBIA. Putumayo: Umbría, 0° 54' N, 76° 10' W, alt 325 m, Dec 1930 (fl), *Klug 1880* (BM, G, GH, MO, NY, WIS). Meta: Sierra de la Macarena, Caño Yerly, 450 m, 21 Nov 1949 (fl), *Philipson et al 1528* (BM, F, US); Sierra de la Macarena, Caño Entrada, 550 m, 23 Jan 1950 (fl), *Philipson et al 2202* (BM, US). ECUADOR. Napo: Road to Coca (Puerto Francisco de Orellana), oil wells of the Acua district, ca 38 km S of Coca, 10 Jan 1973 (fl), *Lugo 2593* (NY, S); Armenia Vieja at Río Napo, ca 12 km SW of Coca (Puerto Francisco de Orellana, *Lugo 2705* (NY, S). PERU. Loreto: Chambira, Yurimaguas, 14 Sep 1948 (fl), *Ferreyra 4933* (USM); Balsapuerto (lower Río Huallaga basin) alt 150-350 m, 28-30 Aug 1929 (fr), *Killip & Smith 28564* (US); Mishuyacu, near Iquitos, alt 100 m, Oct-Nov 1929 (fl), *Klug 350* (US), Feb-Mar 1930 (fl), *Klug 865* (F); above Pongo de Manseriche, mouth of Río Santiago, alt 200 m, 6 Dec 1931 (fl), *Mexia 6228a* (GH, NY); San Miguel, Yurimaguas, alt 172 m, 11 Oct 1963)fl), *Schunke 6355* (F); prov. Maynas, alto Nanay, along the trail N from Santa María de Nanay, 25 Feb 1969 (fr), *Simpson 741* (F); Nanay

Hills, May-Jun 1929 (fl), *Williams 281* (F); Yurimaguas, Jul 1902 (F), *Ule 6302* (MG); lower Río Huallaga, Oct-Nov 1929 (fl), *Williams 3941* (F). BRAZIL. Amazonas: Esperança (Bôca do Javarí), 12 Mar 1944 (fl), *Ducke 1802* (A, US); Rio Ucayali, Cauchauaya pueblo, 6 Nov 1898 (fl), *Huber 1455* (MG); Rio Negro, próximo ao Rio Arara, 27 Apr 1973 (fl), *Loureiro et al INPA 37801* (NY).

Ecology. *Gustavia longifolia* is an understory tree of *terra firme* (= well drained) forests.

All large-leafed individuals of *Gustavia* with cauline inflorescences, 4 calyx lobes, and usually more than 28 pairs of lateral veins which come from western Amazonia are considered by me to belong to this species. *Gustavia coriacea* of southern Venezuela is very closely related to *G. longifolia,* differing only in its slightly fewer pairs of lateral veins, somewhat more rounded leaf base, and more robust flowers. Another species, *G. excelsa,* of the Magdalena Valley of Colombia also has strong affinities with *G. longifolia* however it has considerably longer inflorescences.

Local names. COLOMBIA. Cocora *(Klug 1880).* PERU. Chope *(Ferreyra 4933);* Sacha-manga *(Mexia 6228a);* Chope Masha *(Schunke 6355);* Mangua *(Williams 281);* Sacha Chope *(Simpson 741);* Tripa de Pollo *(Acosta-Solis 13908).* BRAZIL. Chope *(Huber 1455),* Sachavaya *(Huber 1455).*

36. Gustavia gigantophylla Sandwith, Kew Bull. **1955:** 471. 1955. Fig 54.

Trees, unbranched or sparsely branched, to 10 m tall, the leaf-bearing branches 9-15 mm in diameter, the leaves tightly grouped at their ends. Leaf blades oblanceolate, 69-110 × 18-25 cm, glabrous, chartaceous, with 34-48 pairs of lateral veins, narrowly tapered from the middle to an acute base; apices acuminate; margins serrulate or serrate. Petioles 4-26 × 5-7.5 mm, semicircular in cross section. Inflorescences cauline, racemose, densely rusty-pubescent, with 3-6 flowers, the rachis 40-130 mm; pedicels 20-50 mm, subtended by a single caducous bract and bearing at or above the middle 2 ovate to oblong bracteoles 6-12 × 4-12 mm. Flowers 13-14 cm in diameter; calyx with 4 broadly triangular lobes, 3.5-5 × 8-14 mm, rusty-pubescent, the margins somewhat ciliate; petals 8, narrowly oblong, narrowly obovate, or oblanceolate, 50-90 × 15-33 mm, puberulous, white; connate androecial base 11-17 mm high, creamy-yellow, the outermost filaments 10-24 mm, white; anthers 2.5-3.5 mm; ovary without costae, rusty-pubescent, 7-8 locular?, the summit white-tomentose with some glabrous spots; style 2.5 mm. Fruits globose, truncate at the apex, 37-65 × 50-67 mm in diameter, without persistent calyx lobes or costae. Seeds angular in cross section, 22 × 22 mm, without distinctive funicles.

Type. *Fanshawe 4537* (= *Maguire & Fanshawe 22888)* (Lectotype, K, here designated; isolectotypes, K, US). Guyana. Essequibo River, Kamuni Creek, Groete Creek, 18 Apr 1944 (fl, fr).

Distribution. This species is known only from Guyana and northeastern Venezuela.

VENEZUELA. Sucre: Paria, Cerro de Río Arriba, oeste de Cerro Humo, al largo de Río Santa Isabel, alt 600-700 m, 9 Aug 1966 (fr), *Steyermark & Rabe 96235* (VEN). Bolívar: Río Nichare (afluente del Río Caura), abajo de la desembocadura con el Río Cicuta (Icuta), lat 6° 25' N, long 64° 50' W, alt 150 m, 24 Apr 1966 (fl), *Steyermark & Gibson 95782* (NY, US, VEN). GUYANA. Nov 1886 (fl), *Jenman 2377* (NY).

Ecology. Fanshawe, in Sandwith (1955), reports "This is a very distinct localized species apparently confined to lateritic soils. It has a very different habit from *G. augusta,* rarely branched, with this crown of very large leaves. The flowers are always cauliflorous. The tree only grows to 20 ft high and 4 in diameter, and occurs both in Mora and miscellaneous forest. The only fruit found (now in Kew Herb.) is depressed-globose, greenish, with the capitulum (sic, i e, the intracalycary zone, or the "operculum" of Miers) below the level of the top of the fruit."

Steyermark and Rabe *(96235)* have since collected the species in Sucre, Venezuela in evergreen forest at between 600-700 meters. Their collection differs from those made at lower elevations by having fewer, more widely spaced lateral veins.

Local names. VENEZUELA. Cacao Cimarrón *(Steyermark & Rabe 96235);* Cola Pava *(Steyermark & Gibson 95782).*

37. Gustavia latifolia Miers, Trans. Linn. Soc. London **30**(2): 182. 1874. Fig 54.

Japarandiba latifolia (Miers) Niedenzu in Engler & Prantl, Nat. Pflanzenfamilien 3(7): 37. 1892.

Tree, slender, to 9 m tall. Leaf blades narrowly obovate or oblanceolate, 28-41 × 11-13 cm, glabrous, chartaceous, with 17-19 pairs of lateral veins; apices abruptly acuminate; bases long cuneate; margins entire. Petioles 35-95 × 3 mm, subterete in cross section. Inflorescences cauline, contracted, racemose, rusty-tomentose, with 4-7 flowers, the rachis 12-21 mm; pedicels 35-55 mm, subtended by a single caducous bract and bearing 3/4 the distance from the base to the ovary 2 ovate, tomentose bracteoles 2-3 × 3 mm. Flowers 9-10 cm in diameter; calyx entire; petals densely pubescent in bud; connate androecial base 14-18 mm high, the outermost filaments 15 mm; anthers 2.5-3 mm; ovary without costae, rusty-tomentose, the summit pubescent in lines radiating from the style; style 1.5 mm; stigma with 4 lobes. Fruits and seeds unknown.

Type. *Hartweg 981* (lectotype, K, here designated; isolectotype, K). Colombia. Cundinamarca: At hacienda de Palmar near Guaduas, without date (fl).

Distribution. This species is known only from the type collection.

Gustavia latifolia is most closely related to *G. nana* subsp *rhodantha,* differing in its entire instead of 4-lobed calyx and long cuneate instead of usually obtuse or rounded leaf bases.

38. Gustavia superba (Kunth) Berg, Linnea **27:** 444-445. 1856; Woodson, Ann. Missouri Bot. Gard. **45**(2): 120-122, *fig 37.* 1958. Figs 1B, 6, 10A, 16E, 42B, 54.

Pirigara superba Kunth, Synops. Plant. Aeq. 3: 426. 1824. Type. Same as for *Gustavia superba* (Kunth) Berg.

Gustavia superba (Kunth) Berg var *salviniae* Hemsley, Biol. Centr. Am. Bot. 1: 413, *t 22.* 1885. Type. *Salvin 2* (K). Panama. Obispo Station, 10 May 1873 (fl).
Japarandiba superba (Kunth) O. Kuntze, Rev. Gen. 1: 240. 1891.

Trees, to 20 m × 25 cm, sparsely branched, the leaf-bearing branches 5-20 mm in diameter, often arching upwards, the leaves tightly compacted at their ends. Bark brown, slightly fissured. Leaf blades oblanceolate, 25-128 × 6-25 cm, glabrous, chartaceous, with 16-36 pairs of lateral veins, long tapered to an acute or cuneate base; apices acuminate; margins serrate. Petioles 5-150 × 1-9 mm, semi-circular in cross section. Inflorescences cauline, racemose, puberulous, with 3-12 flowers, the rachis 10-64 mm; pedicels 29-85 mm, subtended by a single ovate to oblong basal bract 1.8-4 × 1.5-5 mm and bearing at or below the middle 2 ovate, cucullate bracteoles 1-6 × 1.5-5.5 mm wide, the latter often fused at their bases to form a cup-like structure which encircles the pedicel, the cup often with inconspicuous nectaries in the axils (only easily seen in pickled young flowers). Flowers 10-15 cm in diamter; calyx entire or very slightly 4-lobed; petals (7-)8(-9), obovate, oblanceolate, or oblong, 33-67 × 12-37 mm, glabrous or puberulous, white with pink at the apex and with pink speckles throughout; connate androecial base 8-15 mm high, the outermost filaments 10-23 mm, yellow at base pink at apex; anthers 2.5-4 mm, yellow; ovary smooth, puberulous, (5-)6-locular, with 18-30 ovules per locule, puberulous at the summit; style 1-2 mm; stigma with 6(-7) lobes. Fruits globose or depressed globose, 30-90 × 40-100 mm, the opercular region sunken below the fruit surface and less than 1/2 the diameter of the fruit diameter, the calyx forming a raised, entire, circular rim, yellow at maturity; mesocarp orange. Seeds usually angled in cross section, 12-35 × 11-22 mm, without distinctive funicle. x = 34.

Type. *Humboldt & Bonpland 1411* (holotype, P; isotypes, F, GH photo, P). Colombia. Bolívar: "Crescit prope Turbaco Novo-Granatensium, Floret Martio" (from protologue), without date (fl).

Distribution. *Gustavia superba* ranges from southwestern Costa Rica, throughout Panama and into northwestern Colombia.

Representative specimens examined: PANAMA. Veraguas: Santa Lucía (Río San Pablo, near Pueblo Nuevo, Varagua), 1-2 Mar 1839 (fl), *Barclay 2804* (BM). Coclé: El Valle de Anton-Floor, 600 m alt, 7 Feb 1947 (fl), *Allen 4206* (MO). Colón: Tres Brazos Sawmill, Icacal, between Salud and Boca de Río Indio, 29 Jun 1969 (st), *Howell 67* (MO). Panamá: Trapiche, Perlas Islands, 4 Jul 1941 (fr), *Allen 2610* (MO); Isla Taboquilla, 20 Oct 1962 (st), *Duke 5887* (MO); Isla Casaya, 26 Feb 1967 (fl), *Duke 10375* (MO); San José Island, Pearl Archipelago, 18 Jul 1945 (fr), *Erlanson 45* (GH, US); near Tapla River, Juan Díaz region, 1-3 Jun 1923 (fl), *Maxon 6746a* (US); Taboga Island, Dec 1923 (st), *Standley 27934* (US); Penonome and vic, 23 Feb-22 Mar 1908 (fl), *Williams 435* (NY). Canal Zone: Barro Colorado Island, 8 Jun 1931 (fr), *Bailey & Bailey 58* (F); near mouth of Río Chagres, 15 Mar 1935 (fl), *Allen 880* (F, GH, K, MO, NY, US); Pipeline Road, 2.5 miles from gate, 4 Apr 1970 (fl), *Croat 9348* (MO); Fort Sherman, ca 1/2 mile before entering gate, 19 Dec 1966 (fl), *Duke 9249* (MO); along NW side of road leading to the Miraflores locks, across from Ft. Clayton, 12 Mar 1971 (fl), *Nee & Mori 3584* (MO, NY, US, WIS); Obispo, 19 Jan 1924 (st), *Standley 31709* (US); Madden Dam area near road. Transisthmian Highway, 31 May 1959 (fl), *Stern et al 47* (GH, MO, US). Darién: Vicinity of Pinogana, 20 m alt 4 Mar 1947 (fl), *Allen 4310* (MO, NY); Pico Piriaque, 24 Apr 1966 (fl), *Duke 8147* (MO); Río Sabana, ca 4 miles above Santa Fé, alt 25 m, 15 Feb 1967 (fl), *Duke 10204* (MO, WIS); Isla Saboga, 25 Feb 1967 (fr), *Duke 10342* (MO, WIS); trail from Río Pucro to Quebrada Maskia, 22 Jun 1967 (fr), *Duke 13062* (MO, WIS); junction of Río Conglon with Río Chucunaque, N of Yaviza, 21 Nov 1967 (fl), *Mori 373* (MO, WIS). COLOMBIA. Chocó: 2-4 mi NW of Teresita, alt ca 100 m, 18 May 1967 (fr), *Duke 11065* (NY, WIS). Antioquia: Los alrededores de Antioquia, alt 550 m, 8 Feb 1948 (fl), *Barkley & Arboleda 5* (US); ca 1 km NW of Santa Fé de Antioquia on road to Turbo, 4 Jul 1971 (fl), *Nee & Mori 4276* (COL, US, WIS); Bolívar: Guimari, Cordillera Occidental, vertiente oriental, alt 500 m, 17 Apr 1949 (fl), *K. von Sneidern 5745* (F); along trail from Luruaco to Pinar de Candelaria, alt 100-200 m, 10 Oct 1937 (st), *Dugand 1153* (F).

Ecology. This species, known throughout its range as "Membrillo," is one of the most conspicuous elements of tropical moist and wet forests where it occurs. Its large leaves, tufted at the ends of stout branches make this understory tree easily recognizable. Because of its ability to sprout from cut stems it is common in secondary as well as undisturbed habitats.

Flowering occurs from the middle of January through May (early dry season to early wet season) and fruits are produced from March through August (late dry season to middle wet season). Mori and Kallunki (1976) have studied the floral biology and phenology of *G. superba* in considerable detail.

The pedicellary bracteoles of *G. superba* are usually fused at the bases and margins to form a small, shallow cup which surrounds the pedicel. Within the cup there are small structures which appear to function as nectaries. If they are nectaries their function may be to attract ants which in turn protect the flowers against insect attack. I have seen no evidence of similar nectaries in other species of *Gustavia.*

Local names. PANAMA. Membrillo *(Duke 8147, 8253, 9249, 10278; K. von Sneidern 5745; Standley 27443, 27934, 31253, 31447; Tyson et al 3823);* Membrillo Hembra *(Howell 67);* Vaga-local (Chocó language, *Tyson et al 3823);* Wild Mango *(Standley 29917).* COLOMBIA. Membrillo *(Dugand 1153),* Paco *(Duke 11065).*

39. Gustavia flagellata Mori, Brittonia **28**(3): 293-297, *figs 1B-1E,* 3, 4. 1976. Figs 57, 58.

Trees to 20 m tall, 16 cm dbh; leaf-bearing branches 7-16 mm diameter, the leaves aggregated at their ends, the petiole scars touching to 16 mm apart. Bark brown, irregularly fissured. Leaf blades oblong, elliptic, obovate, or oblanceolate, 28-81 × 10-31 cm, glabrous, chartaceous, with 15-23 pairs of lateral veins, the apices acuminate to long acuminate, the bases acute, cuneate, or obtuse, the margins entire to serrulate. Petioles 40-195 mm long, 2-6 mm thick, subterete in cross section. Inflorescences cauline, racemose, densely rusty- to grayish-white-tomentose, with up to 17 flowers, the rachis to 108 cm at maturity of the fruits; pedicels 20-75 mm, subtended by a single widely ovate or oblong caducous bract 8-20 × 4-12 mm and bearing usually above the middle 2 oblong or ovate, cucullate bracteoles 3-10 × 3-6.5 mm. Flowers 7.7-13.5 cm diameter, calyx with 4 broadly triangular to rounded lobes, 2-4 × 10-12 mm, green or greenish-yellow; petals (6-)8, oblong, narrowly obovate or widely obovate, 40-68 × 16-44 mm, white inside, white outside with varying amounts of pink especially towards the apex; connate androecium base 8-15 mm high, yellow, the outermost filaments 14-20 mm, pink, often puberulous, the inner ones progressively shorter, yellow; the anthers 3-4 mm, yellow; ovary smooth or with 2-5 costae, rusty-gray-pubescent, (4-)6-locular, puberulous to white-tomentose, often with glabrous spots at the summit; the style 1-3 mm; the stigma (4-)6-lobed. Fruits globose, truncate at the apex, with or without costae, to 60×76 mm, with persistent, broadly triangular calyx lobes. Seeds angular in cross section, ca 34×26 mm, 1-4 per fruit, without a distinct funicle.

Type. *Nee & Mori 4058* (holotype, WIS; isotypes, K, MO, NY, P, US, VEN). Venezuela. Miranda: Parque Nacional Guatopo, on Hwy 12, ca 9 km S of junction with Hwy 1, 25 Apr 1971 (fl, fr).

Key to the Varieties of *Gustavia flagellata*

1. Pedicellary bracteoles oblong, early caducous, 10×4-5 mm; ovary without costae; plants of inland forests (usually found at ca 500 m elevation). a. var *flagellata.*
1. Pedicellary bracteoles usually ovate, often persistent, 2.5-6×3-6.5 mm, ovary costate; plants of moist coastal forests (usually found at less than 200 m). b. var *costata.*

39a. **Gustavia flagellata** Mori var **flagellata** Fig 57, 58.

Leaf blades narrowly obovate to elliptic, 33-72×13-31 cm with a length to width ratio of 2.2-2.9, with 18-23 pairs of lateral veins; the bases usually obtuse, occasionally acute. Pedicellary bracteoles oblong, early caducous, 10×4-5 mm. Ovary smooth.

Distribution. This variety is apparently confined to the State of Miranda, Venezuela. Two trees have been introduced into the botanical garden of the "Instituto Botánico" in Caracas.

VENEZUELA. Distrito Federal: Garden of the "Instituto Botánico" in Caracas, *Nee & Mori 4174* (WIS), *4175* (COL, MO, NY, US, VEN). Miranda: Carretera Sta. Teresa-Altagracia de Orituco, *Aristeguieta 1795* (NY, VEN); Camino de la Guzmanera, Parque Nacional de Guatopo, *Aristeguieta & Agostini 6346* (US, VEN); Aguas Blancas, 400-500 m alt, Miranda-Guárico, *Medina 534* (NY); Hwy 1, 8 km NW of junction with Hwy 12, about 22 km SE of Santa Teresa, *Nee & Mori 4064* (NY, US, VEN, WIS); Parque Nacional de Guatopo, 43 km NNW of Altagracia de Orituco, 41.5 km SE of Santa Teresa, alt 500 m, *Steyermark 87082* (NY, VEN).

Ecology. This variety is a relatively large tree of the second story of moist, forested slopes at around 500 meters elevation. It is common in the forests of the "Parque Nacional Guatopo" of Venezuela.

The only flowering collections were made in April while fruiting material has been gathered in April, June and September.

In the "Parque Nacional Guatopo" clouds of bees were observed swarming around the pendent inflorescences. Unfortunately the flowers were too far from the ground for detailed observation of the pollinators.

Gustavia flagellata is the only *Gustavia* with the inflorescences commonly over 15 cm in length and sometimes as long as 108 cm. The specific epithet alludes to the long whiplike rachis of the inflorescences.

39b. **Gustavia flagellata** Mori var **costata** Mori, Brittonia **28**(3): 297, *figs 1B, 4.* 1976. Fig 58.

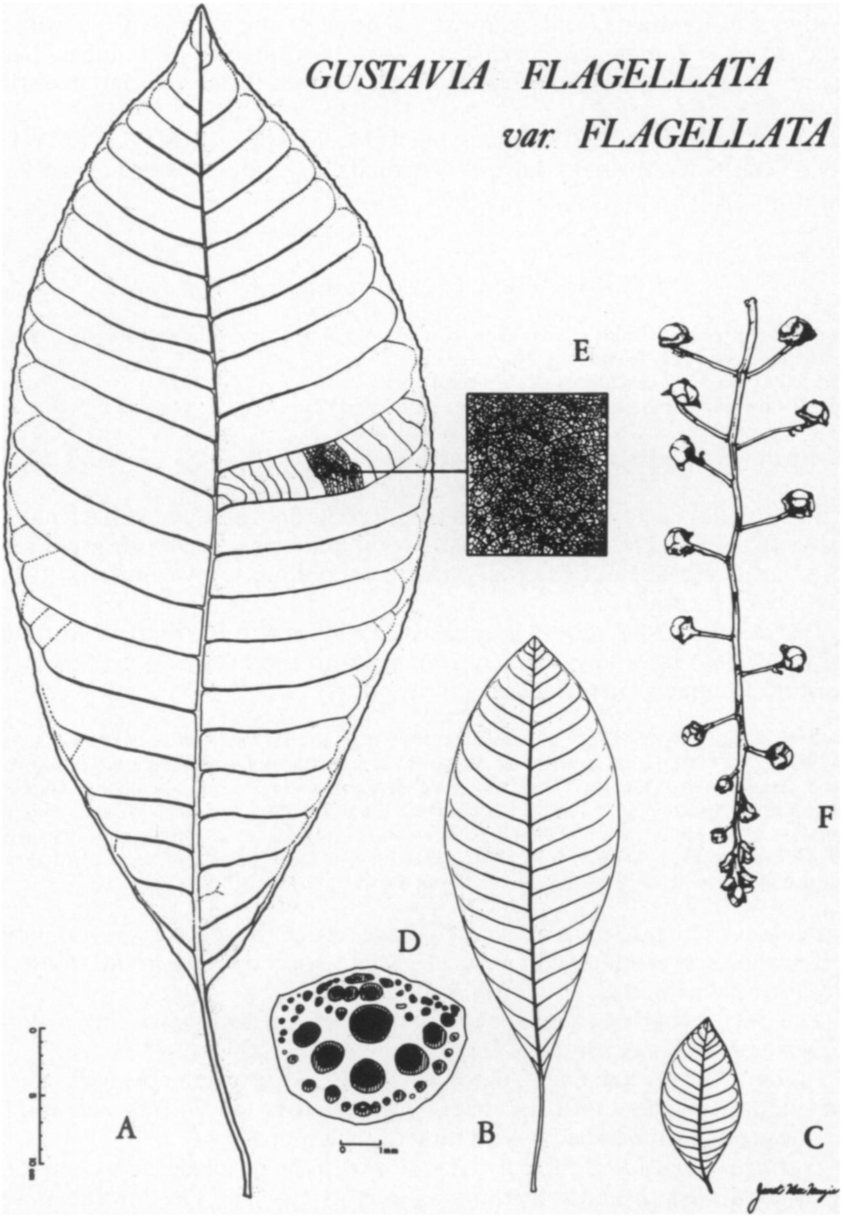


FIG 57. *Gustavia flagellata* var *flagellata (Nee & Mori 4058):* A, Large leaf, found proximally in a given growth flush; B, Smaller leaf, found distal to the leaf shown in A; C, Smallest leaf, found directly below the bud and distal to the leaves shown in A and B; D, Petiole cross section made at the juncture of the petiole and blade; E, Quaternary and higher orders of venation; F, Inflorescence with all flowers still in bud.

Leaf blades narrowly obovate, oblong, or oblanceolate, 34-81 × 10-30 cm, with a length to width ratio of 1.8-3.6, with 15-23 pairs of lateral veins; the bases acute, cuneate, or obtuse. Pedicellary bracteoles usually ovate, persistent, 2.5-6 × 3-6.5 mm. Ovary costate.

Type. *Nee & Mori 4035* (holotype, WIS; isotypes, P, US, VEN). Venezuela. Distrito Federal: Between Los Caracas and Oritopo on coastal Hwy 1, 7 km E of Los Caracas, 25 Apr 1971 (fl).

Distribution. This variety is known only from moist coastal forests below 200 m of the Distrito Federal and Miranda, Venezuela.

VENEZUELA. Distrito Federal: Between Los Caracas and Oritopo on coastal Hwy 1, ca 7 km from Los Caracas, *Nee & Mori 4031* (P, US, VEN, WIS); on coastal Hwy 1, 28 km E of Los Caracas, *Nee & Mori 4048* (MO, WIS); between Los Caracas and Oritopo, 1 mi E of Hacienda Uritapo, 12 mi E of Los Caracas, *Steyermark 91512* (US, VEN). Miranda: Entre Los Caracas y Cabo Codera, *Aristeguieta 4843* (NY, VEN); región baja del Río Guapo, a unos 20 km de Río Chico, *Aristeguieta 2736* (VEN); coastal Hwy 1, 19 km E of La Sabana, *Nee & Mori 4053* (WIS); 1 mile E of El Guapo, *Nee & Mori 4078* (NY, WIS); cerca del puente del Río Guapo, *Rutkis 182* (VEN).

Ecology. This variety is restricted to the moist forests of the Distrito Federal and the state of Miranda. Although much of this area, especially of the Distrito Federal, is covered by semi-deciduous forest there are finger-like projections of moist evergreen forest that reach the coast. *Gustavia flagellata* var *costata* is found in those "quebradas," stream sides, and river valleys with enough moisture to support evergreen forest. In these areas it is a common plant which is easily recognized by its large leaves tufted at the ends of the branches.

This variety flowers from March to June and bears fruit from June to September. Flowering coincides with the dry season and fruits mature in the wet season.

The principal differences between this and the preceding variety are summarized in the key to the varieties. The varietal epithet refers to the costate ovary.

Local names. Venezuela: Camburito *(Rutkis 182)*.

40. **Gustavia excelsa** R. Knuth in Engler, Pflanzenreich IV. **219a:** 24. 1939. Fig 54.

Trees, slender, unbranched or sparsely branched 3.5 to 11 m tall, the leaves in 1 or more verticels grouped at the branch ends. Leaf blades oblanceolate, possibly sessile, to 115 × 25 cm wide, with 60 pairs of lateral veins, lower 1/3 tapered to a retuse base (fide Knuth); apices short acute (fide Knuth); margins entire to minutely serrulate. Inflorescences cauline, racemose, rusty-tomentose, with 2-5 flowers, the rachis 100-200 × 5 mm; pedicels 50-55 mm, with a single caducous bract and bearing near the middle 2 broadly ovate, obtuse, caducous bracteoles (fide Knuth). Flowers 12 cm in diameter; calyx an entire somewhat irregular rim, 3.5-6.5 mm wide; petals 8, oblong, obovate, or narrowly obovate, to 70 × 30 mm, puberulous at anthesis, rose or lilac; the outermost filaments 15-20 mm; anthers 2-3 mm; ovary without costae, rusty-tomentose, the summit white-tomentose, style 1 mm; stigma with (5-)4 lobes. Fruits unknown.

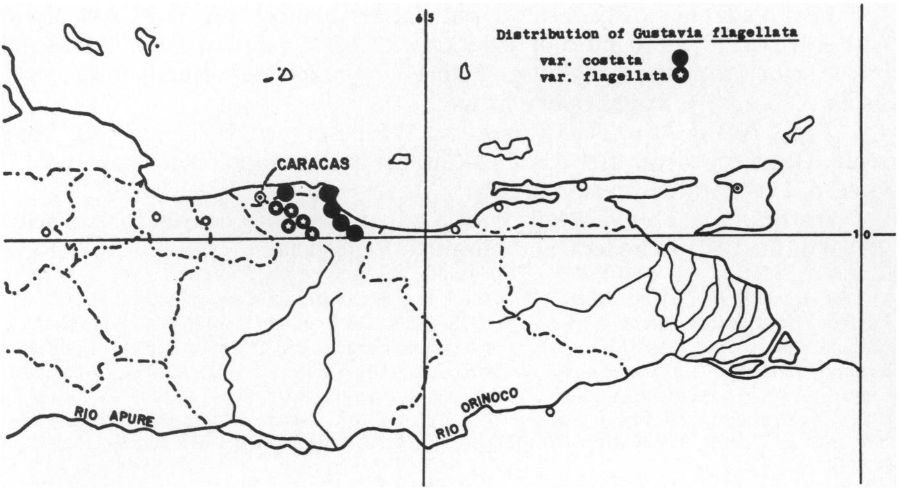


FIG 58. Distribution of *Gustavia flagellata.*

Type. *Haught 1636* (lectotype, US 1592098, here designated; isolectotype, US 1592099). Colombia. Santander: Vicinity of Puerto Berrío, between Carare and Magdalena Rivers, alt 100-700 m, 12 Apr 1935 (fl).

Distribution. This species is known only from the Magdalena Valley of Colombia.

COLOMBIA. Santander: Campo Capote (6° 38' N, 73° 55' W) and vicinity, alt 100-200 m, 8 Jul 1971 (st), *Nee & Mori 4294* (COL, MO, WIS), 8 Jul 1971 (st), *Nee & Mori 4298* (VEN, WIS); 10 leguas al SE de Barrancabermeja, a 8 km de la margen izquierda del Río Opón, alt ± 200 m, 28 Aug 1954 (fl), *Romero-Castañeda 4747* (COL, US), 31 Aug 1954 (fl), *Romero-Castañeda 4784* (US).

Ecology. Within its restricted range *G. excelsa* is a relatively common understory tree in forests on well drained sites.

This is a poorly known species which has its closest affinity with *G. longifolia* of western Amazonia.

Saplings may possess as many as 10 verticels of leaves.

Excluded Species

Gustavia valida de Candolle, Prodromus **3:** 290. 1828 =*Planchonia valida* (Blume) Blume, fide Kartawinata.

Gustavia globosa Spanoghe, Linnaea **15:** 204. 1841 =*Planchonia valida* (Blume) Blume, fide Kartawinata.

Gustavia alata Spanoghe, Linnaea **15:** 204. 1841 =*Planchonia timorensis* Blume, fide Kartawinata.

Gustavia brasiliensis Morren, Belg. Hort. **16:** 201. 1866.

Morren's description is not sufficiently detailed to allow positive identification of *G. brasiliensis.* However, the description does state that the leaves are large and that the collection upon which the description was based came from the Rio Negro. Based on this information I feel that *G. brasiliensis* is synonymous with either *G. augusta* or *G. pulchra.*

Gustavia integrifolia Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **4:** 240. 1929 = *Grias cauliflora* L.

Gustavia gracilipes R. Knuth, Repert. Spec. Nov. Regni Veg. **35:** 338. 1934. I have not been able to match the description with any collections studied nor have I seen the type which was probably destroyed during World War II.

GRIAS
by
SCOTT A. MORI

3. **Grias** Linnaeus, Syst. ed. 10. 1075. 1759; Miers, Trans. Linn. Soc. London **30**(2): 171-172, 298-301, *t 36c.* 1874; Niedenzu in Engl. & Prantl, Nat. Pflanzenfam. **3**(7): 37. 1892; Fawcett & Rendle, Flora of Jamaica **5:** 298-299. 1926; Knuth, Pflanzenreich IV. **219a:** 28-33, *fig 7.* 1939; Macbride, Publ. Field Mus. Nat. Hist., Bot. Ser. **13**(4): 236-238. 1941; Woodson, Ann. Missouri Bot. Gard **45:** 122-125. 1958; Adams, Flowering plants of Jamaica. 508. 1972.

Trees, to 30 m tall, with large leaves clustered at the ends of stout branches. Leaf blades petiolate or sessile, oblanceolate or spathulate, 26-167 × 4-41 cm, glabrous or infrequently pubescent on abaxial surface, with inconspicuous papillae or punctae on abaxial surface, coriaceous, with 11-86 pairs of lateral veins; apices acuminate or attenuate; bases cuneate, narrowly cuneate or auriculate, often decurrent; margins entire or infrequently serrate, slightly revolute, with inconspicuous reddish-brown scars representing attachment of caducous marginal teeth; leaves at end of growth flush often smaller, with fewer pairs of lateral veins, more sessile, and more auriculate at base than leaves at beginning and middle of flush. Inflorescences on trunk or branches, infrequently in axils of lowermost leaves, distinct racemes or fascicles, when racemose the rachis several to 350 mm long; pedicels with a single triangular, ovate, or oblong basal bract, 1-13 × 1-9 mm and two well developed *(G. neuberthii)* or scarcely developed and scale-like bracteoles (remaining species) inserted from directly under the hypanthium to at the base of the pedicel. Flowers 2.5-8 cm in diam.; calyx of 4 distinct lobes, of 2-4 irregular lobes or an entire rim at anthesis, in bud with 4 distinct lobes or enclosed except for an apical pore or completely enclosed, the completely enclosed bud with circumscissle dehiscence or splitting into 2-4 irregular lobes; petals 4, thick and fleshy, cucullate or flat, ascending or spreading at anthesis, 10-35 × 6-27 mm, white or yellow; androecium symmetrical, the connate androecial base 1-9 mm high; stamens 85-210, in 3 to 5 concentric rings, curved inwards, the filaments fleshy, angular, constricted at the apex, the outermost filaments 6-15 mm, the inner ones progressively smaller, the anthers small, 0.5-1.0 mm, the anther sacs divergent, extending below point of filament attachment, i e versatile, with lateral dehiscence; ovary 4-locular, each locule with 2-4 ovules, the ovules pendant, attached to the septum at or towards the apex of the locule; style lacking or short, conical, 1-2.5 mm; stigma with 4 lines. Fruits indehiscent, fusiform or pyriform, 38-120 × 22-60 mm, the mesocarp with 8-10 ribs, these best seen in cross section. Seeds fusiform, 1 per fruit, 30-51 mm long, without cotyledons, retained with the fruit, penetrating the pericarp upon germination. $x = 17$.

Type. *Grias cauliflora* L. The generic name was taken by Linneaus from Apuleius.

Distribution. The six described species of *Grias* are limited to Central America, Jamaica and northwestern South America where they range from southern Belize to central Peru (Fig 37).

Taxonomic History of *Grias*

A species of *Grias* was described and illustrated for the first time by Hans Sloane (1725). Linnaeus (1759) named this species *Grias cauliflora.*

As with *Gustavia,* there have been differences of opinion as to the affinities of *Grias.* For example, Antoine Laurent de Jussieu (1789) placed *Grias* in the Guttiferae, A. P. de Candolle (1828) put it in his "Myrtaceae dubiae," and Bentham and Hooker (1865) felt its relationships were with their subtribe Barringtonieae of the Lecythidaceae.

However, all monographers of the Lecythidaceae (Miers, 1874; Knuth, 1939b; Mori, 1974; Prance and Mori, 1977) recognize its affinities with other lecythid genera, most often placing it in our equivalent of the subfamily Lecythidoideae. In addition, chromosome number *($n = 17$ for G. caulifora)* and pollen type (tricolpate) support its inclusion in this subfamily (Kowal et al, 1977; Muller, 1972, 1973).

Key to the Species of *Grias*

1. Inflorescences fascicular, i e without a well defined rachis or, if present, the rachis less than 5 mm long.
  2. Leaf blades with 45-86 pairs of lateral veins, pilose or with scattered hairs on the abaxial surface. Young pedicels and calyces whitish pubescent. Stamens less than 85. 1. *G. multinervia.*
  2. Leaf blades with 17-45 pairs of lateral veins, glabrous on abaxial surface, infrequently puberulous on the veins. Young pedicels and calyces glabrous or rusty pubescent. Stamens 85-210.
    3. Calyx with an apical pore in bud. Plants of Jamaica, Central America, and northwestern Colombia. 2. *G. cauliflora.*
    3. Calyx completely enclosing the bud. Plants of southern Colombia, Ecuador, and Peru.
      4. Leaf blades spathulate, sessile, more or less auriculate at the base. Inflorescences in leaf axils or on young branches. Plants of southern, coastal Colombia. 3. *G. colombiana.*
      4. Leaf blades elliptic to oblanceolate, the petioles 4-110 mm long, cuneate, acute or obtuse at the base. Inflorescences on larger branches and trunk. Plants of Ecuador and Peru. 4. *G. peruviana.*
1. Inflorescences racemose, the rachis greater than 5 mm long.
  5. Pedicel with 2 well developed, keeled bracteoles directly subtending the hypanthium. Calyx with 4 distinct lobes in bud. 5. *G. neuberthii.*
  5. Pedicel without 2 bracteoles or if present vestigial, not keeled and inserted near the base of the pedicel. Calyx without 4 distinct lobes in bud.

6. Young pedicels and calyces glabrous. Petals white. Plants of northwestern Colombia. 6. *G. haughtii.*
6. Young pedicels and calyces densely pubescent. Petals yellow or white. Plants of southern Colombia, Ecuador and Amazonian Peru. 4. *G. peruviana.*

1. **Grias multinervia** Cuatrecasas, Fieldiana, Bot. **27**(2): 97, *fig 6. 1951. Fig 61.*

Trees, to 20 m. Leaf blades oblanceolate, 110-145 × 24-35 cm, with reddish papillae and scattered hairs on abaxial surface, with 45-86 pairs of lateral veins; apices acuminate; bases long and narrowly cuneate; margins entire. Inflorescences cauline, fascicular, with 1-4 flowers per fascicle; pedicels ca 7 mm, white-pubescent especially in bud, with an ovate bract 1.7 × 1 mm at the base, bracteoles inconspicuous at anthesis. Flowers ca 30 mm in diam at anthesis; calyx completely enclosing the bud, apiculate, splitting irregularly to form an incised rim at anthesis; petals 4; androecium with 56-62 stamens, the outermost filaments 5.5 mm, the innermost 1.5 mm, the anthers 0.8 mm; ovary 4-locular, with 2 ovules per locule; style 1 mm; stigma with 4 lobes. Fruits oblong to elliptic, to 100 × 50 mm, with 8 longitudinal ribs when dry. Seeds, when dried, chestnut brown, rugose, 77 × 30 mm.

Type. *Cuatrecasas 14208* (lectotype, F 1358434; isolectotypes, F 1358435, 1358436, 1358437). Colombia. Cauca: Costa del Pacifico, Río Micay, orilla derecha, en Caliche, 5-10 m alt, 26 Feb 1943 (fr).

Distribution. Known only from southern coastal Colombia and northern coastal Ecuador.

ECUADOR. Los Ríos: Hacienda Clementina, between Babahoyo and Montalve, secondary monsoon forest and cultivated land, 5 Aug 1967 (fl), *Sparre 17902* (S).

The type has 86 pairs of lateral veins whereas Sparre's collection *(17902)* has only 45 pairs.

2. **Grias cauliflora** Linneaeus, Syst. ed. 10. 1075. 1759. Figs 9, 11F-J, 59.

Grias fendleri Seemann, Bot. Voy. Herald 126. 1854. Type. *Fendler* 187 (lectotype, K, here designated; isolectotypes, BM, GH, MO, US). Panama. Chagres, 12 Feb 1850 (fl).

Gustavia integrifolia Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. **4**: 240. 1929. Type. *Englesing* 225 (holotype, F 579727; isotype, K). Nicaragua. Region of Bragman's Bluff, 19 Apr 1928 (fl).

Grias integrifolia (Standley) R. Knuth in Engler, Pflanzenreich IV. **219a**: 30. 1939.

Grias pittieri R. Knuth in Engler, Pflanzenreich IV. **219a**: 29. 1939. Type. *Pittier 6552* (holotype, US 716619). Panama. Darién: Forests around Pinogana, 16-21 Apr 1914 (fl).

Grias gentlei Lundell, Wrightia **2**(3): 122. 1961. Type. *Gentle 5194* (holotype, LL; isotypes, F, UC, S). Honduras. Toledo District, upper reach Temash River, Feb 1945 (fl).

Grias darienensis Dwyer, Ann. Missouri Bot. Gard. **52**: 353-354, *fig 2.* 1965. Type. *Stern et al* 119 (holotype, MO; isotypes, GH, US). Panama. Darién: Vicinity of El Real, Río Tuira, 1 mile down from Pinogana near Quebrada Chuito, 6 Jun 1959 (young fr).

Grias duckei Dwyer, Ann. Missouri Bot. Gard. **52**: 357-358, *fig 4.* 1965. Type. *Duke 5090* (holotype, MO). Panama. Darién: Río Pirre, 2-5 miles above El Real, 23 Jun 1962 (fr).

Grias sternii Dwyer, Ann. Missouri Bot. Gard. **52**: 354. 1965. Type. *Stern et al 772* (holotype, MO; isotypes, GH, US). Panama. Darién: El Real, Río Tuira, 1 Jul 1959 (fr).

Trees, to 30 m × 45 cm; leaf-bearing branches to 23 mm in diam. Leaf blades oblanceolate, often with the margins somewhat concave towards the base, 35-110 × 7-28 cm, with inconspicuous reddish papillae or punctae abaxially, coriaceous, with 25-45 pairs of lateral veins; apices acuminate; bases narrowly cuneate or auriculate; margins entire, slightly revolute; leaves at end of growth flush smaller, with fewer pairs of lateral veins, more sessile, and more auriculate than leaves at beginning and middle of flush. Petioles lacking to 110 × 4-11 mm, semicircular in cross section, often canaliculate. Inflorescences fascicular, from small warty outgrowths on the trunk and large branches, with 2-4 flowers, the rachis mostly much reduced, infrequently to 25 mm; pedicels 3-20 mm, subtended by a single ovate or triangular, cucullate basal bract 1-5 × 1-5 mm and bearing just above the base 2 caducous bracteoles less than 1 × 1 mm. Flowers 2.5-5 cm in diam.; calyx enclosing the bud except for an apical pore, rim-like or of irregularly split lobes at anthesis; petals 4, oblong or obovate, 2 mm thick, ascending and cucullate at anthesis, 10-23 × 6-15 mm, white or creamy-white; androecium with 85-150 stamens in 3 concentric rows, the connate base 1-5 mm high, the outermost filaments 6-8 mm, the anthers 0.5-0.8 mm; ovary glabrous, (3-)4-locular, each locule with 2-4 ovules, glabrous or puberulous at the summit; style lacking; stigma with 4 lobes. Fruits fusiform, obovate, or pyriform, brown, 38-90 × 22-40 mm, the pericarp 5-8 mm thick. Seeds 35-50 mm long. $x = 17$.

Type. Tabla 216 in Sloane, Hist. Jam. **2:** 122-123, *t 216-217.* 1725.

Distribution. In Jamaica and south from Guatemala and Belize into northwestern Colombia. *Grias cauliflora* is found only in areas with relatively high rainfall. For example, in the Canal Zone it occurs only on the Caribbean side which is much wetter than the Pacific side. In fact, the only Pacific localities are the Darién of Panama and the Osa Peninsula area of Costa Rica and adjacent Panama which are wetter than the remainder of the Pacific Coast of Central America.

Representative specimens examined. JAMAICA. Trelawny: Windsor, alt 100-150 m, 3 Apr 1931 (st), *Miller 1489* (US). St. Elizabeth: Vicinity of Frenchman, at sea level, 3 Dec 1971 (st), *Prance 16539* (BM, NY). St. Ann: Roaring River, 12 Mar 1961 (fl), *Proctor 22127* (GH). Portland: Vicinity of Port Antonio, near Cold Harbor, 25 Sept 1906 (st), *Britton 902* (NY, US). BELIZE: Toledo: Moffredye Creek, near San Antonio, 26 Apr 1945 (st), *Gentle 5350* (F); Río Grande, alt 250 ft, 19 Mar 1933 (fl), *Schipp 1151* (BM, F, GH, K, MICH, MO, NY, UC); Temax River, 7 Aug 1933 (?), *Stevenson 152* (F). GUATEMALA. Izabal: Lower course of Río Oscuro, SW of Lake Izabal, at sea level, 27 Apr 1966 (fl), *Jones et al 3146* (F, NY); shores of Lago Izabal, opposite San Felipe and mouth of Río Juan Vicente, alt 50 m, 19 Apr 1940 (fl), *Steyermark 39682* (F). HONDURAS. Atlántida: Vicinity of Tela, at sea level, 14 Dec-15 Mar 1928 (st), *Standley 54469* (F, GH, MO). Yoro: Guaymas District, farm 39 of the Tela Railroad Co., alt 30 m, 2 Feb 1928 (st), *Standley 55481* (F, GH, US). Gracias a Dios: Mosquitia, Río Platano, 0-4 hours upriver from village of Ras, near sea level, 23 May 1973 (young fr), *Gentry et al 7539* (MO). NICARAGUA. Zelaya: Vicinity of El Recreo, on Río Mico, ca 30 m, 23 Apr-14 May 1942 (st), *Standley 19456* (F, US). COSTA RICA. Heredia: 1.4 km NW of Puerto Viejo, alt 75 m, 24 Jun 1966 (st), *Mori & Anderson 128* (F). Limón: Estrella Valley, 6 miles inland from mouth of Estrella River, 21 Apr 1952 (st), *Stork 4619* (UC). Puntarenas: Vicinity of Jalaca, area between the Río Esquinas and Palmar, 100 ft, 25 Mar 1949 (fl), *Allen 5216* (F, MICH, MO, UC, US); Osa Peninula, Rincón, ca 1 km W of the landing strip, 8 Mar 1971 (fl), *Nee & Mori 3574* (WIS). PANAMA: Bocas del Toro: Fish Creek Hills, vicinity of Chiriquí Lagoon, 8 May 1941 (fl), *von Wedel 2423* (GH, MO, US). Chiriquí: Progreso, Jul-Aug 1927 (fr), *Cooper & Slater 228* (F, GH, NY, US); vicinity of Puerto Armuelles, alt 0-75 m, 28-31 Jul 1940 (young fr), *Woodson & Schery 901* (F, MO, NY). Colón:

Salud, alt 3 m, 5 Aug 1971 (young fr), *Lao & Holdridge 232* (MO, PMA); on the road from Colón to Portobelo, 2.9 miles SW of Portobelo, 16 Mar 1971 (fl), *Nee & Mori 3663* (MO, WIS). Canal Zone: Swampy area along trail along Río Petitpie, between Gatún and Fort Sherman, 30 Apr 1975 (fl), *Mori & Kallunki 5773* (MO); Barro Colorado Island, Gatun Lake, 17 Jan 1924 (st), *Standley 31404* (US). San Blas: Nakka, one of the San Blas Islands, 26 Aug 1965 (fl), *Dwyer 6874* (MO). Darién: Trail between Pinogana and Yavisa, ca 15 m alt, 17 Mar 1937 (?), *Allen 273* (F, GH, MO). COLOMBIA. Antioquia: Inmediaciones de Turbo, 19 Sep 1959 (fl), *Huertas & Hernández 4132* (COL). Chocó: Between Ríosucio and La Nueva, 5 Feb 1967 (fl), *Duke 9790* (NY, WIS); Strand flora between Camp Curiche and Quebrada Changame, 3.7 miles S of Camp Curiche, 24 May 1967 (fr), *Duke 11530* (MICH, NY, WIS); upper Río Truandó, La Teresita (INDERENA camp), ca 100 m alt, 18 Jan 1974 (fl), *Gentry 9340* (MO, NY).

Ecology. *Grias cauliflora* is an understory tree most commonly found in swampy areas or in riverbottom forests. In Jamaica, according to Guppy (1917), this species "is one of the most picturesque trees in the river scenery of Jamaica," and Adams (1972) reports that it is "rather local and gregarious near streams and in marsh forest." My observations of *G. cauliflora* in Panama and Costa Rica demonstrate that it is found in the same habitat in Central America.

In Central America its peak blooming period is from February through April.

Because of its riverine habitat the fruits of *G. cauliflora* often drop into the water where the seeds germinate. However, once they are carried into salt water they die (Guppy, 1917). Old fruits have been collected in the beach drift of San José Island, Panama (Plate 12, fig 4 as unidentified "seed" Johnston, 1949). The disjunct distribution of this species between Jamaica and Central America may be the result of a successful long range dispersal over water.

Sloane (1725, vol. 2, p 123) reports that the Spaniards used to eat the pickled fruits as a substitute for mangos, which may account for the Jamaican common name of the tree, Anchovy Pear. He adds that it is "sent from the Spanish West Indies to Old Spain, as the greatest rarity." Schomburgk (1922, vol. 1, p 33) states that the fruits of *G. cauliflora* are sold in the markets of Georgetown. However, I have no collections to document the natural occurence of this species in the Guianas. The *Grias tetrapetala* of Aublet is actually *Gustavia augusta* and therefore can not be the source of the fruits Schomburgk saw in Georgetown.

Local names. JAMAICA. Anchovy Pear *(Prior sn;* Sloane, Hist. Jam. 1725; Guppy, Plants, Seeds, and Currents, 1917); Wild Tobaco *(Britton 902).* BELIZE. Bombowood *(Gentle 5194, 5350);* Genip *(Schipp 1151);* Wild Mammy *(Gentle 5194).* GUATEMALA. Cayhilla *(Record 48).* HONDURAS. Irayol *(Record & Kuylen H. 10);* Jaguillo *(Standley 54469).* NICARAGUA. Papallon *(Englesing 225).* COSTA RICA. Tabaco *(Allen 5216).* PANAMA. Jaguey *(Cooper & Slater 228);* Madre de Cocoa *(Cowell 355);* Membrillo *(Cooper & Slater 228, Duke 9678, Standley 31404).*

3. **Grias colombiana** Cuatrecasas, Fieldiana, Bot. 27(2): 96. 1951. Fig 61.

Trees, small, to 6 m; leaf-bearing branches to 12 mm in diam., the leaves loosely aggregated in 1 to 3 whorls at their ends. Leaf blades sessile, spathu-

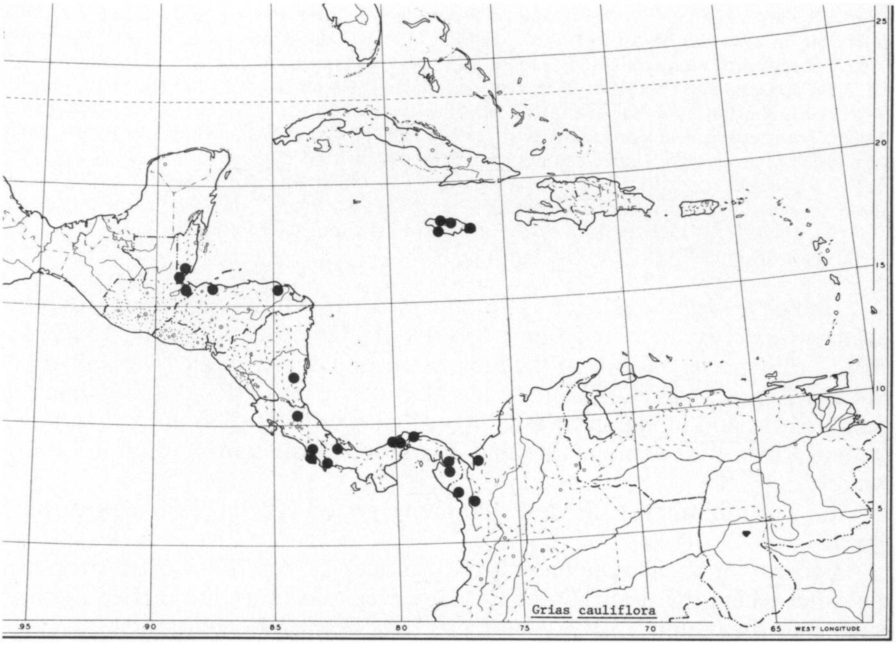


FIG 59. Distribution of *Grias cauliflora*.

late, 25-53 × 7-16 cm, glabrous, with inconspicuous reddish punctae abaxially, coriaceous, with 23-27 pairs of lateral veins; apices acuminate; bases ± auriculate; margins entire towards the base, serrulate towards the apex. Inflorescences fascicular, in axils of lower leaves or from branches just below the leaves, with 3-5 flowers, the rachis much reduced, usually less than 7 mm; pedicels glabrous, subtended by a single oblong or ovate, cucullate bract 2-3 × 2-2.5 mm and bearing just above the base 2 ovate, caducous bracteoles 2 × 2 mm. Flowers ca 4 cm in diam.; calyx enclosing the bud, splitting into an irregularly incised rim at anthesis; petals 4, obovate or elliptic, 14-20 × 7-10 mm, white; androecium with ca 195 stamens, the outermost filaments 7-10 mm, the anthers 0.7 mm; ovary glabrous, 4-locular, each locule with 2 ovules; style lacking; stigma with 4 lobes. Fruits truncate at the apex, 50-60 mm in diam, light yellow at maturity.

Type. *Cuatrecasas 15920* (holotype, F 1358432). Colombia. Valle: Costa del Pacífico, Río Yurumanguí, 5-50 m alt, 3 Feb 1944 (fr).

Distribution. Known only from Pacific coastal Colombia.

COLOMBIA. Chocó: A lo largo del Río Baudó, 15 km desde Pizarro a La Porquera. alt ca 5 m, 2 Feb 1967 (fl, young fr), *Fuchs et al 21701* (COL). Cauca: Costa del Pacífico, Río Micay, brazo Noanamito, El Chachajo, 2-5 m alt, 27 Feb 1943 (fl), *Cuatrecasas 14267* (F).

The relatively small, sessile, spathulate leaves in combination with the fasicular inflorescences in the axils of the leaves or on the branches just below the leaves characterize this species.

4. Grias peruviana Miers, Trans. Linn. Soc. London **30**(2): 301. 1874. Figs 11L, 61.

Grias grandifolia Pilger, Notizbl. Bot. Gart. Berlin-Dahlem **9:** 142. 1924. Type. *Tessmann 3110* (holotype, B probably not extant; isotype, GH photo). Peru. Loreto: Middle Ucayali, Masisea, ca 160 m alt, Aug 1923 (fl).

Grias maranonensis R. Knuth, Repert. Spec Nov. Regni Veg. **35:** 339. 1934. Type. *Kuhlmann* RB *21501* (holotype, B probably not extant; isotypes, S, U). Peru. Loreto: Río Marañón, Perserveranza, 5 Feb 1924 (fl).

Grias tessmannii R. Knuth, Repert. Spec. Nov. Regni Veg. **35:** 340. 1934. *ex char.* Type. *Tessmann 4187* (B fide Knuth, not seen). Peru. Loreto: Mouth of Río Santiago, 160 m alt, 1924.

Trees, to 30 m; leaf-bearing branches 6-12 mm in diam. Leaf blades elliptic or oblanceolate, 9-118 × 4-35 cm, glabrous, often with inconspicuous reddish papillae or punctae abaxially, with 11-47 pairs of lateral veins; apices acuminate or attenuate; bases cuneate, acute, or obtuse; margins entire or serrulate, obscurely revolute, with inconspicuous scars. Petioles lacking to 115 × 2-8 mm, semicircular or subterete in cross section. Inflorescences of 1 to several racemes arising from warty outgrowths on the trunk and branches, with 1-15 flowers, the rachis 5-115 mm; pedicels pubescent, 8-53 mm, subtended by a single bract 1-3 × 2-4 mm and bearing just above the base 2 caducous, inconspicuous, scale-like bracteoles. Flowers 3.5-7 cm in diam; calyx completely enclosing the bud, then usually apiculate, with circumscissle dehiscence and then forming a rim 3-4 mm wide or splitting into 2-4 irregular lobes at anthesis; petals 4, oblong or elliptic, 17-30 × 10-24 mm, usually yellow, infrequently white; androecium with 93-171 stamens, the connate androecial base 2-9 mm high, the outermost filaments 6-15 mm, the anthers 0.6-1.0 mm; ovary pubescent especially in bud, 4-locular, each locule with 2-4 ovules; style 1-2.5 mm; stigma with (3-)4 lobes. Fruits elliptic, fusiform, or obovate, 82-130 × 50-70 mm, brown with a yellow pulp, the pericarp with 8-10 longitudinal ribs.

Type. *Spruce 4541* (lectotype, K; isolectotype, BM). Peru. San Martín: prope Tarapoto, Río de Ventana, 1855-56 (fl, young fr).

Distribution. *Grias peruviana* has populations west of the Andes in northwestern Ecuador and east of the Andes from Ecuador south to near the headwaters of the Huallaga River in Peru.

Representative specimens examined: ECUADOR. Esmeraldas: Río Pambil, near junction with Estero Capuli, 150 m, 3 Jul 1966 (st), *Játiva & Epling 1060* (NY, S, UC, US); about 3 km E of Quinindé, 12 Apr 1943 (fr), *Little 6239* (F, MO, UC, US). Manabí: Río Pescadillo, 1876 (fl), *André 4243* (K); road to Santo Domingo-Chone, Flavio Alfaro, ca 100 m alt, 11 May 1968 (fl), *Harling et al 9418* (NY, S). Pichincha: Kilometer 170-175, via Santo Domingo-Quinindé, alt 300 m, *Acosta-Solis 13615* (F); 20 km W of Santo Domingo de los Santos, 1000 ft alt, 17 Oct 1961 (fl), *Cazalet & Pennington 5054* (K, NY, UC, US); within 3 km of Santo Domingo de Colorado, 1887 ft, 2 Apr 1943 (fr), *Little 6142* (F, K, UC, US); 37 km S of Santo Domingo de los Colorados, 29 Oct 1960 (fl & young fr), *Pennington 64SD* (NY). Napo: Cerro Antisana (0° 30' S, 78° W), Shinguipino Forest between Ríos Napo and Tena, 8 km SE of Tena, 1450 ft alt, 17 Sep 1960 (fr), *Grubb et al 1631* (K, NY). Los Ríos: Río Palenque field station, halfway between Quevedo and Santo Domingo de los Colorados, ca 200 m alt, *Gentry 10103* (MO, S), 24 Oct 1974 (fl), *Gentry 12018* (MO). Pastaza: Basin of Río Pastaza, Pacayacu-Sarayacu region, Río Bobonaza and adjacent tributaries, ca 1000 m alt, Aug-Oct 1938 (st), *Gill 49* (NY). Morona-Santiago: Cordillera Cutucu, ca 2° 40' S, 78° W, 17 Nov-5 Dec 1944 (fl), *Camp 1107* (FHO, MO, NY, WIS); Taisha, 1500 ft alt, 1 Jan 1962 (fl), *Cazalet & Pennington 7539* (K, NY). Zamora Chinchipe: Estación Experimental "El Padmi," 52 km NE de Zamora, lat 3° 42' S, long 78° 38' W, 900 m alt, 11 Sep 1975 (fl), *Little et al 308* (NY). PERU. Loreto: Alto Amazonas, Hacienda Santa María, cerca Yurimaguas, 170-200 m, 15 Sep 1948 (fl), *Ferreyra 4993* (NY, USM); above Pongo de Manseriche, at mouth of Río Santiago, 200 m alt, 17 Nov 1931 (fl, young fr), *Mexia 6115* (BM, F, GH, K, MICH, MO, NY, S, U, UC, US). Amazonas: Río Cenipa, near Huampami, 11 Mar 1973 (fl), *Ancuash 90* (MO), 28 Nov 1972 (fl), *Berlin 417* (MO, NY), 21 Feb 1973 (fr), *Berlin 884* (MO). San Martín: Provincia Cáceres, Madre Mía, 16 Mar 1977 (fr), *Boeke & Ramírez 1325* (K, MO, NY); alto Río Huallaga, Juan Jui, 400-800 m, Jan 1936 (fl), *Klug 4211* (BM, F, GH, K, MO, NY, S, U, UC, US); Provincia Mariscal Caceres, 2 km abajo de Tocache Nuevo, margen derecha del Río Huallaga, 9 Sep 1969 (fl, fr), *Schunke 3404* (K, NY, US). Huanuco: Chapajilla, near Tingo María, 27 Aug 1940 (fl), *Asplund 13343* (S).

Ecology. *Grias peruviana* is usually an understory or less frequently a canopy tree of primary forests of *terra firme* and river margins.

Collections of *G. peruviana* from the Huallaga River basin of Peru have larger more gradually tapered leaves than those from further north. As there is no morphological or geographical discontinuity between collections from the two regions I interpret this variation as clinal.

The disjunct distribution in Ecuador, with populations west and east of the Andes, may be the result of fruit dispersal by man. The fruit pulp is reported to be edible by many collectors *(Boeke & Ramírez 1325, Berlin 884, Grubb et al 1631, Kuhlmann 21501, Mexia 6115, Wurdack 2073),* and the type of *G. grandifolia (Tessmann 3110),* a synonym of *G. peruviana,* comes from a cultivated tree.

Local names. ECUADOR. Aguacate de Monte *(Little 580),* Apaí *(Little et al 308, Little 580),* Llanero *(Little 6239),* Piton *(Cazalet & Pennington 5054, 7539; Grubb et al 1631),* Sapote de Perro *(Rimbach 43).* PERU. Apaí (Aguaruna Jivaro language, *Berlin 884),* Apan (Aguaruna Jivaro language, *Berlin 417),* Mancoa *(Schunke 3404, 7087),* Nakunuk (Aguaruna Jivaro language, *Ancuash 90),* Sacha Mango *(Boeke & Ramírez 1325, Kuhlmann 21501, Mexia 6115, Schunke 4463, Wurdack 2073).*

5. Grias neuberthii Macbride, Publ. Field Mus. Nat. Hist., Bot. Ser. **11**(1): 30. 1931. Figs 10B, 11K, 16L-M, 60, 61.

Grias loretensis R. Knuth, Repert. Spec. Nov. Regni Veg. **35**: 339. 1934. Type. *Killip & Smith 27272* (holotype, B fide Knuth, probably not extant; isotypes, NY, US 1461048). Peru. Loreto: Iquitos, ca 100 m alt, 3-11 Aug 1929 (fl).

Grias foetidissima Dugand, Caldasia **3**: 31-32. 1941. Type. *Ballera sn* (holotype, COL; isotypes, COL). Colombia. Caquetá: Venecia y Río Orteguaza, 30 Sep 1941 (fl, fr).

Trees, to 20 m. Leaf blades oblanceolate with the margins slightly concave towards the base, 32-120 × 12-22 cm, with inconspicuous reddish papillae or punctae abaxially, coriaceous, with 23-42 pairs of lateral veins; apices acuminate; bases attentuate; margins entire, slightly revolute, with inconspicuous scars; leaves at end of growth flush smaller, more sessile and more auriculate than leaves at beginnng and middle of flush. Petioles lacking to 75 × 4-7 mm, semicircular in cross section, somewhat canaliculate when dry, the decurrent blade often obscuring the petiole-blade separation. Inflorescences of 1 to many racemes arising from warty outgrowths of trunk, with 10 to many flowers, the rachis elongated, 50-350 mm; pedicels 6-27 mm, buff-pubescent, subtended by a single oblong, caducous bract 7-13 × 4-9 mm and bearing directly below the hypanthium 2 keeled, lanceolate or widely ovate bracteoles 4-11 × 3-7 mm. Flowers 5-8 cm in diameter; calyx of 4 distinct lobes in bud, the lobes at anthesis ovate to very widely ovate, 6-11 × 5-10 mm; petals 4, fleshy, to 5 mm thick, spreading and flat at anthesis, widely oblong to suborbiculate, usually yellow, infrequently cream, with various tinges of pink and red; androecium with ca 210 stamens in 4 concentric rows, the connate androecial base weakly fused, 2-4 mm high, the outermost filaments 10-15 mm, the anthers 0.8-1.0 mm; ovary gray to rusty-tomentose, 4-locular, each locule with 2 ovules, the summit overlapped by the inner edge of the androecium; style conical, 1.5-2.5 mm long; stigma with 4 lobes. Fruits narrowly to broadly fusiform, 40-125 × 40-55 mm, with 8-10 longitudinal ribs when dried, brown, the pericarp 7 mm thick. Seeds circular in cross section, 30-75 mm long.

Type. *Williams 2337* (lectotype, F 608216; isolectotypes, F 608217, US 1515830). Peru. Loreto: Caballo-Cocha on the Amazon River, Aug 1929 (fl).

Distribution. East of the Andes in Southern Colombia, throughout eastern Ecuador and northern Peru.

Representative specimens examined. COLOMBIA. Cauca: Puerto Limón, bosques en el lado caucano del Río Caquetá, 28-29 Feb 1942 (fl), *Schultes 3312* (GH). Caquetá: 10 km SW of San José del Fragua (SW of Florencia), 320-340 m, 11 Jan 1974 (fr), *Davidse & Gentry 5736* (MO); near Río Orteguaza, La Maria (Hacienda de Ramón Achiardy), 400 m alt, 7 Mar 1944 (fl, fr), *Hermann 11246* (US). Putumayo: Selva higrófila del Río Putumayo, Puerto Porvenir, arriba de Puerto Ospina, hacia la Loma, 230-250 m alt, 17 Nov 1940 (fl, fr), *Cuatrecasas 10594* (F, US); márgenes del Río Güamués entre San Antonio y la desembocadura, 310-370 m alt, 20 Dec 1940 (fl), *Cuatrecasas 11232* (F, NY, US); between Río Chipayacu and (finca) Pedrogoso, en route to Puerto Asis, ca 700 m alt, *Ewan 16733* (NY, US); El Whiskey, 13 km S of Umbría, finca "Santa Marta," ca 300 m alt, 27 Nov 1968 (young fr), *Plowman 2077* (GHK); Río San Miguel o Sucumbios, Conejo y los alrededores, en frente de la Quebrada Conejo, 2-5 Apr 1942 (fr), *Schultes 3479* (GH); Mocoa and vicinity, 1800-2400 ft alt, 16 Mar 1953 (fl), *Schultes & Cabrera 19042* (US). ECUADOR. Napo: Tena, along river, 22 Jul 1977 (fr), *Boeke 2211* (COL, F, K, MO, NY, QCE); 1.5 km S of Lago Agrio on road to Coca, ca 340 m alt, 1 Apr 1972 (fl), *Dwyer & Macbryde 9794* (MO); Río Pucino, first major tributary of Río Aguarico above bridge at Aguarico (near Lago Agrio), ca 250 m alt, 9 Feb 1974 (fl, fr), *Gentry 9756* (MO, S). Pastaza: Between Nalpi and Canelos, 20 Nov 1971 (fl), *Lugo 1487* (NY, S); Río Zupayacu, ca 7 km S of Puerto Sarayacu, 11 Oct 1974 (fl), *Lugo 4077* (NY); ca 4 km S of Pacayacu on the Río Bobonaza, 31 Oct 1974 (fl), *Lugo 4414* (NY); environs of Mera, 22 Nov 1974 (fr), *Plowman & Davis 4486* (NY). Morona-Santiago: 16 km N of Taisha, 2° 11' S, 77° 30' W, 500 m alt, Aug 1976 (st), *Ortega 84* (NY). PERU. Loreto: Along road to Puerto Almendra, 7 km from Río Nanay, 23 Jul 1972 (fl), *Croat 18331* (MO); Quebrada Tahuayo above Tamishiyaco, 29 Aug 1972 (fl), *Croat 19703* (MO); Río Napo at Caserío Bella Vista, 22 Sept 1972 (fl), *Croat 20641* (MO); Iquitos, circa urbem, 14 Nov 1945 (fl), *Ducke 1840* (F, GH, K, NY, US). BRAZIL. Guanabara: Cultivated, grounds of the Río de Janiero Botanical Garden, 23 Feb 1973 (fl), *Prance 16572* (NY).

Ecology. *Grias neuberthii* is a tree of *terra firme* or riverine forests which is often left standing when the forest is cleared, probably because the fruits are edible.

This species is easily recognized by its four well developed calyx lobes in bud and its persistent, keeled pedicellary bracteoles inserted just below the hypanthium. No other species of *Grias* has lobed calyces in bud or persistent bracteoles.

The relatively large flowers, high number of stamens, and persistent bracteoles suggest that, of all species of *Grias, G. neuberthii* is the one with the closest affinity to species of *Gustavia.*

Local names. COLOMBIA. Cocora *(Sprague sn);* Cocorro *(Ewan 16733);* Kokora *(Schultes 3479);* Pepe-guara *(Ballera sn);* Té-Té-ku-chu (Kofán language, *Schultes 3479).* ECUADOR. Piton *(Dwyer & Macbryde 9794, Gentry 9756, Mexia 7232, Mowbray 6908).* PERU. Mangua *(Klug 680);* Sacha Mangua *(Croat 19703, Dodson 2831, Ducke 1840).*

6. **Grias haughtii** R. Knuth in Engler, Pflanzenreich IV. **219a:** 31, 33. 1939; Romero-Castañeda, Frutas Silvestres de Colombia **1:** 202-204, *fig 61a.* 1961. Fig 61.

Trees, to 30 m x 60 cm. Bark brown, smooth. Leaf blades oblanceolate or spathulate, 73-167 x 14-42 cm, glabrous, with inconspicuous reddish papillae abaxially, coriaceous, with 35-45 pairs of lateral veins; apices acuminate; bases cuneate, narrowly decurrent to leaf attachment; margins obscurely revolute, with inconspicuous reddish scars. Petioles lacking to 195 x 9-25 mm, semicircular in cross section. Inflorescences racemose, cauline, glabrous, with 1-2 flowers; pedicels 10-25 mm, with a single ovate, scale-like basal bract 1-4 x 1.5-4 mm, with the bracteoles not evident at anthesis. Flowers 6 cm in diameter; calyx completely enclosing the bud, then apiculate, splitting into 2-4 irregular lobes at anthesis; petals 4, elliptic or oblong, white or yellow, 25 x 10 mm; androecium with 120-180 stamens, the connate androecial base 1.5 mm high, the outermost filaments 7-12 mm, the anthers 0.6-0.8 mm; ovary glabrous or puberulous, (3-)4-locular, each locule with 1-4 ovules; style nearly lacking, less than 0.5 mm; stigma with 4 lobes. Fruits oblong or obovate, brown, 80-110 x 30-48 mm, with 8 longitudinal ribs, the mesocarp orange, 4 mm thick. Seeds 65 x 25 mm, the integument hard, with 7-8 salient vertical lines.

Type. *Haught 1550* (lectotype, US 1592082; isolectotypes, F 929658, 929660, NY, US 1592084). Colombia. Santander: Vicinity of Barrancabermeja, Magdalena Valley between Sogamoso and Colorado Rivers, 100-500 m alt, 28 Jan 1935 (fl).

Distribution. Restricted to northwestern Colombia.

COLOMBIA. Antioquia: hoya del Rio León o Bacuba, from Villa Arteaga to Chigorodó, Río Porroso, La Pradera, about 90 m alt, 3 Oct 1961 (fl), *Cuatrecasas & Willard 26177* (US); Río La Miel, hacienda "La Rica" un poco más abajo de la desembocadura del Río Samana, 8 Aug 1965 (fl), *Fernández P. & Jaramillo 7100* (COL, NY); Municipio de Sonsón, Corregimiento de la Argelia, Quebrada de Ledesma, Oct 1940 (fl), *Galindo 20-A* (COL). Santander: 15 leguas al SE de Barrancabermeja, a 3 km de la margen izquierda del Río Opón, ca 200 m alt, 8 Oct 1954 (fl), *Romero-Castañeda 4993* (US); 8 km N of Río Guapa, 4 Feb 1941 (fl), *Seibert 1681* (MO).

Ecology. Romero-Castañeda (1961) reports that *G. haughtii* prospers on periodically inundated alluvial soils at elevations less than 400 meters.

According to Romero-Castañeda (1961) the pulp of the fruit (=mesocarp) has an agreeable taste and is eaten raw or cooked in syrup. He suggests that its exploitation should be studied because the pulp appears to contain a

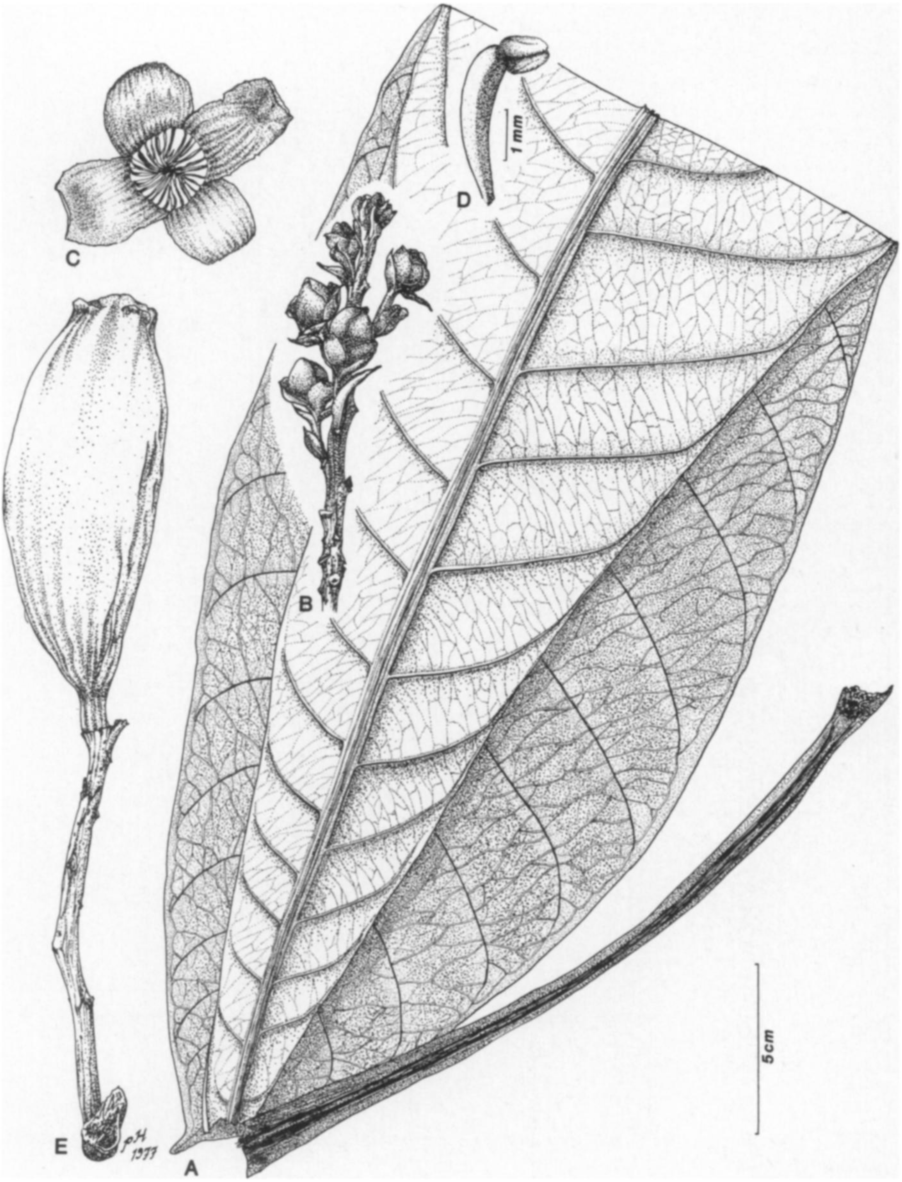


FIG 60. *Grias neuberthii,* A, *(Lugo 1522);* B & E, *(Croat 20641);* C & D, *(Plowman & Davis 4395);* A, Leaf; B, Inflorescence with buds; C, Top view of flower; D, Stamen; E, Old inflorescence with attached fruit.

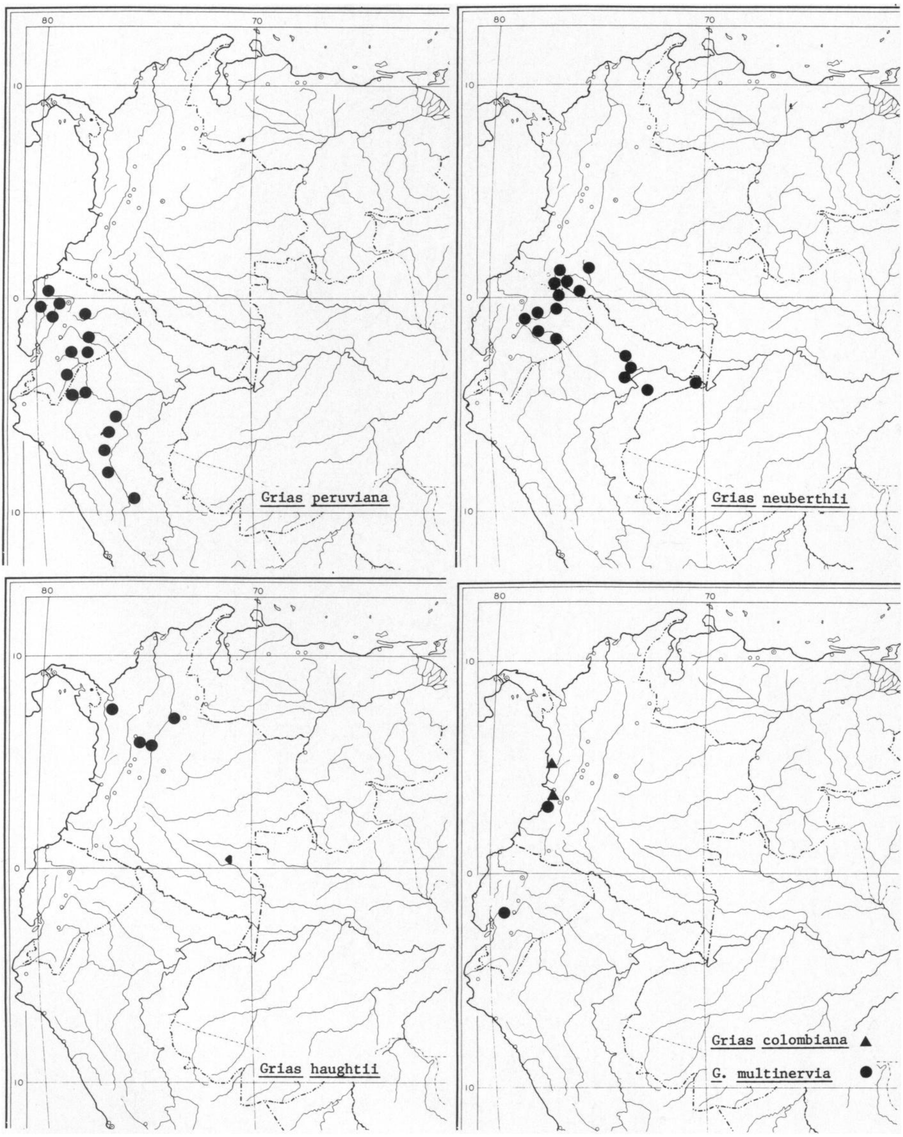


FIG 61. Distributions of *Grias peruviana, G. neuberthii, G. haughtii, G. colombiana, and G. multinervia.*

high percentage of vitamins and the fruits present no difficulties in transportation.

Local names. COLOMBIA. Membrillo *(Cuatrecasas & Willard 26177).*

Excluded Species

Grias aubletiana Miers, Trans. Linn. Soc. London **30**(2): 299-300. 1874 based on *Pirigara tetrapetala* Aublet = *Gustavia augusta* Linnaeus.

Grias tetrapetala (Aublet) Niedenzu in Engler & Prantl, Nat. Pflanzenfamilien 3(7): 37-38. 1892 based on *Pirigara tetrapetala* Aublet = *Gustavia augusta* Linnaeus.

Grias megacarpa Dwyer, Ann. Missouri Bot. Gard. **52:** 354. 1965 = *Pouteria fossicola* Cronquist, Sapotaceae.

ALLANTOMA

by

GHILLEAN T. PRANCE

4. **Allantoma** Miers, Trans. Linn. Soc. London **30:** 170, 291. 1874, pro parte, androphoro excl.; Niedenzu in Engl & Prantl, Nat. Pflanzenfam. **3**(7): 41. 1892, pro parte, androphoro excl.; Ducke, Arch. Jard. Bot. Rio de Janeiro **4:** 155. 1925; Eyma, Polygon. Guttif. Lecythid. Surin. 54-61. 1932; Sprague, J. Bot. **70:** 231. 1932; Knuth, Pflanzenreich IV. **219a:** 39-43. 1939.

Couratari sensu Berg, Mart. Fl. Bras. **14**(1): 506. 1858, pro parte.
Goeldinia Huber, Bol. Mus. Paraense Hist. Nat. **3:** 438. 1902.

Small to medium trees. Leaves alternate, entire, glabrous. Inflorescences racemes or once-branched racemose panicles, terminal or subterminal. Flowers hermaphrodite, 15-22 mm long. Receptacle campanulate. Sepals (5-)6, united at base with triangular small lobes at apex. Petals 6, oblong. Androecium urceolate, only slightly asymmetrical, the apex divided into 8-10 inward-reflexed lacinae with anthers at the apex of most of them, with additional stamens inserted sparsely all over the interior of androecium on short thick reflexed filaments, stamens ca 30, all anthers fertile. Ovary (3-)4-5-locular, with numerous ovules in each loculus. Style short with a rounded undivided stigmatic surface. Pyxidium woody, tubular-cylindrical to cylindrical campanulate, straight or slightly curved, always longer than broad. The operculum tack shaped, 4-5 angular, readily dehiscent from the base of the pyxidium. Seeds narrowly linear-elongate, with a caducous flattened stipe-like funicle, not winged, the exterior of testa verrucose.

Lectotype. *Allantoma torulosa* Miers (= *A. lineata* (Mart. ex Berg) Miers). see Sprague, J. Bot. **70:** 231. 1932. The name *Allantoma* is derived from the Greek αλλ∝ς = sausage, and δμος = like; referring to the long cylindrical pyxidium.

When Miers described the genus *Allantoma,* he included twelve species. Three of these were known from flowering material and nine from fruiting collections. The three flowering species were later included in *Couratari* where they belong *(A. multiflora* (Smith) Miers, *A. subramosa* Miers and *A. fagifolia* (Berg) Miers). The remaining nine of Miers' species belong to *Allantoma* as defined here. Sprague (1932) and Eyma (1932) have both given reasons for regarding the fruiting species as typical of *Allantoma,* and Sprague chose *A. torulosa* Miers as the lectotype. I agree with these workers that *Allantoma* was based more on fruit characters, and can thus be maintained as the valid name for the material included in it in the present work.

Distribution. A single species confined to the river margins of eastern and central Amazonian Brazil, and extending to the upper Río Orinoco in Venezuela (Fig 63).

Taxonomic history of Allantoma

The genus *Allantoma* was described by Miers (1874) to accommodate six species previously placed in *Couratari* and *Lecythis* by their authors, as well as six new species. The three species with flowering material (listed above), and placed in *Allantoma* by Miers, have later been transferred to *Couratari.* The other nine species were known to Miers from fruiting material, six of them by the pyxidium only with no leaves or branches, and they all belong to *Allantoma* as it is defined here. Niedenzu (1892) followed Miers' definition of the genus in his account for Engler's *Pflanzenfamilien.*

In 1902, Huber described the new genus *Goeldinia* in which he included two species that were later included in *Allantoma* by Ducke (1925) who reduced them to synonymy under *A. lineata.* It is not surprising that Huber proposed the new genus *Goeldinia* from his flowering material because of Miers' association of *Couratari* flowers with *Allantoma.*

The circumscription of the genus *Allantoma* was discussed in length and resolved satisfactorily by Eyma (1932) and Sprague (1932) in mutual cooperation. Eyma realized that *Allantoma* was a heterogeneous assemblage, and that it contained two very different elements, i e that the flowering species described by Miers do not belong in the same genus as the fruit described by Miers. This posed a nomenclatural problem and a problem in the typification of the genus since Miers did not select a type species. Eyma decided that the fruiting characters were the most important differences of Miers' genus *Allantoma* from the related genera. The generic name is derived from the shape of the fruit (sausage-like). Consequently Eyma considered the flowers described by Miers as part of *Couratari,* and the fruit as *Allantoma* sensu stricto. Eyma also studied the flowers of *Allantoma* sens. str. which are quite different from those of the three species of *Couratari* originally included in *Allantoma.* Eyma sought the help of Sprague (1932) for the nomenclature of his re-defined *Allantoma.* Sprague chose *A. torulosa* as the lectotype of the genus since that species has fruit typical of those described by Miers. Thus purged of the species of *Couratari, Allantoma* is a most distinct genus which is not easily confused with other genera since it differs in characters of both the flowers and fruit.

Knuth (1939b) followed Eyma's circumspection of *Allantoma.* He included twelve species (nine of Miers and three new ones, one of which was known by an empty pyxidium only), and he divided the genus into two sections: *Pentakolopos* with a five chambered pyxidium, and *Tetrakolpos* with four chambers. He also provided a key to his twelve species which was based entirely on minute differences of the pyxidia. These twelve species are all reduced to a single species, *A. lineata,* in the present study. It is usually possible to collect at least five of the 'species' recognized by Knuth on the same tree. For example, I have collected 4 and 5 chambered fruit on the same tree near to Manaus, yet this was Knuth's primary division of the genus into sections.

In spite of all the confusion in the history of *Allantoma* it is in fact a very distinct genus, and is easily recognized when complete material is studied. The problems arose from the use of inadequate material as has so often been the case in the Lecythidaceae.

1. **Allantoma lineata** (Martius ex Berg) Miers, Trans. Linn. Soc. London **30:** 297, *t 65, fig 4-5.* 1874; Ducke, Arch. Jard. Bot. Rio de Janeiro **4:** 155, *t 16.* 1925; Knuth, Pflanzenreich IV. **219a:** 40. 1939.
Figs 3N, 9, 11S-U, 16I-K, 62, 63, 64, 65.

Couratari lineata Martius ex Berg, Mart. Fl. Bras. **14**(1): 508, *t 7 & 77.* 1858.

Couratari macrocarpa Martius ex Berg, Mart. Fl. Bras. **14**(1): 509, *t 79, fig 9.* 1858. Type. *Martius sn,* Brazil, Pará, fruit only (holotype, M).

Allantoma macrocarpa (Martius ex Berg) Miers, Trans. Linn. Soc. London **30:** 295, *t 64, fig 9.* 1874; Knuth, Pflanzenreich IV. **219a:** 41. 1939.

Couratari aulacocarpa Martius ex Berg, Mart. Fl. Bras. **14**(1): 509, *t 79, fig 2.* 1858. Type. *Martius sn* Brazil, Pará, fruit only (holotype, M).

Allantoma aulacocarpa (Martius ex Berg) Miers, Trans. Linn. Soc. London **30:** 296, *t 65, fig 9.* 1874; Knuth Pflanzenreich IV. **219a:** 42. 1939.

Couratari dictyocarpa Martius ex Berg, Mart. Fl. Bras. **14**(1): 510, *t 79, fig 3.* 1858, synon. nov. Type. *Martius sn,* Brazil, Pará, fruit only (holotype, M).

Allantoma dictyocarpa (Martius ex Berg) Miers, Trans. Linn. Soc. London **30:** 297, *t 64, fig 10.* 1874; Knuth, Pflanzenreich IV. **219a:** 42. 1939.

Allantoma torulosa Miers, Trans. Linn. Soc. London **30:** 293, *t 64, fig 1-3.* 1874; Knuth, Pflanzenreich IV **219a:** 41. 1939, synon. nov. Type. *Farries 65*[5], Brazil, Pará, Culantingo, fr (holotype, BM).

Allantoma cylindrica Miers, Trans. Linn. Soc. **30:** 294, *t 64, figs 4-8.* 1874; Knuth, Pflanzenreich IV. **219a:** 43. 1939. Type. *Farries sn,* Brazil, Pará, Cametá, fruit only (holotype, K).

Allantoma burchelliana Miers, Trans. Linn. Soc. London **30:** 294, *t 65, fig 6-8.* 1874; Knuth, Pflanzenreich IV. **219a:** 41. 1939. Type. *Burchell 9314*[6], Brazil, Pará, (holotype, K not seen; isotype fragment, BM).

Allantoma scutellata Miers, Trans. Linn. Soc. London **30:** 296, *t 65, fig 1-3.* 1874; Knuth, Pflanzenreich IV. **219a:** 41. 1939, synon. nov. Types. *E. Home sn,* Brazil, fruit only (syntype, missing, cited as Linnaean Society Herbarium by Miers, but disposed of to unknown source by the Society when the non-Linnean herbaria were sold); *without data sn,* fruit only (syntype, BM).

Allantoma corbula Miers, Trans. Linn. Soc. London **30:** 297, *t 65, fig 10-11.* 1874; Knuth, Pflanzenreich IV. **219a:** 40. 1939, synon. nov. Type. *Without data sn,* fruit only (holotype, BM).

Goeldinia ovatifolia Huber, Bol. Mus. Paraense Hist. Nat. **3:** 438. 1902. Type. *Huber MG 1859,* Brazil. Pará, Aramá, fl (holotype, MG; isotype, RB 17304).

Goeldinia riparia Huber, Bol. Mus. Paraense Hist. Nat. **3:** 439. 1902. Type. *M. Guedes MG 2223,* Brazil, Pará, Breves, Furo Macujubim, fl (holotype, MG; isotype, RB 17303).

Allantoma dilatata Knuth, Pflanzenreich IV. **219a:** 42. 1939, synon. nov. Type. *Ducke RB 23639,* Brazil, Amazonas, Manaus, fl (holotype, B, lost; isotypes, INPA, RB).

Allantoma caudata Knuth, Pflanzenreich IV. **219a:** 42. 1939, synon. nov. Type. *Ducke RB 23638,* Brazil, Amazonas, Manaus, Tarumã, fl (holotype, B, lost; isotypes, IAN, INPA, K, RB, US).

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[5] Cited as 69 by Miers, but labelled 65 at the British Museum. Miers suggested that the type locality is in fact the Rio Curuatingo which flows into the Amazon east of Santarém.

[6] Part of *Burchell 9314* is the type of *Bertholletia nobilis* Miers = *B. excelsa.*

Small to medium sized tree, usually about 10 m tall, rarely larger, the young branches glabrous. Leaves with laminas usually oblong, but from ovate to oblong-lanceolate, coriaceous, 10.0-29.0 cm long (usually 12.0-20.0 cm long), 5.0-11.5 cm broad, the margins entire or slightly revolute to undulate, long-acuminate to caudate at apex, with acumen 10.0-20.0(-30.0) mm long, rounded to subcuneate at base, glabrous on both surfaces, midrib prominent beneath, prominulous above; primary veins 18-25 pairs, prominulous above, prominent beneath, the secondary venation plane; petioles 12.0-20.0 mm long, canaliculate, glabrous, not winged. Inflorescences terminal or subterminal racemes or little-branched panicles of racemes, the rachis and branches glabrous, conspicuously lenticellate; bracts lanceolate, ca 2.0 mm long, membraneous, early caducous; pedicels 1.0-3.0 mm long, glabrous. Hypanthium campanulate, 7.0 mm long, the lobes 5-6 rather indistinct and little divided, triangular, glabrous on exterior. Petals 5, oblong, fleshy, white, lenticellate. Androecium glabrous, to 10.0 mm long, the apex divided into 8-10 inward-reflexed lacinae with anthers at the apex of most of them, the stamens also borne on short reflexed filaments scattered over the interior surface of the androecium. Ovary 4-5 locular (3 locular in one collection) with numerous ovules in each loculus. Style very short. Pyxidium typically tubular-cylindrical, but varying from campanulate-cylindrical to cylindrical, usually of almost equal width from near top to base, sometimes slightly curved especially when young, 7.0-18.0 cm long, 3.5-6.5 cm broad, crustaceous on exterior, often cracking irregularly when dry, 4-5 locular, the calycine ring 5.0-10.0 cm below apex; operculum 5.0-12.0 cm long, 4-5 angular, the apex convex to deeply concave, usually concave; seeds narrowly linear-elongate, 5.0-6.0 cm long with caducous stipe-like funcile to 2.0 cm long, the exterior of the angled edges verrucose.

Type. *Poeppig 3036,* Brazil, Pará, Colares I., fr (holotype, W; isotype, B, lost; isotype fragment, F).

Distribution. River margins in Amazonian Venezuela and collected in Brazil from Manaus to eastern Pará. Flowering throughout the year, but collected in flower June-January, and flowering most profusely in October and November.

Representative collections: VENEZUELA. Terr. Amazonas: Reserva Forestal El Sipapo, margin of Río cuao between Sipapo and Raudel del Danto, *Blanco 1291* fr (NY, VEN); Orinoco below Caño Yapacana, *Wurdack & Adderley 43035* young fr (NY), below San Fernando de Atabapo, Caño Morocoto, *Gentry et al 10951* fr (MO, NY). BRAZIL. Amazonas: Rio Negro, Barcelos, *Fróes 28348;* Lower Rio Negro, Santa Izabel, *Ducke 166* st (A); Uipiranga, *J. G. Kuhlmann RB 21499*^{7} fl (RB, S, U), Baia de Buiaçú, *Prance et al 10454* fr (INPA, K, MG, NY, U, US), *11498* fl fr (INPA, MG, NY); Manaus, Rio Taruma, *L. Coêlho & Mello INPA 4263* fl (IAN, INPA, MG, NY), *Ducke 1414* fl (A, F, IAN, MG, NY, R, US), *2080* fl (IAN, R75273, U), *Mello INPA 3027* fl (MG 21161, INPA), *Prance et al 11618* fr (INPA, MG, NY), *17549* fl (INPA, NY), *23254* fr (INPA, NY, S), *Rodrigues et al 8705* fl (INPA), *Schultes & Rodrigues 26143A* fl (INPA); Manaus, Ponta Negra, *Ducke RB 23640*^{7} fl (G, K, P, RB, S, U, US); Manaus and vicinity, *Chagas & D. Coêlho INPA 3267* fl (IAN, INPA, MG, NY), *D. Coêlho INPA 2256* fl (INPA, MG), *L. Coêlho INPA 1044* st (INPA, MG), *INPA 2215* fl (INPA, MG), *INPA 4273* fl (INPA, MG, NY), *INPA 6331* fr (INPA), *Ducke 298* fl (A, F, K, MO, NY, R, S, US), *Rodrigues & Chagas 2128* fr (INPA, MG), *Rodrigues & Monteiro 9105* fr (INPA, NY); Rio Preto, Manaus-Itacoatiara road km 80, *D. Coêlho INPA 35208* fr (INPA), *Prance et al 3160* fl (INPA, MG, NY); Rio Urubu, near Cachoeira Lindoia, *Rodrigues 303* fl (INPA); Rio Cuieiras, *Ongley & Ramos P21748* fr (INPA, NY). Pará: Rio Trombetas, Jacaré, *Ducke RB 21481*[7] fl (K, RB, S, U, US); Rio Mapuera, *Ducke MG 9036* fl (MG, RB 17305, US); Santarém, *Dahlgren & Sella sn* fr only (F); Acará, Jacarequara, *M. Silva 582* fr (MG); Rio Macujubim, Breves, *Ducke RB 15899* fr (RB); Belém and vicinity, *Archer 7829* fl (IAN, NY, US), *Black 827* fl (IAN, NY, U), *Cavalcante 344* fl (MG), *372* fl (IAN, MG), *T. Guedes 216* fl (IAN), *Ducke MG 15506*[7] fl (MG, P, RB 145140, US), *RB 17300* fl (RB, S, U), *Pereira 4923* fl (F, NY), *Pires 6991* fl (IAN), *12185* fl (IAN), *51738* st (NY, US), *Pires & Black 729* st (IAN), *1530* fr (IAN, R, RB), *M. Silva 709* fr (MG), *N. T. Silva 482* st (IAN), *57850* fl (NY, US); Santa Izabal, *Museu Goeldi 10126* fl (MG, RB 17301); Castanhal, *M. Guedes MG 1662* fr (MG, RB 17302, US); Rio Moju, *Black 54-16306* fl (IAN), *Fróes 33163* fr (IAN), Rio Anapú, *Fróes 32993* fr (IAN), *Oliveira 1263* fl (IAN). Guanabara: Cultivated in Rio de Janeiro Botanic Garden, *Brade RB 29074* fl (RB), *J. G. Kuhlmann RB 78322* fl (RB).

Local names and uses. Venezuela: *Tabari.* Brazil: *Cerú, Cherú, Churú, Xurú, Tauarí.* The nut is edible and is known in English as "Skittle-nut," but is not widely used. The bark is used as a cigarette wrapper in Venezuela.

The twelve species of *Allantoma* recognized by Knuth (1939b) are a good example of the multiplication of species of Lecythidaceae based on inadequate material, using minute differences with little attention to the biology of the group. Eight out of the twelve species recognized by Knuth were originally described from pyxidia alone without any material of the leaves or flowers. Furthermore, the pyxidia of two species *(A. corbula* Miers and *A. aulacocarpa* (Mart. ex Berg) Miers) are empty; they lack seeds and opercula. Four of these eight fruits were described as separate species by Miers (1874), three by Berg (1858), and one by Knuth (1939b), who recognized all the species of the former authors.

As can be seen above, I have reduced into synonymy under *Allantoma lineata* three of the four species of *Allantoma* described by Berg (1858) in the genus *Couratari.* Since *A. lineata* was the only Berg species based on adequate material (leaves and fruit), it is chosen as the name in preference to the other three Berg names.

The main characters used to separate the "species" by previous authors were the number of loculi of the pyxidia, and differences in size and shape of the pyxidia and opercula. Knuth (1939b), divided the genus into two sections based on the number of locules in the pyxidia (Section *Pentakolpos* with 5; and Section *Tetrakolpos* with 4). This is an absolutely false division since the number of compartments is not even a specific character. I have collected pyxidia with both four and five compartments from the same tree at Tarumã near Manaus *(Prance et al 11618).* Since the major key character used by Knuth breaks down, his key and his division of the genus into twelve species is meaningless. The number of loculi of the ovary and fruit has been much over-used as a taxonomic character in the Lecythidaceae. Its use has led to the creation of too many genera and species. Even in *Couratari* a genus characterized by the 3-partite pyxidium there are a few individuals with 4-partite pyxidia. The ovary of several collections of *Allantoma* was found to vary from 4-5 locular within the same individuals.

The other main characters used to separate the species of *Allantoma* were

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[7] Paratypes of *A. dilatata.*

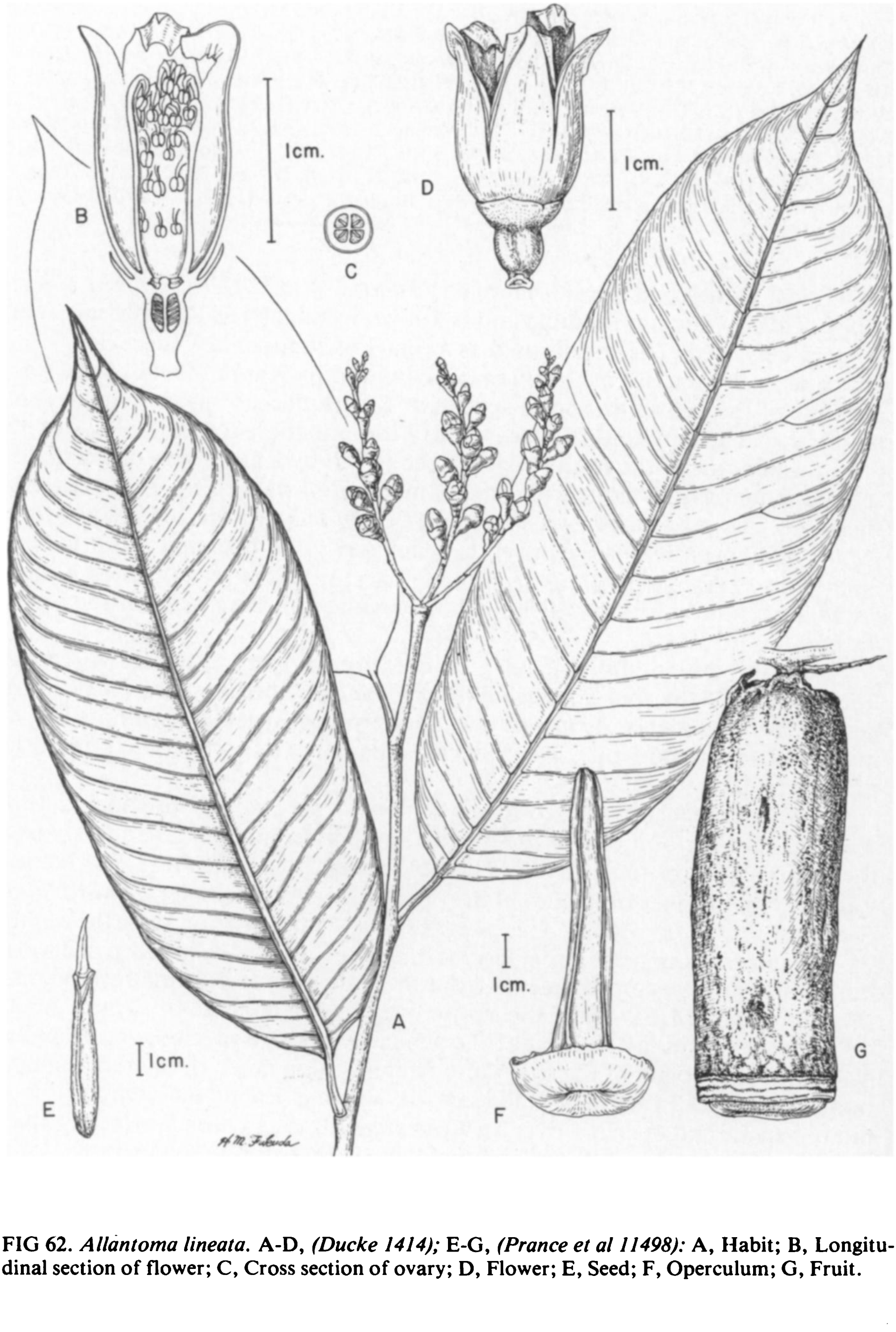

FIG 62. *Allantoma lineata.* A-D, *(Ducke 1414);* E-G, *(Prance et al 11498):* A, Habit; B, Longitudinal section of flower; C, Cross section of ovary; D, Flower; E, Seed; F, Operculum; G, Fruit.

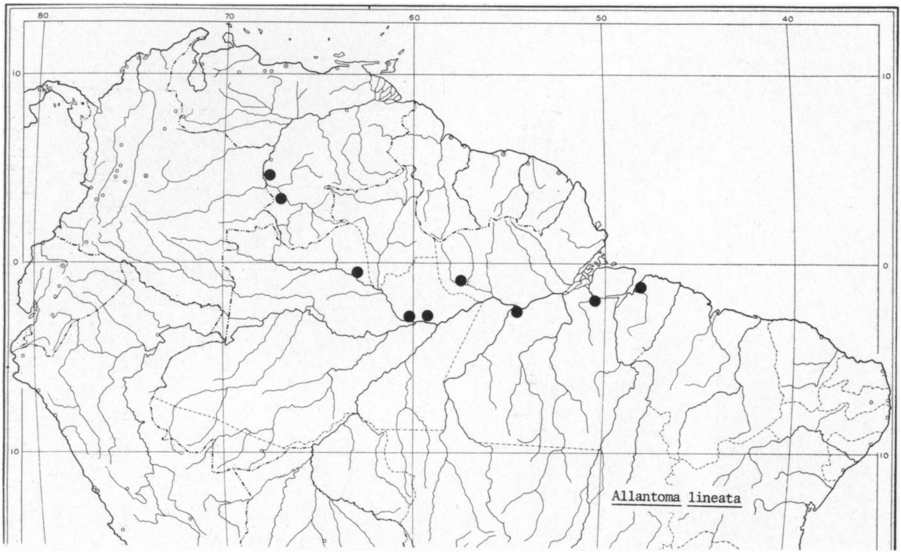

FIG 63. Distribution of *Allantoma lineata.*

small differences in size and shape of the pyxidia. These differences are in fact due to collections made at different stages of fruit development, and they are also due to the effect of minor ecological differences and to natural variation within the same individuals. For example: *Allantoma dictyocarpa* (Mart. ex Berg) Miers, was described from a single very young and immature fruit which naturally differs in size and shape from the adult fruit; *Allantoma aulacocarpa* (Mart. ex Berg) Miers was described from a single very old and half-rotted pyxidium which has a different surface texture because the outer layers have rotted off exposing the fibrous ridged inner layer of the pericarp. The method of drying and the stage of maturity of the collection considerably affect the outer texture of the pericarp and the opercular shape, e g *Prance 11478* was dried in an oven and consequently has many fissures and cracks in the pericarp, but *Prance 11618* was air dried and has a smooth pericarp. The operculum may remain convex or become concave according to the drying procedure and the stage of maturity when collected. These are all features which have been used as taxonomic characters to separate species by previous workers. Figures 64 and 65 illustrate some of the type specimens for *Allantoma* and also the variation from a single gathering.

The two species proposed by Knuth, *Allantoma caudata* and *A. dilatata* were based on minor variation of fruit and leaf shape which fall well within the range of variation of *A. lineata.*

In light of the above facts a large synonymy is presented here. Ducke (1925), has already suggested that four of Miers' species of *Allantoma* are synonymous with *A. lineata.*

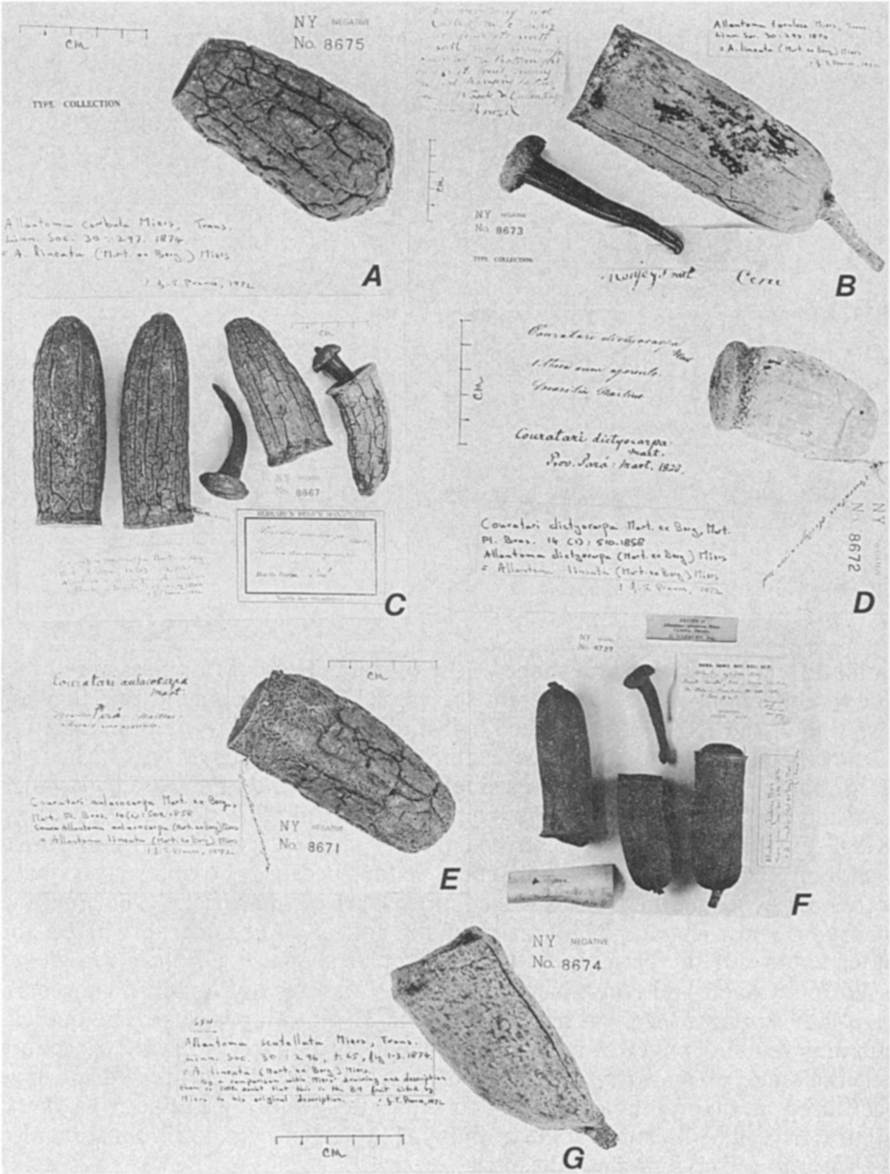

FIG 64. The holotypes of seven 'species' of *Allantoma* described from empty pyxidia only. This shows how pyxidia in various stages of development and deterioration have been described as new species. All seven are synonyms of *A. lineata,* and the total variation is little more than the fruit collected from a single tree illustrated in Fig 65. A, C and E are old fruit in various stages of deterioration probably picked up off the ground; B and F are mature fruit as they appear on the tree, and D and G are young fruit collected while still immature. A, *A. corbula* Miers (without collector's name); B, *A. torulosa* Miers *(Farries 65);* C, *A. macrocarpa* (Mart. ex Berg) Miers *(Martius sn);* D, *A. dictyocarpa* (Mart. ex Berg) Miers *(Martius sn);* E, *A. aulacocarpa* (Mart. ex Berg) Miers *(Martius sn);* F, *A. cylindrica* Miers *(Farries sn);* G, *A. scutellata* Miers *(Home sn).*

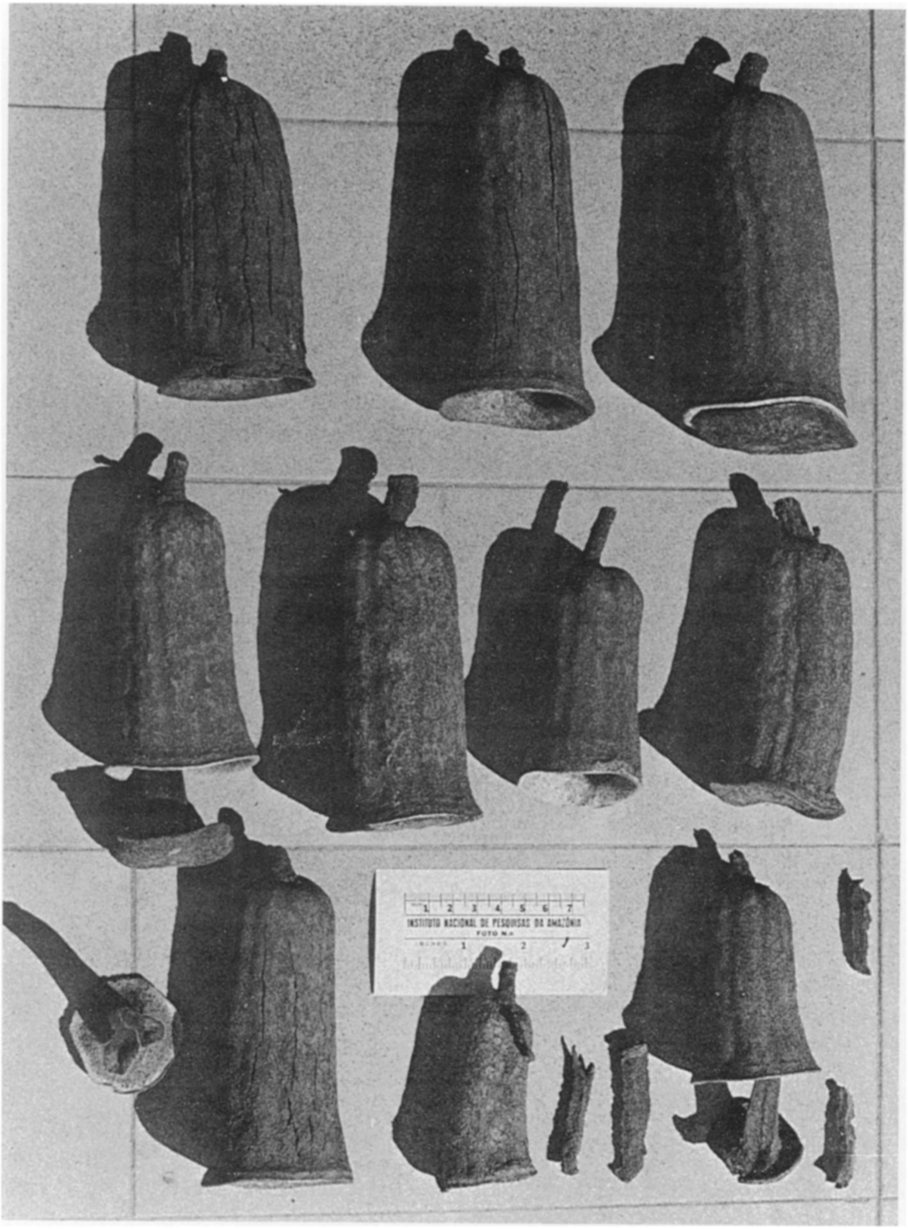

FIG 65. The variation of the fruit of a single collection of *Allantoma lineata* (Prance et al 11618).

The collection *Wurdack & Adderley 43035,* from the Rio Orinoco, Amazonas, Venezuela, is particularly interesting since it is geographically far removed from all other collections studied. *Allantoma lineata* is otherwise known only from the lower Rio Negro of Brazil, eastwards to eastern Pará. This collection is also the only one studied with very young developing fruit. These young fruit still have the persistent corolla and androecium above the fruit. The petals are still closed in all the flowers even in those which persist above quite well developed fruit. This is indicative of self-pollination.

Dubious species

Allantoma impressa Knuth, Pflanzenreich IV. **219a:** 41. 1939. Type. Without data, Brazil, fruit only (holotype, B, lost).

Since the holotype of this species was without any collector's data, and was lost at Berlin, it is unlikely that material of it will be found. Judging from the description in the protolog, it is probable that *A. impressa* is also part of *A. lineata,* but I hesitate to place it in synonymy without studying the type.

Excluded Species

Alantoma multiflora (J. E. Smith) Miers, Trans. Linn. Soc. London **30:** 291. 1874 = *Couratari multiflora* (J. E. Smith) Eyma.

Allantoma subramosa Miers, Trans. Linn. Soc. London **30:** 292. 1874. Flowers = *Couratari multiflora* (J. E Smith) Eyma; leaves = *Couratari guianensis* Aubl.

Allantoma fagifolia (Miquel) Miers, Trans. Linn. Soc. London **30:** 298. 1874 = *Couratari fagifolia* (Miq.) Eyma = *Couratari multiflora* (J. E. Smith) Eyma.

CARINIANA

by

GHILLEAN T. PRANCE

5. **Cariniana** Casaretto, Nov. Stirp. Bras. Dec. **4:** 35-37. 1842; Miers, Trans. Linn. Soc. London **30:** 169, 284-291. 1874; Niedenzu in Engl. & Prantl, Nat. Pflanzenfam. **3**(7): 40. 1892; Knuth, Pflanzenreich IV. **219a:** 33-39. 1939; Macbride, Publ. Field Mus. Nat. Hist., Bot. Ser. **13**(4): 238-239. 1941.

Couratari pro parte auct. div. non Aublet viz, de Candolle, Prodromus **3:** 294. 1828; Berg, Linnaea **27:** 462-463. 1856; Benth. & Hook., Gen. Pl. **1**(2): 722. 1865; etc.

Couratari section *Cariniana* Berg, Mart. Fl. Bras. **14**(1): 510-514. 1858.

Amphoricarpus Spruce ex Miers, Trans. Linn. Soc. London **30:** 288. 1874, in syn. sub. *Cariniana,* non *Amphoricarpus* Visiani.

Medium to large trees. Leaves alternate, entire, glabrous or with pubescence of simple hairs, or with hair-filled domatia. Inflorescences racemes or panicles, usually terminal, rarely axillary. Flowers hermaphrodite, 7.0-15.0 mm long. Receptacle conical to campanulate. Sepals 6, small. Petals 6, oblong. Androecium obliquely hood-shaped, only slightly asymetrical, with stamens inserted in a complete circle either all over the interior or at the apex only; the stamens 10-150, often markedly reflexed inwards, all anthers fertile. Ovary 3-locular with numerous ovules in each loculus. Style very short with a 3-partite stigmatic surface. Pyxidium woody, cylindrical, campanulate or conical, always longer than broad. The operculum tack-shaped, readily dehiscent from the base of pyxidium, the columella triangular. Seeds with long unilateral wings.

Type. *Cariniana brasiliensis* Casaretto (= *C. legalis* (Mart.) Kuntze). The genus was named in honor of Prince Eugene de Savioe-Carignan who sponsored Casaretto's 1839-1840 voyage to Brazil.

Knuth (1939b) cited *C. excelsa* as the type of the genus, but this cannot be so since *C. brasiliensis* was described together with the generic description in Casaretto's fourth Decas (1842) while *C. excelsa* was not published until the following year in Decas five (1843).

Distribution. One species in northern Colombia and Venezuela, the rest in Amazonia and the coastal part of eastern central Brazil, but predominantly an Amazonian genus.

Taxonomic History of *Cariniana*

The genus *Cariniana* was described by Casaretto (1842) based on the species *C. brasiliensis.* The following year Casaretto (1843) published a second species, *C. excelsa.* The genus *Cariniana,* as defined here, is quite distinct, but both Casaretto's names are now in synonymy because older names existed in *Couratari* for both species *(C. brasiliensis* = *C. legalis* (Mart.) Kuntze and *C. excelsa* = *C. estrellensis* (Raddi) Kuntze).

Berg (1856) reduced *Cariniana* into synonymy under *Couratari* and he placed *Cariniana brasiliensis* as a synonym of *Couratari legalis.* Two years later, Berg (1858), in his account for Martius' *Flora Brasiliensis,* divided *Couratari* into two sections; *Eucouratari* and *Cariniana.* Section *Cariniana* contained three species: *C. legalis* and *C. domestica* described by Martius (1837) and *C. estrellensis* described by Raddi (1820). Section *Eucouratari* contained eight species now placed in *Couratari* and *Allantoma* and one new species, *Couratari uaupensis* which has later been transferred to *Cariniana.* Bentham and Hooker (1865) also treated *Cariniana* as a synonym of *Couratari.* Miers (1874) correctly reinstated the genus *Cariniana* which clearly differs from *Couratari* in the androecium and the seeds. Miers included seven species, four of which were mentioned above: *C. excelsa, C. domestica, C. brasiliensis* and *C. uaupensis.* The other three were new species, *C. rubra, C. exigua* and *C. pyriformis.* These species all belong to *Cariniana* although their nomenclature has since been somewhat altered. Niedenzu (1892) followed Miers exactly and listed the same seven species.

During the present century various species have been added to *Cariniana,* but the circumscription of the genus has not changed since Miers reinstated it. Knuth (1939b) included thirteen species which with one exception belong to *Cariniana. Cariniana paraensis* (Mart. ex Berg) Knuth, which was transferred from *Couratari* to *Cariniana* by Knuth, is a *Couratari.* Since Knuth's monograph only two species, *C. pauciramosa* Rodrigues (1974) and *C. penduliflora* Prance & Anderson (1976) have been added to the genus.

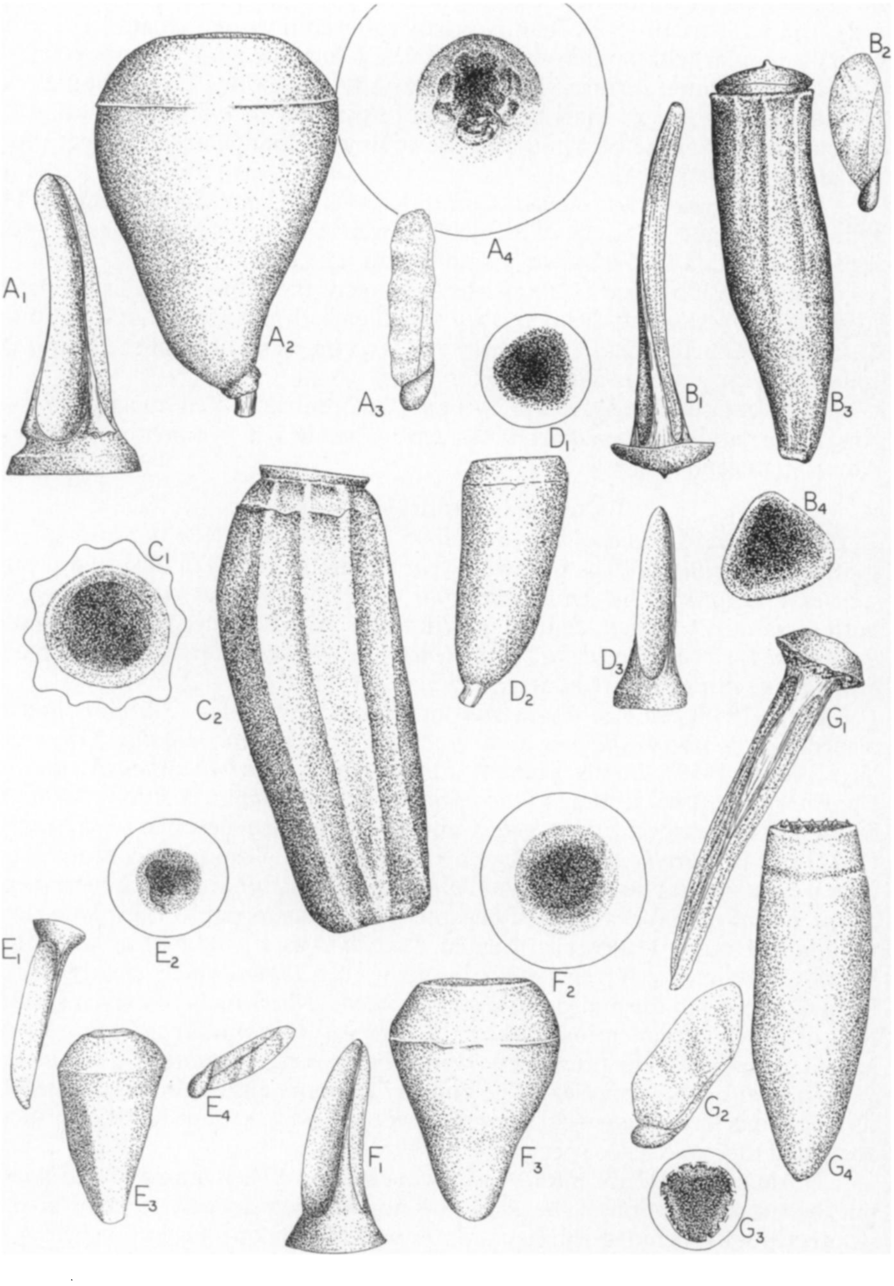

FIG 66. Fruit of species of *Cariniana:* A, *C. micrantha (Krukoff 5095);* B, *C. decandra (Krukoff 1375);* C, *C. multiflora (Krukoff 8624);* D, *C. legalis (Barreto 1562);* E, *C. domestica (Krukoff 5597);* F, *C. pyriformis (Pennell 4090)* G, *C. estrellensis (Irwin et al 8885).* All ×0.47.

Key to Species of *Cariniana*

1\. Inflorescence predominantly terminal and subterminal; pyxidium without teeth at line of opercular dehiscence.

2\. The leaf undersurface with distinct small domatia at junction of primary veins and midrib, the domatia with a tuft or a few pilose hairs; pyxidium extremely thick, ca 8.0-12.0 mm at line of opercular dehiscence.

3\. Leaf laminas oblong to lanceolate, 2.0-3.2 cm broad, the acumen straight, the midrib glabrous; petioles 3.0-4.0 mm long; pyxidium conical, smooth not ridged, 4.5-5.5 cm diameter at calycine ring, the operculum diameter 3.0 cm (Northern Colombia and Venezuela). 1. *C. pyriformis.*

3\. Leaf laminas oblong-ovate, 4.0-6.5 cm broad, the acumen curved, the midrib puberulous; petioles 5.0-10.0 mm long; pyxidium campanulate, slightly costate on exterior, 3.0-4.5 cm diameter at calycine ring, the operculum diameter 1.5-2.5 cm.

4\. Petioles 5.0-10.0 mm long; inflorescence erect.

5\. Leaves 6.0-12.0 cm long, tapering to apex from well above mid-point, the primary veins 19-25 pairs; pyxidium warted on exterior, 4.0-4.5 cm broad at calycine ring (Amazonia). 2. *C. domestica.*

5\. Leaves 10.5-16.0 cm long, tapering to apex from well below mid-point, the primary veins 24-29 pairs; pyxidium smooth not warted on exterior, 3.0-3.7 cm broad at calycine ring (Brazil-Goiás). 3. *C. rubra.*

4\. Petioles 15.0-18.0 mm long; inflorescence pendulous. (Brazil-Rondônia). 4. *C. penduliflora.*

2\. The leaf undersurface without domatia and glabrous at junction of primary veins and midrib; the pyxidium rarely thick at line of opercular dehiscence, usually quite thin (less than 4.0 mm thick).

6\. Leaves 22.0-30.0 cm long; inflorescence branches crustaceous (Upper Rio Negro, Brazil). 5. *C. uaupensis.*

6\. Leaves to 23.0 cm long in *C. multiflora,* but usually much shorter; inflorescences branches usually smooth, crustaceous only in *C. pachyantha.*

7\. Fertile stamens 10-25, always strongly reflexed; leaf margins entire or serrate, leaves 6-23 cm long.

8\. Leaf margins crenate.

9\. Leaf primary veins 22-40 pairs, closely spaced; inflorescence multiple branched; pyxidium with distinct calycine ring ± 1 cm below apex. 7. *C. multiflora.*

9\. Leaf primary veins 9-20 pairs, widely spaced; inflorescence little branched (2-5 branches); pyxidium without distinct calycine ring or only small supracalycine area and indistinct calycine ring.

10\. Inflorescence twice branched; petioles 15-40 mm long × 1.5-2 mm thick, not winged, fruit not lipped at opercular opening. 8. *C. kuhlmannii.*

10\. Inflorescence 4-6 branched; petioles 12-15 mm long × 3 mm thick, winged; fruit lipped at opercular opening. 9. *C. pauciramosa.*

8\. Leaf margins entire.

11\. Primary leaf veins 17-19 pairs; the inflorescence branches crustaceous (Western Amazonia). 6. *C. pachyantha.*

11\. Primary leaf veins 9-12 pairs; inflorescence branches smooth, not crustaceous.

12\. Leaves coriaceous, apex acute or shortly obtuse-acuminate; fruit not costate (Central Amazonia). 10. *C. integrifolia.*

12\. Leaves chartaceous, apex with finely pointed distinct acumen; fruit longitudinally costate (Southern Amazonia). 11. *C. decandra.*

7\. Fertile stamens 40-150, often erect; leaf margins serrate to crenulate, leaves to 10.0 cm long.

13\. Petioles 3.0-7.0 mm long; leaf margins finely serrate-crenulate; petals 5.0-8.0 mm long.

14\. Primary leaf veins 18-25 pairs; pyxidium 7.0-10.0 cm long, 4.5-7.0 cm broad at broadest point; operculum diameter 2.5-3.7 cm (Amazonia). 12. *C. micrantha.*

14. Primary leaf veins 9-11 pairs; pyxidium 4.5-6.5 cm long, 1.5-3.0 cm broad at broadest point; operculum diameter 1.0-1.5 cm (Eastern Brazil). 13. *C. legalis.*

13. Petioles 12.0-17.0 mm long; leaf margins coarsely serrate; petals 11.0-15.0 mm long (Eastern Brazil). 14. *C. ianierensis.*

1. Inflorescence axillary; pyxidium with distinct teeth around rim of line of opercular dehiscence (Eastern Central Brazil and Acre). 15. *C. estrellensis.*

1. **Cariniana pyriformis** Miers, Trans. Linn. Soc. London **30:** 290, *t 63, fig 11-23.* 1874; Pittier, Trop. Woods **1:** 13. 1925; Pittier, J. Wash. Acad. Sci. **19:** 182. 1929; Curran, Trop. Woods **19:** 24. 1929; Knuth, Pflanzenreich IV **219a:** 38. 1939. Figs 17D, 66F, 67

Cariniana exigua Miers, Trans. Linn. Soc. London **30:** 289. 1874. Type. *Prestoe sn,* Trinidad, fr (holotype, K; isotype fragment, BM).

Cariniana clavata Novikova, Trudy Bot. Inst. Akad. Nauk SSSR, Ser. 1, Fl. Sist. Vyss. Rast. 2: 250. 1936. Types *Bosse sn,* Colombia (not seen), *Woronov sn,* Colombia (not seen).

Tree to 50.0 m tall, the young branches sparsely puberulous, soon becoming glabrous. Leaves with laminas lanceolate to oblong 4.5-7.5 cm long, 2.0-3.2 cm broad, the margins crenate, acuminate or cuspidate at apex, the acumen 5.0-20.0 mm long, straight, the base broadly subcuneate, not decurrent; midrib prominent on both surfaces, glabrous beneath; primary veins 18-22 pairs, with domatia and a tuft of hairs at junction with midrib beneath, prominulous and slender on both surfaces, 2.0-4.0 mm apart at base; petiole 3.0-4.0 mm long, puberulous, canaliculate, not winged. Inflorescences of terminal panicles 6.0-12.0 cm long, the rachis and branches tomentellous, pedicels 0.5-1.2 mm long, tomentellous. Calyx ca 3.0 mm long, the lobes triangular, tomentellous on exterior. Petals oblong-lanceolate, 7.0-9.0 mm long, 2.0-3.0 mm broad, rose. The androecium ca 2.0 mm in diameter, white, the stamens ca 50, erect, attached mainly to top of androecium, the anthers globose. Style short. Pyxidium 7.0-8.0 cm long, conical, ca 4.5-5.5 cm broad at calycine ring, the supracalycine zone 1.5-2.0 cm wide, the pericarp very thick at line of opercular dehiscence, 6.0-6.5 cm long, the columella triangular. Seeds pyriform, 8-24 per fruit, 1.3 cm long, 0.7 cm broad, with long unilateral wings.

Type. *Anthoine sn,* Colombia, Córdoba, Plato, Río Sinú (holotype, K).

Distribution. Forests of northern Colombia and northeastern Venezuela. Cultivated outside this range in Trinidad and Jamaica. Collected in flower in December, and in fruit April-May. Cultivated at Singapore Botanic Garden, *(Krukoff 362* st, NY).

COLOMBIA. Chocó: between Río Curiche and Camp Curiche, *Duke 11594* fl (MICH, NY); Bahía Solano, *Killip & García-Barriga 33636* fr only (US); Río Atrato, *Martínez R. sn* st (US); confluence of Ríos Chinadó and Truandó, *Romero-Castañeda 4690* st (COL); Río Truandó, La Teresita, *Gentry 9389* fr (MO, NY). Córdoba: Sahagun, *Pennell 4090* fr only (NY). Norte de Santander: between Puerto Barco and Caño Brandy, La Motilonia, *García-Barriga & Lozano 18416* fr (COL). Bolívar: Estrella, Caño Papayal, lands of Loba, *Curran 353* fr (GH, NY, US); Amaryamiento Rico, lands of Loba, *Curran sn* fr only (US). Santander: Campo Capote, *Nee & Mori 3729* st (NY, WIS). Boyacá: Guaguaqui, *Whitford & Pinzón 11* fr (A, GH, US). VENEZUELA. Zulia: road Machiques to Colon, *Aristeguieta et al 6776* fr (NY, VEN); Sierra Perija, vicinity of Quebrada de Koshida, *Steyermark 99964* fr (NY, VEN). Trujillo, Río Lavo, *Pittier 10934* fl (G, GH, NY, P, US, VEN). TRINIDAD. Cult. *Bot. Garden 1365* fl (K), *3821* fl (K, MICH), *4503* fl (F, US); *Broadway 5086* fl (BM, F, FHO, G, MO, S), *sn* fr only (F); *Eggers sn* fr only (F); *Petford 14055* fr only (F).

FIG 67. Distributions of *Cariniana pyriformis, C. rubra,* and *C. penduliflora.*

Local names and uses. Colombia: *Abarco, Chibuga.* Venezuela: *Bacú.* English: *Colombian Mahogany.* The wood has been exported under the name of Colombian Mahogany, but it is hard to work, the inner bark fiber is used for tying and is very strong.

Ecology. The fruiting season of *C. pyriformis* in the Chocó of Colombia is from November to April (Betancur and Raigosa, 1973).

Cariniana pyriformis is most closely related to *C. rubra, C. domestica* and *C. penduliflora.* These four species form a complex readily distinguished from the other species of the genus by the presence of leaf domatia and by the very thick pericarp of the pyxidium. *Cariniana pyriformis* differs from the three other related species by the narrower oblong-lanceolate leaves with an erect not curved acumen, the shorter petioles, and by the shape of the pyxidium which is also smooth not costate, and is much broader at the calycine ring region.

I have not yet been able to locate type material of *C. clavata,* but judging from the type description and the illustrations it falls well within the range of variation of *C. pyriformis. Cariniana clavata* represents another species described from small differences of pyxidium morphology which do not hold true when further material is studied.

2. **Cariniana domestica** (Martius) Miers, Trans. Linn. Soc. London **30:** 286, *t 63, fig 4-5.* 1874; A. C. Smith, Phytologia **1:** 126. 1935; Knuth, Pflanzenreich IV. **219a:** 36. 1939; Macbride, Publ. Field Mus. Nat. Hist., Bot. Ser. **13**(4): 239. 1941. Figs 11M-O, 66E, 68, 69.

Couratari domestica Martius, Flora **20**(Beibl. 2): 127. 1837; Berg, Mart. Fl. Bras. **14**(1): 510, *t 80.* 1858.

Tree to 50.0 m tall, the young branches puberulous, becoming glabrous but not conspicuously lenticellate. Leaves with laminas oblong-ovate, 6.0-12.0 cm long, 4.0-6.5 cm broad, the margins crenulate, tapered from above the midpoint to apex, acuminate at apex, the acumen 5.0-10.0 mm long, curved, subcuneate at base, slightly decurrent onto petioles, glabrous beneath; midrib prominulous above, prominent beneath, sparsely puberulous on both surfaces becoming glabrous with age; primary veins 19-24 pairs, prominulous on both surfaces, 2.0-5.0 mm apart at base; with distinct domatia at junction with midrib and most veins, the domatia with a small pilose tuft of hair; petioles 5.0-10.0 mm long, slightly winged, sparsely puberulous when young. Inflorescences terminal and subterminal racemose panicles to 15.0 cm long, the rachis and branches sparsely puberulous, not crustaceous; pedicels 0.5-1.0 mm long. Calyx ca 3.0 mm long, turbinate, the lobes triangular, sparsely puberulous on exterior. Petals obovate, ca 6.0-8.0 mm long, usually red, rarely white. The androecium ca 2.0 mm in diameter with numerous (over 50) stamens on filaments inserted all over the inner surface. The style very short. Ovary trilocular. Pyxidium 5.5-7.0 cm long, 3.0-4.0 cm maximum diameter near apex, usually slightly costate on exterior, but not warted, the calycine ring 1.0-1.5 cm below apex, the pericarp thick, to 1.0 cm at line of opercular dehiscence, smooth, without teeth at mouth. Operculum 1.5-1.8 cm diameter at apex, to 5.5 cm long, the columella triangular. The seed wings to 3.0 cm long, the seed more or less pyriform, 8.0 cm long, 4.0 mm broad.

Type. *Silva Manso sn (Herb. Martius 207),* Brazil, Mato Grosso, Cuiabá, fl (holotype, BR; isotypes, FI, G, LE[8], M, NY, P, W; frag, K).

Distribution. Forest on non-flooded ground in southern Amazonian Brazil from Acre to Pará and extending south of Amazonia into the gallery forests of the northern part of the Planalto of central Brazil. Collected in flower September-March.

BRAZIL. Pará: Jurutí Velho, *Ducke RB 21484* fl (RB); Mid Rio Tapajós, Frances, *Ducke RB 15903* fl (G, K, P, RB, S, U, US); Serra do Cachimbo, *Pires et al 6360a* st (IAN, NY); Conceição de Araguaía, *Fróes 29924* fr (IAN); Rio Jamanxim, *L. Coêlho sn* fr (INPA 42004). Maranhão: 35 km S of Loreto, *G. & L. T. Eiten 4304* fr (US). Acre: mouth of Rio Macauhan, tributary

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[8] One LE sheet with this number is a Dilleniaceae.

of Iaco, *Krukoff 5597* fr (A, BM, F, G, GB, K, LE, M, MO, NY, S, SP, U, US); Sena Madureira, *Prance et al 7967* fl fr (INPA, MG, NY, S, U, US), path from Rio Acre to Palmares, *J. G. Kuhlmann 780* fl (RB 21497). Terr Rondônia: 2-4 km E of Mutumparaná, *Prance et al 8834* fl fr (INPA, MG, NY, S, U, US). Mato Grosso: Rio Tapajós, *J. G. Kuhlmann 1083* fl (R 91166); Rio Jaurú, *Hoehne 855* fl (R 53404); Xavantina, *Prance & Silva 59135* fr (F, GH, K, NY, RB, S, U, UB, US), *Ratter et al 565* st (K, NY); Cuiabá, *Hoehne 4015* fl (R 53407), *Lhotzky 92* fl (G); Rio Aripuanã, Salto Dardanelos, *Berg et al P18497* fr (FHO, INPA, NY, S, U, US). Without locality: *Lhotzky sn* fl (W); *Pohl sn* fl (W). BOLIVIA. Beni: Riberalta, *Cárdenas 4164* fl (GH, US); *J. G. Kuhlmann RB 21492* fl fr (K, RB, S, U, US).

Local names. *Cachimbeira, Jequitibá.*

Cariniana domestica is most closely related to *C. pyriformis* and *C. rubra* (see notes under those species for the differences).

The original description does not cite the type collection, but the locality is given as Cuiabá. The material in the Martius Herbarium at Bruxelles was collected by Silva Manso at Cuiabá and this is the type with the duplicates labelled only 'Herb. Martius No. 207.'

3. **Cariniana rubra** Gardner ex Miers, Trans. Linn. Soc. London **30:** 288, *t 63, fig 10.* 1874; Knuth, Pflanzenreich IV. **219a:** 36. 1939, pro parte. Fig 67

Couratari rubra Gardner ex Miers, Trans. Linn. Soc. London **30:** 288. 1874, nom. nud. in syn.

Cariniana carajarum Toledo, Revista Mus. Paulista, Nov. Sér. **4:** 382. 1950, synon. nov. Type. *H. Schultz sn,* Brazil, Goiás, Rio Araguaia, Ilha do Bananal, fruit only (holotype, SP 44809; isotype, NY).

Tree to 15.0 m tall, the young branches glabrescent, not conspicuously lenticellate. Leaves with laminas elliptic, 10.5-16.0 cm long, 4.0-7.3 cm broad, the margins crenulate, gradually tapered to apex from below or at midpoint, acuminate at apex, the acumen 9.0-15.0 mm long, curved, rounded to subcuneate at base, slightly decurrent onto petiole, glabrous beneath; midrib prominulous above, prominent beneath, sparsely puberulous on both surfaces, becoming glabrous with age; primary veins 24-30 pairs, prominulous on both surfaces, 2.0-5.0 mm apart at base, with distinct domatia at junction with midrib and primary veins, the domatia with a small pilose tuft of hair; petioles 7.0-10.0 mm long, slightly winged, sparsely puberulous when young. Inflorescences terminal and subterminal racemose panicles, to 25.0 cm long, the rachis and branches sparsely puberulous, not crustaceous, sparingly lenticellate; pedicels ca 0.5 mm long. Calyx ca 2.5 mm long, turbinate, the lobes triangular, sparsely puberulous on exterior. Petals obovate, ca 8.0 mm long, red. The androecium ca 2.0 mm in diameter, with numerous (over 50) stamens on filaments inserted all over the inner surface. Style very short, ovary trilocular. Pyxidium 7.0 cm long, 4.0-4.5 cm maximum diameter at apex, slightly costate and warted on exterior, the calycine ring 1.5 cm below apex, broadest at the ring, the pericarp thick, 1.3 cm thick at apex, smooth without teeth at line of opercular dehiscence. Operculum 2.0-2.5 cm diameter at apex.

Type. *Gardner 3743,* Brazil, Goiás, Natividade, fl (holotype, BM; isotypes, CGE, K, OXF).

Distribution. Known only from the States of Goiás and Mato Grosso, Brazil. Collected in flower January-March, fruiting around June.

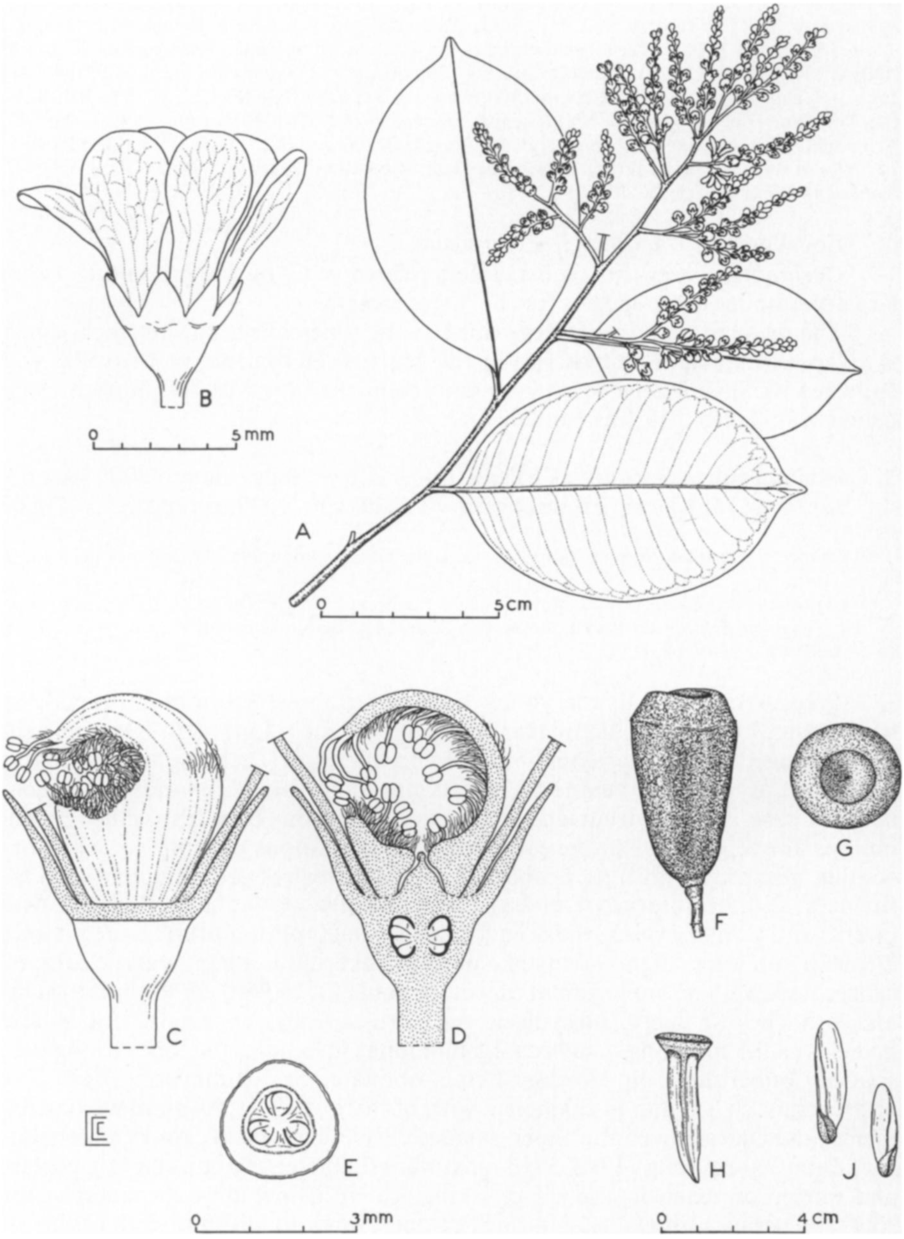

FIG 68. *Cariniana domestica.* A, *(Prance et al 7967);* B-E, *(Prance et al 8834);* F-J, *(Krukoff 5597):* A, Habit; B, Flower; C, Androeciun. in position on summit of ovary, petals removed; D, Longitudinal section of flower; E, Cross section of ovary; F, Lateral view of fruit; G, Apical view of fruit; H, Operculum; J, Seeds.

FIG 69. Distribution of *Cariniana domestica.*

BRAZIL. Goiás: Araguaina, *Irwin et al 21284* fl (IAN, NY); 27 km S of Paraíso, *Irwin et al 21625* fl (IAN, NY, UPS); 8 km S of Cavalcante, *Irwin et al 24195* fr (IAN, NY, UPS); Pousada Quente, Caldas Novas, *Barroso et al sn* fl (RB 141430), *Heringer & Eiten 14105* fl (U, UB); *M. Kuhlmann sn* fl fr (NY, SP). Mato Grosso: Arinos, Piavore, *J. G. Kuhlmann 1086* fl (R 91159); Km 274 Xavantina-Cachimbo road, *Philcox & Ferreira 3902* fl (K, NY), *Santos & Souza R 1655* st (IAN, K, NY); Aripuanã, Salto Dardanelos, *Rosa 77* fr (IAN).

Local names. *Cachimbeira, Cachimbo de macaco, Jequitibá.*

Cariniana rubra is very closely related to *C. domestica* and may ultimately prove to be part of that species. However, it is distinct in a number of small but well correlated characters, and is also only partially sympatric with *C. domestica. Cariniana rubra* as defined here is different from the circumscription of Knuth (1939b) who separated *C. rubra* and *C. domestica* entirely on the corolla color; white in *C. domestica,* and red in *C. rubra.* That distinction is quite artificial since both red and white petals occur in *C. domestica.* The difference between the two species as defined are listed in Table XIII below. *Cariniana rubra* differs from *C. domestica* mainly in the large leaves of a slightly different shape.

Table XIII.
Differences between *Cariniana rubra* and *C. domestica*

Character	*C. domestica*	*C. rubra*
Leaf shape	Leaves tapering to apex from above midpoint	Leaves tapering to apex from well below midpoint
Leaf length	6.0-12.0 cm	10.5-16.0 cm
No. Primary veins	19-25 pairs	24-29 pairs
Pyxidium	Exterior not warted	Exterior warted

Cariniana carajarum, which was described from some empty pyxidia used by the Carajá Indians as pipes, is synonymous with *C. rubra.* There is no difference at all to separate *C. carajarum.*

4. **Cariniana penduliflora** Prance, Brittonia **28:** 298-300. 1976. Figs 67, 70.

Tree to 12.0 m tall, the young branches glabrescent, not conspicuously lenticellate. Leaves with laminas elliptic, 10.0-14.0 cm long, 5.0-8.2 cm broad, the margins crenulate, tapering to base from about midpoint, acuminate at apex, the acumen 10.0-12.0 mm long, curved, rounded at base, slightly decurrent onto petioles, glabrous beneath; midrib prominulous above, prominent and glabrous beneath; primary veins 25-33 pairs, prominulous on both surfaces, 2.0-5.0 mm apart at base, with distinct domatia at junction with midrib and primary veins, the domatia with a few short hairs or glabrous; petioles 12.0-16.0 mm long, slightly winged, glabrous. Inflorescences terminal and subterminal racemose panicles with many branches, pendulous, the rachis and branches sparsely puberulous, not crustaceous, not lenticellate; pedicels ca 0.5 mm long. Calyx 2.5 mm long, turbinate, the lobes triangular, very sparsely puberulous on exterior. Petals obovate ca 6.0 mm long, orangish-red. The androecium ca 2.0 mm in diameter, with ca 40 stamens inserted all over the inner surface. The style very short. Ovary trilocular. Pyxidium not seen.

Type. *Prance, Rodrigues, Ramos & Farias 8811,* Brazil, Terr. Rondônia, Road Mutumparaná to Porto Velho, 2-4 km east of Mutumparaná, fl (holotype, INPA; isotypes, MG, NY).

Distribution. Known only from the type gathering collected in flower in November, and growing in forest on high non-flooded ground.

Cariniana penduliflora is very close to *C. rubra* and *C. domestica,* having the leaf domatia characteristic of those species. In some respects *C. penduliflora* is intermediate between *C. rubra* and *C. domestica* as it has large leaves similar to those of *C. rubra* but which are the shape of the leaves of *C. domestica. Cariniana penduliflora* differs from both of the above species in the longer petioles and in the pendulous inflorescence which is much branched.

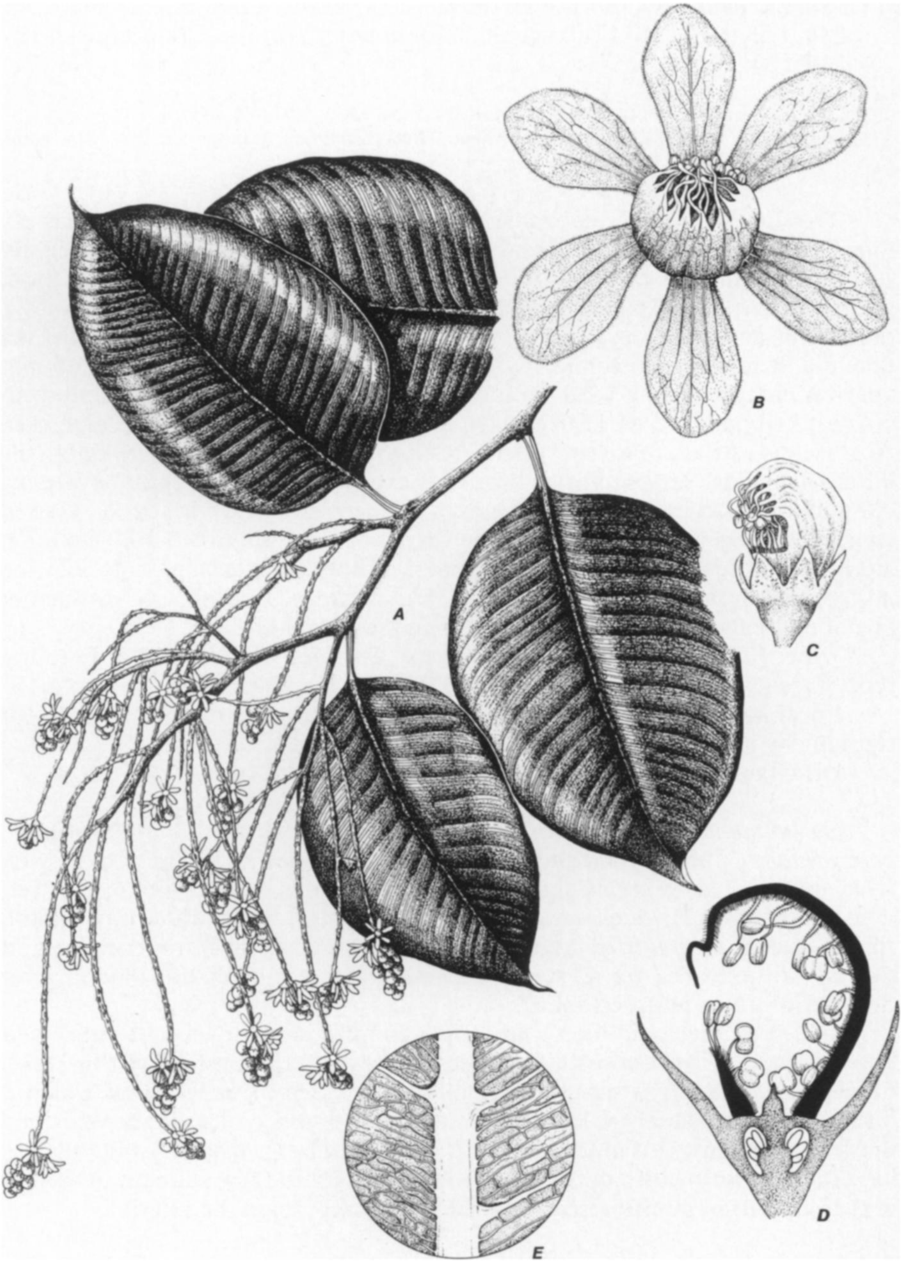

FIG 70. *Cariniana penduliflora (Prance et al 8811):* A, habit, ×0.47; B, flower viewed from above, ×3.84; C, flower, viewed from side, petals removed, ×3.84; D, flower section, ×7.68; E, leaf and midrib undersurface, showing domatia, ×3.84.

5. Cariniana uaupensis (Spruce ex Berg) Miers, Trans. Linn. Soc. London **30:** 288, *t 63, fig 9.* 1874 sub sphalm *'Uahupensis';* Knuth, Pflanzenreich IV. **219a:** 34. 1939. Fig 71.

Couratari uaupensis Spruce ex Berg, Mart. Fl. Bras. **14**(1): 508, *t 78.* 1858.
Amphoricarpus uaupensis Spruce ex Miers, Trans. Linn. Soc. London **30:** 288. 1874, nom. nud. in syn.

Trees to 30.0 m tall, the young branches glabrous. Leaves with laminas oblong, 22.0-30.0 cm long, 9.0-12.0 cm broad, the margins entire but slightly revolute, acuminate at apex, the acumen ca 2.0 cm long, cuneate at base, slightly decurrent onto petiole, glabrous beneath; midrib prominulous above, prominent and glabrous beneath; primary veins 20-27 pairs, without distinct domatia at junction with midrib, prominent on both surfaces, 10.0-15.0 mm apart at base; petiole 1.5-2.0 cm long, slightly winged, glabrous. Inflorescences terminal panicles, ca 11.0-22.0 cm long, the rachis and branches glabrous, crustaceous, striate. Flowers sessile. Calyx ca 2.0 mm long, turbinate, the lobes triangular, very small, glabrous on exterior. Petals oblong-obovate, ca 7.0 mm long. Androecium ca 2.0 mm in diameter at base, with ca 11 reflexed stamens arising from apex only. Style very short. Pyxidium 9.5-10.0 cm long, 5.0 broad at apex, campanulate, broadest at apex, not costate, calycine ring not apparent, the pericarp ca 7.0 mm thick at apex, smooth, not toothed at line of opercular dehiscence; operculum and seeds not seen.

Type. *Spruce 2510,* Brazil, Amazonas, Panuré, Rio Uaupés, fl fr (holotype, K; isotypes, BM, BR, C, E, F, G, GH, LE, NY, OXF, P, W).

Local names and uses. *Chorão, Choro.* The bark is stripped and used for smoking by natives of the upper Rio Negro.

Distribution. Known only from the type gathering.

Cariniana uaupensis together with the next four species, *C. multiflora, C. pachyantha, C. integrifolia* and *C. decandra* form another group of closely related species. This group is characterized by the much smaller number of fertile stamens (10-25) which are inserted terminally on the androecium, and all species except *C. multiflora* have entire leaf margins. In all other species of *Cariniana* there are over 40 sterile stamens which are often attached all over the interior of the androecium.

Since two species in the *C. uaupensis* complex are known only from their type collections it is impossible to assess the exact relationships at this stage. *Cariniana uaupensis* is most closely related to *C. pachyantha* from which it differs in the much larger leaves with a greater number of primary veins and the fewer stamens. It is also close to *C. multiflora* but is distinct in the slightly larger leaves with entire not crenulate margins and the few stamens as well as in the very different inflorescence which is crustaceous on the exterior.

6. Cariniana pachyantha A. C. Smith, Amer. J. Bot. **26:** 411. 1939; Knuth, Pflanzenreich IV. **219a:** 136. 1939. Fig 71.

Large trees to 40.0 m tall, the young branches glabrous. Leaves with laminas ovate-elliptic, 8.0-13.0 cm long, 4.5-9.0 cm broad, the margins entire and slightly revolute, abruptly acuminate at apex, the acumen 7.0-12.0 mm long, rounded at base, slightly decurrent onto petiole, glabrous beneath; midrib prominulous above, prominent and glabrous beneath; primary veins 14-19 pairs, without domatia at junction with midrib, prominulous above, prominent beneath, 3.0-9.0 mm apart at base; petiole 4.0-7.0 mm long, winged, canaliculate, glabrous. Inflorescences terminal and subterminal panicles to 13.0 cm long, the rachis and numerous branches glabrous, crustaceous, striate. Flowers sessile. Calyx 2.0 mm long, turbinate, glabrous, the lobes triangular, very small and thick, glabrous on exterior. Petals oblong-obovate, ca 6.0 mm long, thick. The androecium 2.0 mm diameter at base, with 17-25 stamens with reflexed filaments. Style very short. Ovary trilocular with 10-12 ovules in each loculus. Pyxidium unknown.

Type. *Krukoff 8690,* Brazil, Amazonas, Creek Belém, municipality of São Paulo de Olivença, fl (holotype, NY; isotypes, A, BM, BR, F, G, K, LE, MICH, MO, S, U, US).

Cariniana pachyantha is most closely related to *C. uaupensis;* see differences given under that species.

7. **Cariniana multiflora** Ducke, Arq. Inst. Biol. Veg. **2:** 65. 1935; Knuth, Pflanzenreich IV. **219a:** 36. 1939. Figs 66C, 71.

Tree to 45.0 m tall, the young branches glabrous. Leaves with laminas oblong to oblong-elliptic, 12.0-23.0 cm long, 4.5-9.0 cm broad, the margins crenulate, abruptly acuminate at apex, the acumen 8.0-13.0 mm long, rounded to subcuneate at base, slightly decurrent onto petiole, glabrous beneath; midrib prominulous above, prominent and glabrous beneath; primary veins 22-40 pairs, without domatia at junction with midrib, prominent on both surfaces, 4.0-7.0(-9.0) mm apart at base; petioles 10.0-20.0 cm long, glabrous, winged, canaliculate. Inflorescences terminal and subterminal panicles to 30.0 cm long, the rachis and branches glabrous, smooth. Flowers sessile. Calyx ca 2.0 mm long, the lobes triangular, small, thick, glabrous on exterior. Petals obovate, ca 7.0 mm long, very thick. The androecium ca 2.0 mm basal diameter, with ca 14 stamens with reflexed filaments. Style short. Ovary trilocular with 10 ovules in each loculus. Pyxidium 12.0-13.0 cm long, ca 3.5 cm broad at apex, the calycine ring 1.0 cm below apex, the pericarp thin at apex, smooth not toothed at line of opercular dehiscence; operculum and seeds not seen.

Type. *Ducke RB 23889,* Brazil, Amazonas, São Paulo de Olivença, fl (holotype, RB; isotypes, G, K, P, S, U, US; photo, F, US).

Distribution. Forest on non-flooded ground in western Amazonia. Collected in flower October and November.

COLOMBIA. Vaupés: Jinogoje, Río Apaporis, *R.E.D. Baker sn* fr only (K); *García-Barriga 14368* fr (COL, US). PERU. Loreto: Yurimaguas, *Soria S. 29* fl (F, NY). BRAZIL. Amazonas: Creek Belém near São Paulo de Olivença, *Krukoff 8624* fr (A, BM, F, K, MO, NY, S, U); Palmares, near São Paulo de Olivença, *Krukoff 8164* fr (A, BM, BR, F, G, K, LE, MICH, MO, NY, P, S, U, US), *8508* fl (A, BM, BR, F, G, K, LE, MICH, MO, NY, P, S, U, US).

Local names. Colombia. *Enic-nirika* (Makuna). Peru. *Machimango.*

FIG 71. Distributions of *Cariniana legalis, C. integrifolia, C. pachyantha, C. uapensis,* and *C. multiflora.*

All Brazilian collections cited above are from the immediate vicinity of São Paulo de Olivença. *Cariniana multiflora* is quite close to *C. pachyantha* and *C. uaupensis,* but differs from those species in the inflorescence, the crenate leaf margins and the large number of closely spaced primary leaf veins. It differs from *C. decandra* in the much larger leaves with more primary veins and crenate margins, and in the larger pyxidium.

The species *Cariniana multiflora, C. decandra, C. kuhlmannii, C. pauciramosa* and *C. integrifolia* form a group of very closely related species which are distinct in a number of small characters only. They share in common very similar flowers with a low number of stamens, but there is considerable variation in inflorescence fruit and leaf characters. The principal differences are given in Table XIV.

Table XIV

Differences between 5 related species of *Cariniana*

	C. multifora	*C. decandra*	*C. kuhlmannii*	*C. pauciramosa*	*C. integrifolia*
Leaf margin	crenate	entire	crenate	crenate	entire
Leaf length	12-19 cm	6.5-13(-19)	8-12	6-15(23,5)	7-11.5
Leaf 2° vein number	22-40	9-14	14-18	12-18(25)	7-9
Supracalycine zone width	1 cm below apex	1 cm below apex	apical	apical	1 cm below apex
Fruit costate	no	yes	no	no	no
Inflorescence	multiple branches	6-8 branches	4 branches	twice branched	6-10 branches
Petiole length	15 × 5 mm	15-25 × 1-4	15-20 × 3	20-40 × 2	10-15 × 1.5-2

8. Cariniana kuhlmannii Ducke, Arch. Jard. Bot. Rio de Janeiro **4:** 154, *t 16.* 1925; A. C. Smith, Bull. Torrey Bot. Club **60:** 384. 1933; Knuth, Pflanzenreich IV. **219a:** 37. 1939. Fig 72.

Tree to 15 m tall, the young branches glabrous, lenticellate. Leaves with laminas elliptic to oblong-ovate, 8.5-15 cm long, 4.5-8.0 cm broad, the margins crenulate, acuminate at apex, the acumen 10-15 mm long, finely pointed, subcuneate at base and decurrent onto petiole, glabrous on both surfaces; midrib prominulous above, prominent and glabrous beneath; primary veins 14-18 pairs prominulous on both surfaces, 3.0-8.0 mm apart at base, without domatia at junction with midrib; petiole 15-20 mm long × 0.3 mm broad, glabrous, slightly winged to base, not canaliculate. Inflorescences terminal and subterminal panicles to 11 cm long, 4 branched (in single type specimen examined), the rachis and branches glabrous, not crustaceous. Flowers sessile. Calyx ca 2.0 mm long, campanulate, the lobes triangular, acute, glabrous, ca 1 mm long. Petals oblong, 6-7 mm long, creamish-white. The androecium ca 2 mm in diameter at base, with 13-14 stamens, reflexed, 6-7 terminal, and 7-8 inserted on interior. Style very short. Ovary trilocular with numerous ovules in each loculus. Pyxidium not distinctly costate longitudinally, the calycine ring apical or absent, not lipped at line of opercular dehiscence and without teeth.

Type. *J. G. Kuhlmann 2206,* Brazil, Terr. Rondônia, Cataqui-Iamain, Campos dos Urupás, fr fr (holotype, RB).

Distribution. Known only from the type collection, collected in flower in January.

9. Cariniana pauciramosa W. Rodrigues, Acta Amazonica 4(1): 8-9. 1974. Figs 3P, 9, 11P-R, 72.

Tree to 25 m tall, the young branches glabrous, lenticellate. Leaves with laminas elliptic, 6-15(-23) cm long, 3.5-7.5(-10) cm broad, the margins serrulate to crenulate, acuminate at apex, the acumen 0.5-3 cm long, subcuneate and shortly decurrent to petiole at base, glabrous on both surfaces; midrib prominulous above, prominent and glabrous beneath; primary veins 12-20 pairs, without domatia at junction of midrib, prominent on both surfaces, 5-15 mm apart at base; petioles (15-)18-40 mm long, glabrous, slightly winged next to lamina, not winged near base, slightly canaliculate. Inflorescences terminal or subterminal, little-branched panicles (2-3 branched), branches 2-4 cm long, glabrous, not crustaceous. Flowers sessile. Calyx campanulate, ca 2.0 mm long, the lobes acute, 1 mm long, glabrous on exterior. Petals 4.0-8.0 mm long, oblong-ovate, glabrous, yellow. The androecium ca 3.5-4.0 mm basal diameter, 3 mm tall, yellow, with 10-12 reflexed stamens, 7-9 apical and 3-4 inserted on interior. Style short. Ovary trilocular. Pyxidium 6.5-10.0 cm long, 2.7-3.2 cm broad at apex, slightly 3 sided, not conspicuously costate, the calycine ring ca 0.3 cm below apex, the line of opercular dehiscence distinctly lipped, smooth not toothed; operculum 2.3 cm diameter at apex, convex, the columella triangular. Seeds not seen.

Type. *Prance, Rodrigues, Lleras, Coêlho & Monteiro 17516,* Brazil, Amazonas, Manaus-Itacoatiara road, Km 69, fl (holotype, INPA; isotypes, NY, S).

Distribution. Known only from the type locality from two trees on high non-flooded forest east of Manaus. Collected in flower in September.

BRAZIL. Amazonas, Manaus-Itacoatiara road, Km 69, *W. Rodrigues & Monteiro 9114* fl (Paratype, INPA), *W. Rodrigues 8790* fr (INPA); Km 139, *L. Coêlho & A. Miranda INPA 36013* fr (INPA, NY).

Local name. *Tauari.*

This species is closest to *Cariniana kuhlmannii* but differs in the fruit, the petioles and the less branched inflorescence, see discussion of this group of species under *C. multiflora.*

The species in this group have been separated largely by leaf characters. The various collections of *C. pauciramosa* made at different times of the year from the same tree demonstrate considerable variation in leaf size, shape and number of veins, as well as in the petiole. This is certainly also true in *C. decandra* and demonstrates the caution needed in using these types of characters in the family.

10. Cariniana integrifolia Ducke, Trop. Woods **31:** 18. 1932; Knuth, Pflanzenreich IV. **219a:** 34. 1939. Fig 71.

Cariniana integrifolia var *ovatifolia* Ducke ex Knuth, Pflanzenreich IV. **219a:** 34. 1939. Type. *Ducke RB 23642,* Brazil, Amazonas, Manaus, fl (holotype, B lost; isotypes, G, P, RB, S, U, US; frag INPA).

Tree to 30.0 m tall, the young branches glabrous, lenticellate. Leaves with laminas obovate-elliptic to oblong-elliptic, 7.0-11.5 cm long, 4.0-7.5 cm broad, the margins entire, rounded to short-obtuse-acuminate at apex, the acumen 0-4.0 mm long, subcuneate to cuneate at base, slightly decurrent onto petiole, glabrous beneath; midrib prominulous above, glabrous, prominent and flattened beneath; primary veins 7-9 pairs, without domatia at junction with midrib, prominulous beneath, 6.0-12.0 mm apart at base; petiole 10.0-15.0 mm long, slightly winged, canaliculate, glabrous. Inflorescences terminal and subterminal panicles to 9.0 cm long, the rachis and branches glabrous, not crustaceous; pedicels ca 1.5 mm long. Calyx ca 3.0 mm long, turbinate, the lobes triangular, small, thin, glabrous on exterior. Petals obovate, 6.0-7.0 mm long, white. The androecium ca 2.0 mm in diameter at base, with ca 11 stamens with reflexed filaments which arise from the top of the androecium only. Style very short. Ovary trilocular with ca 10 ovules in each loculus. Pyxidium 11.0 cm long, 3.5 cm broad, the calycine ring ca 5.0 mm below apex, the pericarp thin and without teeth at line of opercular dehiscence; operculum ca 2.5 cm diameter at apex, to 9.0 cm long, the columella triangular; seed wings ca 5.0 cm long, 2.0 cm broad, the seed more or less pyriform, to 2.0 cm long, 1.0 cm broad.

Type. *Ducke RB 23641,* Brazil, Amazonas, Manaus, fl (holotype, RB; isotypes, K, S, US, frag INPA).

Distribution. Forest on non-flooded ground in the vicinity of Manaus. Collected in flower August-October.

BRAZIL. Amazonas: Manaus, Cachoeira Baixa do Tarumã, *Rodrigues & D. Coêlho 7724* fr (INPA 17029, NY); Manaus, Aleixo road, *Ducke 18* fl (A, F, MO, NY, R, S, US), *18* (2nd col.) fl fr (IAN, K, MG, US); vicinity of Manaus, *Ducke 78* fl (F); *78a* fl (A, F), *RB 23884* fl (K, RB, US), *Killip & Smith 30127* fl (BM, GH, NY, S, US) collected from type tree at the same time as type, *Rodrigues 8665* fr (INPA); Reserva Florestal Ducke, Manaus, *Albuquerque INPA 5541* st (INPA); *L. Coêlho INPA 6010* fr (INPA), *E. Ferreira 143/57* fl (IAN, INPA 5901, MG, NY); Manaus-Itacoatiara road km 170, *Rodrigues 7609* fr (INPA), km 185, *Rodrigues 7628* fl (INPA).

Local names. *Cerú, Churú, Tauarí.*

Cariniana integrifolia belongs to the *C. uaupensis* species complex and is most closely related to *C. decandra* from which it differs in the blunt or very shortly acute leaf apex and the thicker coriaceous leaves.

Knuth (1939b) described the variety *ovatifolia* which Ducke mentioned in the original description of the species but never proposed formally. This variety falls well within the leaf variation of this species and cannot be maintained.

11. Cariniana decandra Ducke, Arch. Jard. Bot. Rio de Janeiro **4:** 153, *t 16.* 1925; Knuth, Pflanzenreich IV. **219a:** 37. 1939. Figs 66B, 72.

Tree to 40.0 m tall, the young branches glabrous, lenticellate. Leaves with laminas ovate to oblong-ovate, 6.0-12.0(-19) cm long, 3.0-7.0(-8.5) cm broad, the margins entire, often slightly undulate, acuminate at apex, the acumen 5.0-15.0 mm long, subcuneate at base, slightly decurrent onto petiole, glabrous beneath; midrib prominent on both surfaces, glabrous; primary veins 9-14 pairs, prominulous to plane above, prominent beneath, 3.0-11.0 mm apart at base, without domatia at junction with midrib; petiole 10.0-25.0 mm long × 1-4 mm broad, glabrous, slightly winged towards lamina, lower portion not winged, plane or slightly canaliculate above. Inflorescences terminal and subterminal panicles to 12.0 cm long, the rachis and branches glabrous, not crustaceous. Flowers sessile. Calyx ca 2.0 mm long, campanulate, the lobes oblong, acute, glabrous. Petals oblong, 4.0-5.0 mm long. The androecium ca 1.5 mm in diameter at base, with ca 11 stamens inserted at the apex, the anthers reflexed. Style very short. Ovary trilocular with numerous ovules in each loculus. Pyxidium 11.0-13.0 cm long, 3.0-3.5 cm broad at broadest point, distinctly costate longitudinally, broadest at calycine ring which is very distinct and 7.0-15.0 mm below apex, the pericarp thin at apex (ca 1.5 mm thick), without teeth at line of opercular dehiscence; operculum triangular at apex, ca 2.5 cm broad, to 10.0 cm long, the columella triangular; seed wings 5.0-7.0 cm long, to 2.0 cm broad, the seeds to 2.5 cm long, rounded-triangular.

Types. *Ducke RB 324,* Brazil, Pará, Rio Tapajós, Bella Vista, fl (lectotype, RB); *Ducke RB 17295,* Brazil, Pará, Rio Tapajós, Flechal, fr (syntype, RB).

Distribution. Forest on non-flooded ground in Amazonian Brazil and Peru. Collected in flower December-February.

PERU. Loreto: Mishuyacu near Iquitos, *Klug 979* fl (US). BRAZIL. Amazonas: Creek Belém, Mun. São Paulo de Olivença, *Krukoff 8717* fr (A, BR, F, G, K, LE, MICH, MO, NY, P, S, U, US); Manaus, Flores, *Ducke RB 23888* fr (INPA, RB, US); Manaus, Reserva Florestal Ducke, *O. Pires 27* fr (INPA 27836), *M. Silva et al 13* fr (INPA); Manaus-Itacoatiara Road Km 145, *W. Rodrigues & D. Coêlho 9073* fr (INPA); Santa Cruz, Rio Maici, *Krukoff 5819* fr (A, G, K, NY, U); between Rios Livramento and Ipixuna, Mun. Humaitá, *Krukoff 7193* fr (A, BR, F, G, IAN, K, MICH, MO, NY, RB, S, U, US); Rio Madeira between Borba and Rio Aripuanã, *L. Coêlho sn* fl (INPA 39603); Lago Castanho-Mirim, *Albuquerque et al 873* fr (INPA 39214). Acre: Cruzeiro do Sul, Estrada Alemanha, *Maas et al P12805* fr (INPA, NY), *Prance et al 11884* fr (INPA, MG, NY), Cruzeiro do Sul airport, *Rosa 625* fr (IAN, NY). Terr. Rondônia: Upper Rio Machado, Tabajara, *Krukoff 1375* young fr (A, BM, F, G, K, MICH, MO, NY, P, S, U, US), Rio Madeira, *RADAM 13231* st (IAN).

Local names. *Cerú, Tauarí.*

Cariniana decandra is related to the preceding four species, for differences, see notes under those species, especially under *C. multiflora.*

12. Cariniana micrantha Ducke, Arch. Jard. Bot. Rio de Janeiro **5:** 175. 1930; Gleason and Smith, Bull. Torrey. Bot. Club **60:** 384. 1933; A. C. Smith, Phytologia **1**(3): 126. 1935; Knuth, Pflanzenreich IV. **219a:** 37. 1939. Figs 17A-C, 30, 66A, 73.

Tree to 65.0 m tall, the young branches soon glabrous, lenticellate. Leaves with laminas oblong to elliptic, 5.5-9.5 cm long, 2.5-4.5 cm broad, the margins finely crenulate, acuminate at apex, the acumen 5.0-12.0 mm long, subcuneate at base, not decurrent onto petiole, glabrous beneath; midrib prominulous and glabrous beneath; primary veins 18-25 pairs, without domatia at junction with midrib, prominulous on both surfaces, anastomosing near margins, 2.0-4.0 mm apart at base; petiole 4.0-7.0 mm long, glabrous, canaliculate, with very small wings. Inflorescences terminal and subterminal panicles, 4.0-10.0 cm long, the rachis and branches tomentellous; pedicels ca 0.5 mm long, tomentellous. Calyx ca 3.0 mm long, campanulate, the lobes oblong, acute, thin, tomentellous on exterior. Petals oblong to ovate-lanceolate, 5.0-8.0 mm long, white. The androecium ca 2.0 mm in diameter at base, with numerous, ca 50, stamens all over the interior, white. Style short. Ovary trilocular with ca 6 ovules in each loculus. Pyxidium pyriform, 7.0-10.0 cm long, 4.5-7.0 cm broad at broadest point below the calycine ring, the calycine ring 1.5-2.5 cm below apex, the pericarp very thick at apex (ca 1.5 cm thick), smooth not toothed at line of opercular dehiscence; operculum 2.5-3.7 cm diameter at apex, to 8.5 cm long, the columella triangular; the seed wings 4.0-5.5 cm long, 1.2 cm broad, the seeds to 1.5 cm long, 8.0 mm broad, triquestrous, pyriform.

TYPES. *Ducke RB 17294,* Brazil, Pará, Rio Tapajós, Bella Vista, fr (syntype, RB fruit and leaf only; isosyntypes, K, U fruit only, US fruit only); *Ducke RB 20589,* Brazil, Amazonas, Rio Curuçá, near Maués, fl fr (lectotype, RB; isolectotypes, G, K, P, S, U, US, VEN).

Distribution. Forest on non-flooded ground in Amazonian Brazil. Collected in flower November and December.

BRAZIL. Amazonas: Tabatinga, *Ducke 1797* fl fr (A, F, IAN, K, MG, NY, RB, US); São Paulo de Olivença, *Ducke 71* st (F), *RB 23637* fl fr (G, K, P, RB, S, U, US); Creek Belém, Mun. São Paulo de Olivença, *Krukoff 8796* fl fr (BM, F, G, K, LE, MICH, MO, NY, P, S, U, US); near mouth of Rio Envira tributary to Rio Tarauacá, *Krukoff 5095* fr (A, BM, F, K, LE, M, MICH, MO, NY, RB, S, SP, U, US); Rio Capitarí, *Fróes 26538* fr (IAN); Manaus, Reserva Florestal

FIG 72. Distributions of *Cariniana decandra, C. pauciramosa, C. ianeirensis* and *C. kuhlmannii.*

Ducke, *Aluisio 186* fl (INPA), *234* fl (INPA), *Lourteig 1827* fr only (NY, P), *W. Rodrigues et al 5334* fl (INPA, RB), *8127* fl (INPA), *8132* st (INPA); Manaus-Itacoatiara highway, km 32, *W. Rodrigues & L. Coêlho 1774* fr (INPA), km 54, *D. & L. Coêlho INPA 25948* fl (INPA, NY), km 56, *W. Rodrigues et al 8548* fl (INPA, NY), km 84, *W. Rodrigues 7263* st (INPA), km 165, *W. Rodrigues 7629A* fr (INPA), Manaus-Caracarai, Km 148, *Berg et al P18145* fr (INPA, NY, S), Km 220, *Prance et al 24271* fl (INPA, NY); 30 km W of Lábrea, *Campbell et al P21261* fr (INPA, NY); Manaus-Porto Velho road km 510, *Prance et al 22995* fr (INPA, NY). Terr. Rondônia: Upper Rio Machado, Tabajara, *Krukoff 1439* fl (A, BM, F, G, K, MICH, MO, NY, P, S, U, US); between Fortaleza de Rio Abunã and São Sebastião mines, *Prance et al 8499* fl fr (INPA, MG, NY, S, U, US).

Local name. *Tauarí.*

Cariniana micrantha is an easily recognized distinct species, but is closely related to *C. rubra* and *C. domestica* differing in the smaller narrower leaves, without domatia, and in the smooth not costate pyxidium.

FIG 73. Distributions of *Cariniana micrantha* and *C. estrellensis.*

13. Cariniana legalis (Martius) Kuntze, Rev. Gen. **3**(2): 89. 1898; Knuth, Pflanzenreich IV. **219a:** 38. 1939. Figs 7, 66D, 71.

Couratari legalis Martius, Flora **20**(Beibl. 2): 88. 1837; Berg, Mart. Fl. Bras. **14**(1): 512, *t 7, fig 151.* 163, *t 82.* 1858.

Cariniana brasiliensis Casaretto, Nov. Stirp. Bras. Dec. **4:** 36. 1842; Walpers, Bot. Syst. **5:** 757. 1846; Miers, Trans. Linn. Soc. London **30:** 287, *t 63, fig 1-2.* 1874. Type. *Casaretto 584,* Brazil, Rio de Janeiro (holotype, TO; isotype, G, photos, F, GH, US).

Tree to 25.0 m tall, the young branches glabrous, sparsely lenticellate. Leaves with laminas oblong, 3.0-6.5 cm long, 1.5-3.2 cm broad, the margins weakly serrate-crenulate, rarely crenate, acuminate at apex, the acumen 1.0-5.0 mm long, straight, the base cuneate, decurrent onto petiole and the decurrent part characteristically revolute in dried material; midrib prominulous above, prominent beneath, glabrous beneath; primary veins 9-11 pairs, without domatia at junction with midrib, prominulous on both surfaces, anastomosing near margins, 2.0-10.0 mm apart at base; petiole 3.0-5.0 mm long, the upper portion winged. Inflorescences terminal and subterminal little-branched panicles or racemes, the rachis and branches puberulous; pedicels 0.5-1.0 mm long, sparsely puberulous. Calyx 2.5-3.0 mm long, the lobes obscure, rounded, sparsely puberulous on exterior. Petals oblong-ovate, ca 4.0 mm long, white. The androecium ca 3.0 mm in basal diameter, with ca 50 stamens mostly attached to apex with a few free filaments arising from base of the androecium, reddish-purple. Style very short. Pyxidium 4.5-6.5 cm long, 1.5-3.0 cm broad, the calycine ring indistinct, 0.4-0.8 cm below apex, the pericarp 2.0-3.0 mm thick at apex, the line of opercular dehiscence smooth not toothed; operculum 1.0-1.5 cm diameter.

Type. *Luschnath, Herb. Martius No. 60,* Brazil, Rio de Janeiro, fl (holotype, BR; isotypes, K, M, MO, W).

Distribution. Eastern coastal Brazil from Pernambuco to São Paulo, in high coastal forest. Collected in flower January-May.

BRAZIL. Pernambuco: Forest of Uzina Mussurepe, Itaboraí, near Recife, *Ducke 2300* fr (R), *Lima 52-1018* fl (IAN). Bahia: Road Ubaitaba-Ubata, *Belém & Pinheiro 2204* fl (IAN, NY, RB, U, UB), *2216* fl (NY, RB, UB); Ipiaú, *Belém & Pinheiro 3393* fl (NY), *3395* fl fr (NY); Ilheus, *Hage 61* fr (NY), *Raimundo S.P. 1164* fl (NY), *T. S. Santos 380* fl (INPA), *Velloso 844* st (R); Rio Grongogi Basin, *Curran 16* fr (US), *29* fl fr (K, S, US); São José, *Castellanos & Lana 25525* st (INPA). Minas Gerais: near Tombos, *Barreto 1562* fr (R, US), *J. E. de Oliveira sn* fl (IAN); near Lagoa Santa, *Duarte 8141* fr (R); Mun. Coronel Fabriciano, Rio Piracicaba, *Fróes 33399* st (IAN); Agua Limpa, *Heringer 2524* fl (SP); Rio Pomba, *Heringer 2524-2842* fl (INPA, RB); Paraopeba *Heringer 5483* fl (RB), *7505* fl (RB); Coronel Pacheco, *Heringer 1175* fl (SP), Ilheus, *Mexia 4989* st (A, F, GB, MICH, MO, P, PH, UC, US); without locality, *Widgren sn* fl (S). Espírito Santo; Collantina, *Whitford & Silveira 79* st (F, GH, US), *93* st (GH, US); between Frederico Pretti & Dulcolmo, *Giacomino RB 86207* fl (RB); Linhares, *T. S. Santos 1501* fl (INPA), *2005* fr (NY). São Paulo: Itatuba, *Amaral sn* fl (F, NY, SP 30302); Campinas, *Novaes 528* fl (SP), *785* fl (SP, US); Rio Claro, *Andrade 165* fl (R 91148, US), *Veechi sn* fl (R 16254); Indaiatuba, *Estanislau sn* fl (SP 30302); Itú, *Gehrt sn* fr (SP 31588); Ibiti, *M. Kuhlmann & Gonçalves 1423* st (SP); Ampara, *M. Kuhlmann 538* fr (SP); Queluz, *sine col 13* st (SP 22400); without locality, *Guillemin 1018* fl (P). Rio de Janeiro: Avellar, *Machado Nunes 32* fl (RB); Corcovado, *Glaziou 6164* st (BM, C, K, MO, P, S, US), *7645* fl (BR, C, F, G, GH, LE, P, R, S), *12719* fl (C, K, P), *Nadeaud sn* st (P); Horto Florestal, *J. G. Kuhlmann RB 136139* fl (NY, RB); Gavea, *Constantino RB 16204* fl (INPA, RB, S, U, US), *J. G. Kuhlmann RB 136981* fl (INPA, RB); Itahangá, *O. A. da Silva 31* st (RB 114750); Laranjeiras, *Miers 3616* fr (K); Mesa do Imperador, *Duarte 6209* fl (INPA, K, NY, RB 132165); Botanical Garden, *J. G. Kuhlmann 6255* fl (RB 54412), *Pessoal de Tecnología RB 69908* fl (INPA, RB); Alto da Boa Vista, *Angeli 274* fl (IAN, INPA), *311* fr (IAN, INPA); Estrada de Camorim, *Lanna 266* st (INPA); without locality, *Allemão sn* fl (G), *Glaziou sn* fl (P), *Riedel 1238* fl (F, FI, G, GH, K, LE, M, NY, P, RB, S, U, UPS, W, frag BM), *St. Hilaire C2-154* fl (P). Without State locality: *Andrade sn* fl (R); *Inspectoria Florestal 32* fl (R); *Miers sn* fr (P); *Silva Manso sn, Herb Martius No. 29* fl (BR); *Sellow sn* fl (BM, BR-Herb Martius, C, G, K, P, U, UPS, W).

Local names and uses. *Jequitibá, Jequitibá branco, Jequitibá rosa, Jequitibá vermelho, Pau carga.* The wood is much used commercially. The bark is said to have medicinal properties.

Cariniana legalis is the only species of the genus in which, in addition to the apical filaments, there are a few distinct solitary filaments arising from the base of the androecium and rising to its apex. In other species all the filaments are either short and attached all over the interior of the androecium, or they are at the apex of the androecium.

The lamina base of *C. legalis* is usually folded inwards providing a character for quick identification of sterile material. *Cariniana legalis* is a distinct species which is not easily confused with the other species of the genus.

In the original description of *Couratari legalis* Martius did not cite the type, and the Martius herbarium at Bruxelles contains six sheets from various collectors. Knuth (1939b) cited *Martius 60* as the type but he apparently only studied the Munich material. In this study the same collection is chosen as the type, but the Bruxelles sheet from the Martius herbarium is the lectotype. Martius herbarium 60 is labelled at Bruxelles as *Luschnath 60* and it is probable that Luschnath was the collector of the type. Another apparent duplicate of the same collection at Bruxelles is labelled Herb Martius 20.

An interesting anecdote about a tree of *C. legalis* concerns the very large tree cultivated at the Rio de Janeiro Botanical Garden. Albert Einstein was shown the tree and told about its good wood and medicinal properties. He admired the tree so much that he was moved to kneel down and kiss the surface roots of the tree.

14. **Cariniana ianeirensis** R. Knuth, Repert. Spec. Nov. Regni Veg. **35:** 340. 1934; Pflanzenreich IV. **219a:** 38. 1939. Fig 72.

Large tree, the young branches glabrescent. Leaves with laminas ovate-elliptic, 5.5-9.0 cm long, 2.3-5.0 cm broad, the margins crenate, acuminate at apex, the acumen 1.0-1.5 cm long, straight, cuneate at base, slightly unequal, not decurrent onto petiole; midrib prominulous above, prominent beneath, glabrous; primary veins 12-15 pairs, without domatia at junction with midrib, prominent on both surfaces, anastomosing near margins, 3.0-8.0 mm apart at base; petioles 12.0-17.0 mm long, not winged, terete. Inflorescences terminal racemes, 3.0-6.0 cm long, the rachis glabrous; pedicels ca 1.0 mm long, glabrous. Calyx 3.0-4.0 mm long, the lobes broadly triangular, glabrous. Petals obovate, 10.0-15.0 mm long, yellowish-white. The androecium ca 4.0 mm in basal diameter, with numerous, ca 150, stamens on short filaments inserted throughout the inner surface. Style short. Ovary trilocular. Pyxidium not seen.

Type. *Glaziou 13883,* Brazil, Rio de Janeiro, São Cristovão, fl (holotype, B, lost; lectotype, C; isotypes, A, BM, BR, C, E, F, G, GH, IAN, K, MO, NY, P, RB, S, US).

Distribution. Known from three collections from near Rio de Janeiro.

BRAZIL. Rio de Janeiro: *Without collector 48* fl (R 91139); Without collector, Serra da Tijuca fl (RB 65027 [Herb Schwacke 4704, Herb Saldanha 7532]; Itaocara, *Castellanos 24011* st (INPA). Without locality: *Warming sn* fl (C).

Cariniana ianeirensis is apparently distinct. It differs from *C. estrellensis* and *C. legalis,* the other species of the genus found around Rio de Janeiro, in the much larger flowers and the longer unwinged petioles. It also differs from *C. estrellensis* in the terminal inflorescences and the short pedicels, and from *C. legalis* in the crenate leaf margins, the longer acumen and the straight not folded leaf bases.

The Warming collection cited above is marked as collected by Warming but may possibly be a duplicate of the type. The sterile collection *Glaziou*

6163, referred to *C. estrellensis* by Knuth, probably belongs to *C. ianeirensis.*

15. Cariniana estrellensis (Raddi) Kuntze, Rev. Gen. **3**(2): 89. 1898; Knuth, Pflanzenreich IV. **219a:** 39. 1939; Macbride, Publ. Field Mus. Nat. Hist., Bot. Ser. **13**(4): 229. 1941. Figs 3-0, 66G, 73, 74.

Couratari estrellensis Raddi, Mem. Soc. Modena **18**(Fis.): 403. 1820, Mem. Pl. Bras. Add. 25, *t 2.* 1821; Poiteau, Mém. Mus. Hist. Nat. **13:** 161. 1825; de Candolle, Prodr. **3:** 294. 1828; Berg, Mart. Fl. Bras. **14**(1): 511, *t 79, fig 2.* 1858.

Cariniana excelsa Casaretto, Nov. Stirp. Bras. Dec. **5:** 46-47. 1843; Walpers, Rep. Bot. Syst. **5:** 757. 1846; Miers, Trans. Linn. Soc. London **30:** 285, *t 63, fig 6-8.* 1874. nom. illegit.

Cariniana excelsa var *puberula* Chodat & Hassler, Bull. Herb. Boisser II. **4:** 77. 1904. Type. *Hassler 5183,* Paraguay, Sierra de Maracayu, fl (holotype, G; isotypes, A, K, MO, NY, S, W).

Couratari glaziovii Taubert ex Glaziou, Bull. Soc. Bot. France 54, Mém. **3c:** 240. 1908, nom. nud. Type. *Glaziou 17008,* Brazil, Rio de Janeiro (A, BM, BR, C, IAN, K, LE, MO, NY, P, RB, W).

Tree to 50.0 m tall, the young branches sparsely puberulous, soon becoming glabrous. Leaves with laminas oblong-elliptic, 3.0-11.0 cm long, 1.5-6.0 cm broad, the margins serrate, acuminate at apex, the acumen 2.0-5.0 mm long, slightly curved, the base subcuneate, decurrent onto petiole; midrib plane above, prominent beneath, glabrous or slightly puberulous beneath; primary veins 11-18 pairs, without domatia at junction with midrib, prominulous above, prominent beneath, anastomosing near margins, 2.0-5.0 mm apart at base; petioles 5.0-13.0 mm long, slightly winged. Inflorescences axillary racemes or racemose panicles 3.0-6.0 cm long, the rachis puberulous; pedicels 2.0-5.0 mm long, puberulous. Calyx 1.0-1.5 mm long, campanulate, the lobes broadly triangular, sparsely puberulous on exterior. Petals obovate, 4.0-7.0 mm long, creamish-white. The androecium ca 2.0 in basal diameter, white, the stamens numerous, ca 40, inserted all over the interior but denser towards the apex. Style very short. Pyxidium 6.5-9.5 cm long, 3.0-3.5 cm broad, the calycine ring ca 1.0 cm below apex, the pericarp thin, ca 1.0 mm thick at apex, thicker below, with a row of tooth-like protrusions all around the line of opercular dehiscence; operculum 1.5-2.5 cm in diameter at apex, to 7.0 cm long, the columella triangular; seed wings to 3.5 cm long, 1.2 cm broad, the seeds more or less pyriform, 1.2 cm long, 0.6 cm broad.

Type. *Raddi sn,* Brazil, Rio de Janeiro, fl (holotype, FI).

Distribution. Mainly found in central Brazil and southwards to Santa Catarina, but extending north to the State of Acre. Flowering October-April.

BRAZIL. Acre: near mouth of rio Macauhan, tributary of rio Iaco, *Krukoff 5568* fr (A, BM, F, G, K, LE, M, MICH, MO, NY, RB, S, U, US); trail Rio Acre to Palmares, *J. G. Kuhlmann 779* fl (RB 21498). Distrito Federal: Caetetinho, *Duarte 9361A* st (INPA, RB 130294); Parque do Gama, *Heringer 10670* fl (NY, UB); Planaltina, *Irwin et al 8885* fl fr (NY); Lagôa Feia, *Irwin et al 13175* fr (NY); Córrego Maranhão, *Pires et al 9492* fr (RB); without locality, *Sucre 491* fr (NY, RB, UB). Bahia: Ilheus, *Almeida 216* fl (NY), *Belém et al 1379* fr (NY, UB); Hage 60 fr (NY); Road Ubaitaba-Itacaré, *Belém & Pinheiro 2967* fl (NY, UB); Itabuna, *Lanna 952* st (IAN, INPA). Minas Gerais: Conceição Aparecida, *Andrade 1208* fl (R 126514); S of Barreiro, Ará, *Barreto 11560* fr (US); São Gonçalves, *J. G. Kuhlmann RB 2597* fl (RB, S, U); Jaguara, *Riedel 773* fl (G, GH, K, LE, NY, P, S, U, UPS); Santa Terezinha, *Macedo 1251* fl (BM, MO, S, RB, US); Caldas, *Regnell III-597* fl (C, F, FI, GH, K, LE, P, PH, R, S, U, UPS, US); Mun. Coronel Fabriciano, *Fróes 33373* st (IAN); Vale de Rio Paranaiba, Mun. Presidente Olegário, *Fróes 33454* fr (IAN); Fazenda Cruzeiro do Sul, headwaters of Rio São Francisco, *Fróes 33964* fr (IAN); vicinity of Cordisburg, *Fróes 33328* fr (IAN); Estaçao Experimental Coronel Pacheco, *Heringer 50* fl (RB); Estação Experimental Agua Limpa, *Heringer 2787* fl (RB); Figueiras, Serra do Ibitunue, *J. G. Kuhlmann 305* fr (RB 136141); Belo Horizonte Botanical Garden, *Barreto 3359* fr (F, R), *8259* fl (F, R), *Sampaio 7409* fr (R); Serra do Taquaril, Mun. Belo Horizonte, *J. E. de Oliveira sn* fr (IAN); Viçosa, *Almeida sn* fl (INPA 39612), *J. G. Kuhlmann 2438* fl (RB 5513); Pomba, *Heringer 2498* fl (INPA, RB); Paraopeba, Horto Florestal, *Heringer 3311* fl (INPA, RB); Fazenda do Rasgão, Paraopeba, *Heringer 5419* fl (F, M, RB); without locality, *Gomes 2586-2480* fl (INPA, RB 97643). São Paulo: São Paulo Botanical Garden, *Hoehne SP 28170* fl (F, NY, P, RB, SP, US), *M. Kuhlmann 2805* fl (NY, SP76439, US); Aguas do Prata, *Andrade EF 336* fl (A, US); Rio Claro, *Chevalier sn* (P); Cubatão, *sine col* st (SP 22401); Pinhal, Bairro do Tres Fazendas, *Gonçalves & Kuhlmann 1560* fl (NY); Santa Rita do Passo Quatro, *Hemmendorf 243* st (S); Buetas, Fazenda, N. S. da Gloria, *Mello RB 136140* fl (RB); Piracicaba, *W. Hoehne 6269* fl (NY), *A. Rodrigues sn* fl (RB 102638); Campinas, *Novaes 784* fl (SP), *Santoro IASP 7480* fl (IAN), *sn* fl (SP 52090); Riolândia, *Marinio 373* fl (SP); Salesopolis, *M. Kuhlmann 1727* fl (SP 76438) *sn* st (SP 76440). Rio de Janeiro: Avelar, *Machado Nunes 10* fl (RB 25737); Engenheiro Passos, *Machado Nunes 10* fl (RB 25736); Teresópolis and vicinty, *Bueno 57* fl (R), *Velloso sn* fl (RB 38388), *sn* fl (R 91126), *Vidal II-5864* fl (R); Petrópolis; *Glaziou sn* fl (R 91130); 64A fl (R); Fazenda Rochinha, *Freire sn* st (R 91152); Cantagalo, *Peckholt sn* st (BR); without locality, *Glaziou 14758* fl (US). Rio de Janeiro: Tijuca, *Glaziou 6165* st (C, P, R, S), *7644* fl (BM, BR, C, F, G, K, LE, NY, P, S, US), *Pereira 4386* fl (INPA, RB); Gávea, *Glaziou 6165bis* fl (C); Horto Florestal, *Almeida RB 1874* fl (K, INPA, RB, S, U, US), *Lage RB 4989* fl (F, RB); near Horto Florestal, *Occhioni RB 5064* fl (K, RB, S, U, US); Itatiago, *Campos Porto RB 665* fl (RB, U); Rio de Janeiro, *Glaziou 12013* fl (BR, C, F, G, K, LE, NY, P, R), *19379* fl (C, K, LE, P); Rio de Funil, *M. Kuhlmann 4059* fl (SP). Without locality, *Glaziou 6160* fl (C, M, UPS), *6162* fl (C, E, GH, K, MO, NY, P, S, US), *8397* fl (BR, C, G, LE, P), *10800* st (C, G, LE, P), *10801* st (BR, C, P), *12012* fl (BR, C, F, G, K, LE, MO, P, RB, US). Paraná: Cerro Azul, *Hatschbach 4246* fl (US); Rio Piquirí, Guaira Mun., *Hatschbach 7964* fl (RB, US); Araruva Mun., Mauá, *Hatschbach 13035* fl (C, F, K, M, NY, U, US); Rio de Cedro, Mun. Guarquecaba, *Hatschbach 18119* fl (C, MICH, MO, NY, S); near Umuarama, *Lindeman & Haas 5519* st (U). Santa Catarina: Itajaí vicinity, *Klein 923* fl (G, NY, U, US), *Klein 1010* fl (NY, U, US); Blumenau, Bom Retiro, *Klein 2299* fl (NY); Horto Florestal, Ibirama, *Reitz & Klein 3136* fl (BR, F, K, L, M, NY), *24530* fr (F); Tres Barras, Garuva, São Francisco do Sul, *Reitz & Klein 4597* fr (BR, G, GH, K, L, NY, U), Serra do Matador, Rio do Sul, *Reitz & Klein 6809* fr (US); Brusque and vicinity, *Klein 83* fl (S, US), *Reitz 2988* fl (IAN, NY, S, US), *4020* fr (G, NY); Hammonia, *Luederwaldt sn* fl (SP). Without precise locality: *Saint Hilaire 29* fl (P); *Sellow sn* fl (K, P), *1109* fl (BR, W); *Warming sn* fl (C). BOLIVIA. La Paz: Yungas Province, Basin of Río Bopi, San Bartolomé, *Krukoff 10308* fr only (NY, U, US), Ascunta near Evenay, *Krukoff 10630* fr (NY). Santa Cruz: Yapacana, *Kuntze 1192* fr (NY, US); Sara Province, Buenavista, *Steinbach 7339* fl (K, NY). PARAGUAY. Esperanza, Sierra de Amambay, *Hassler 670* fl (G), Rojas Herb. *Hassler 10670* fl (C, G, K, MICH, NY, P, RB, S, US, W); Sierra de Amambay, *Rojas 10705* fl (BR, P, W).

Local names. Brazil: *Bingueiro, Estopa, Jequitibá, Jequitibá branco, Mussambe.*

This species is cultivated in Rhodesia *(R. D. Kelly 117, 137,* fl (K).

Cariniana estrellensis is readily distinguished from all other species of the genus by the axillary inflorescences and by the teeth around the margin of the line of opercular dehiscence of the pyxidium.

Excluded Species

Cariniana paraensis (Martius ex Berg) Knuth, Pflanzenreich IV. **219a:** 37. 1939. = *Couratari paraensis* Martius ex Berg, spec. dub.

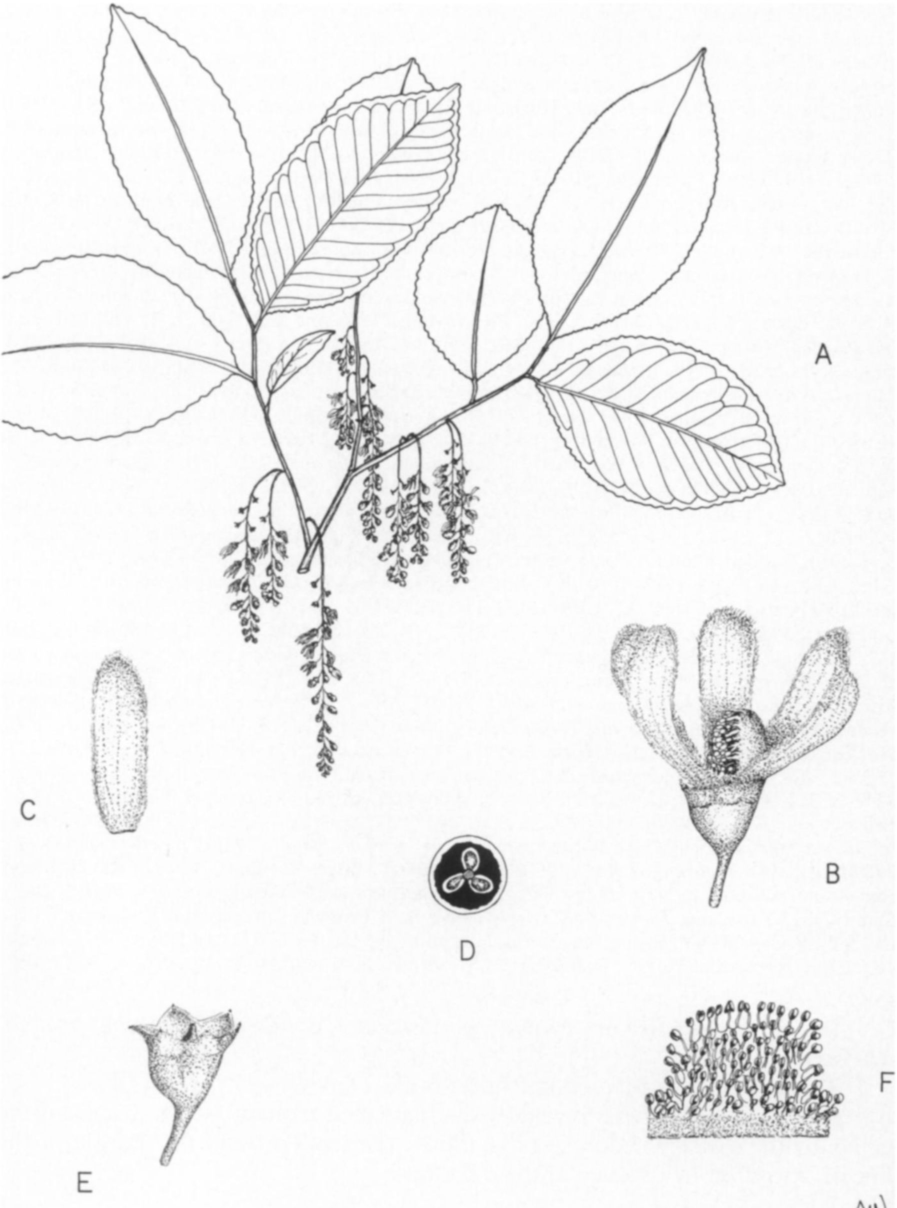

FIG 74. *Cariniana estrellensis (Irwin et al 8885).* A. Habit. ×0.47. B. Flower. ×4.3. C. Petal. ×4.3. D. Cross section of ovary. ×4.3. E. Flower minus petals and androecium. ×4.3. F. Androecium opened up. ×4.3.

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XVI. NUMERICAL LIST OF TAXA

1. *Asteranthos*
   - 1-1. *A. brasiliensis* Desf.
2. *Gustavia*
   - 2-1. *G. brachycarpa* Pittier
   - 2-2. *G. longifuniculata* Mori
   - 2-3. *G. dubia* (Kunth) Berg
   - 2-4. *G. hexapetala* (Aubl.) Smith
   - 2-5. *G. pubescens* Ruiz & Pavon ex Berg
   - 2-6. *G. grandibracteata* Croat & Mori
   - 2-7. *G. sessilis* Mori
   - 2-8. *G. monocaulis* Mori
   - 2-9. *G. angustifolia* Benth.
   - 2-10. *G. petiolata* Mori
   - 2-11. *G. santanderiensis* R. Knuth
   - 2-12. *G. elliptica* Mori
   - 2-12 a. *G. erythrocarpa* Mori
   - 2-13. *G. augusta* L.
   - 2-14. *G. dodsonii* Mori
   - 2-15. *G. terminaliflora* Mori
   - 2-16. *G. verticillata* Miers
   - 2-17. *G. parviflora* Mori
   - 2-18. *G. fosteri* Mori
   - 2-19. *G. macarenensis* Philipson
     - a. subsp *macarenensis*
     - b. subsp *paucisperma* Mori
   - 2-20. *G. speciosa* (Kunth) DC.
     - a. subsp *speciosa*
     - b. subsp *occidentalis* (Cuatr.) Mori
   - 2-21. *G. romeroi* Mori & García-Barriga
   - 2-22. *G. nana* Pittier
     - a. subsp *nana*
     - b. subsp *rhodantha* (Standley) Mori
   - 2-23. *G. tejerae* R. Knuth
   - 2-24. *G. gentryi* Mori
   - 2-25. *G. poeppigiana* Berg
   - 2-26. *G. longepetiolata* Huber
   - 2-27. *G. serrata* Mori
   - 2-28. *G. acuta* Mori
   - 2-29. *G. gracillima* Miers
   - 2-30. *G. foliosa* Cuatr.
   - 2-31. *G. pulchra* Miers
   - 2-32. *G. coriacea* Mori
   - 2-33. *G. inakuama* Mori
   - 2-34. *G. acuminata* Mori
   - 2-35. *G. longifolia* Poeppig ex Berg
   - 2-36. *G. gigantophylla* Sandw.
   - 2-37. *G. latifolia* Miers
   - 2-38. *G. superba* (Kunth) Berg
   - 2-39. *G. flagellata* Mori
     - a. var *flagellata*
     - b. var *costata* Mori
   - 2-40. *G. excelsa* R. Knuth
3. *Grias*
   - 3-1. *G. multinervia* Cuatr.
   - 3-2. *G. cauliflora* L.
   - 3-3. *G. colombiana* Cuatr.
   - 3-4. *G. peruviana* Miers
   - 3-5. *G. neuberthii* Macbride
   - 3-6. *G. haughtii* R. Knuth
4. *Allantoma*
   - 4-1. *A. lineata* (Martius ex Berg) Miers
5. *Cariniana*
   - 5-1. *C. pyriformis* Miers
   - 5-2. *C. domestica* (Martius) Miers
   - 5-3. *C. rubra* Gardner ex Miers
   - 5-4. *C. penduliflora* Prance
   - 5-5. *C. uaupensis* (Spruce ex Berg) Miers
   - 5-6. *C. pachyantha* A. C. Smith
   - 5-7. *C. multiflora* Ducke
   - 5-8. *C. kuhlmannii* Ducke
   - 5-9. *C. pauciramosa* W. Rodrigues
   - 5-10. *C. integrifolia* Ducke
   - 5-11. *C. decandra* Ducke
   - 5-12. *C. micrantha* Ducke
   - 5-13. *C. legalis* (Martius) Kuntze
   - 5-14. *C. ianeirensis* R. Knuth
   - 5-15. *C. estrellensis* (Raddi) Kuntze

XVII. LIST OF EXSICCATAE

Acosta-Solís, M., 6343(2-35); 6948(2-5); 13615(3-4); 13908(2-35).
Agostini, G., 1753(2-25).
Albuquerque, B.W.P. de, 133(2-13); 283(2-13); 873(5-11); INPA 5541(5-10).
Allemão, F. F. et al., sn (5-13); 718(2-13); RB 10896(5-13).
Allen, P. H., 273(3-2); 349(2-22b); 880(2-38); 2610(2-38); 3112a(2-4); 4206(2-38); 4310(2-38); 5216(3-2); 6547(3-2).
Almeida, D., INPA 39612(5-15).
Almeida, H. D., RB 1874(5-15).
Almeida, J. S., 216(5-15).
Alston, A. H. G., 7615(2-25).
Aluisio, J. et al, 186(5-12); 204(2-4); 234(5-12); 312(2-12).
Amaral, E., SP 30302(5-13).
Ancuash, E., 90(3-4).
Andrade, A. G., 1208(5-15).
Andrade, Navarro de, 165(5-13); 336(5-15); R 126517(5-13).
André, E. F., 1772(2-16); 4243(3-4).
Angeli, C., 274(5-13); 311(5-13).
Anthoine, F., sn (5-1).
Appun, C. F., 1856(2-13).
Archer, W. A., 2348(2-25); 2399(2-13); 2551(2-13); 2593(2-13); 2613(2-13); 2864(2-13); 2890(2-13); 7724(2-13); 7829(4-1); 7931(2-13).
Areira, A., 4-10(2-3).
Aristeguieta, L. et al,1268(2-25); 1795(2-39a); 2159(2-28); 2736(2-39b); 4843(2-39b); 5317(2-13); 6346(2-39a); 6776(5-1); 6934(2-25); 7410(2-25).
Asplund, E., 8993(3-5); 10282(2-19a); 10298(2-19a); 13343(3-4); 14076(3-5); 14398(2-19a); 15543(2-13).
Aubréville, A., 18(2-13); 19(2-13).
Aublet, J. B. C. F., sn(2-4).

BAFOG (Bureau Agricole Forestier Guyanais) 270M(2-4); 1018(2-13); 1088(2-13); 1260(2-4); 3221(2-13); 4381(2-13); 4409(2-13); 4471(2-13); 6145(2-13); 7345(2-4); 7351(2-4); 7597(2-4).
Bailey, L. H. & E. Z. Bailey, 58(2-38).
Baker, C. F., 299(2-13).
Baker, R. E. D., sn, 1952-53(5-7).
Baldwin, J. T., 3450(2-31).
Ballera, L., sn, 1941(3-5).
Barclay, G. W., 2804(2-38).
Barkley, F. A. et al, 5(2-38).
Barreto, M., 1562(5-13); 3359(5-15); 8259(5-15); 11560(5-15).
Barroso, G. M. et al., RB 141430(5-3).
Bartlett et al., 16587(2-38).
Bastos, A. M., 2(2-4).
BBS (see Boschwezen)
Beard, J. S., 258(2-25).
Belander, C. P., 119(2-13).
Belém, R. P. et al., 1379(5-15); 2204(5-13); 2216(5-13); 2967(5-15); 3393(5-13); 3395(5-13).
Bena, P., 1018(2-13); 1088(2-13); 1260(2-4); 4192(2-13).
Benoist, R., sn(2-13); 17(2-13).
Berg, C. C. et al., P18145(5-12); P18497(5-2); P19729(2-4).
Berlin, B., 417(3-4); 495(2-33); 656(2-33); 761(2-33); 884(3-4).
Bernal, P., 99(2-22b).
Bernardi, A. L., 1030(2-19b); 6899(2-4); 6948(2-4).
Berry, P. E., 2050(2-31).
Black, G. A. et al., 827(4-1); 828(2-13); 47-1684(2-25); 47-1958(2-4); 48-2980(2-4); 48-3020(2-4); 48-3438(2-13); 49-7945(2-13); 49-8485(2-13); 49-8601(2-13); 50-9298(2-13); 50-10910(2-13); 51-13288(2-13); 54-16306(4-1); 54-17009(2-13); 54-17189(2-13); 56-18861(2-13); 57-18982(2-13).
Blanco, C., 1291(4-1).
Boeke, J. et al., 1325(3-4); 2211(3-5).
Bond, F. E. et al., 196a(2-13); 259(2-25).
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