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CONTENTS

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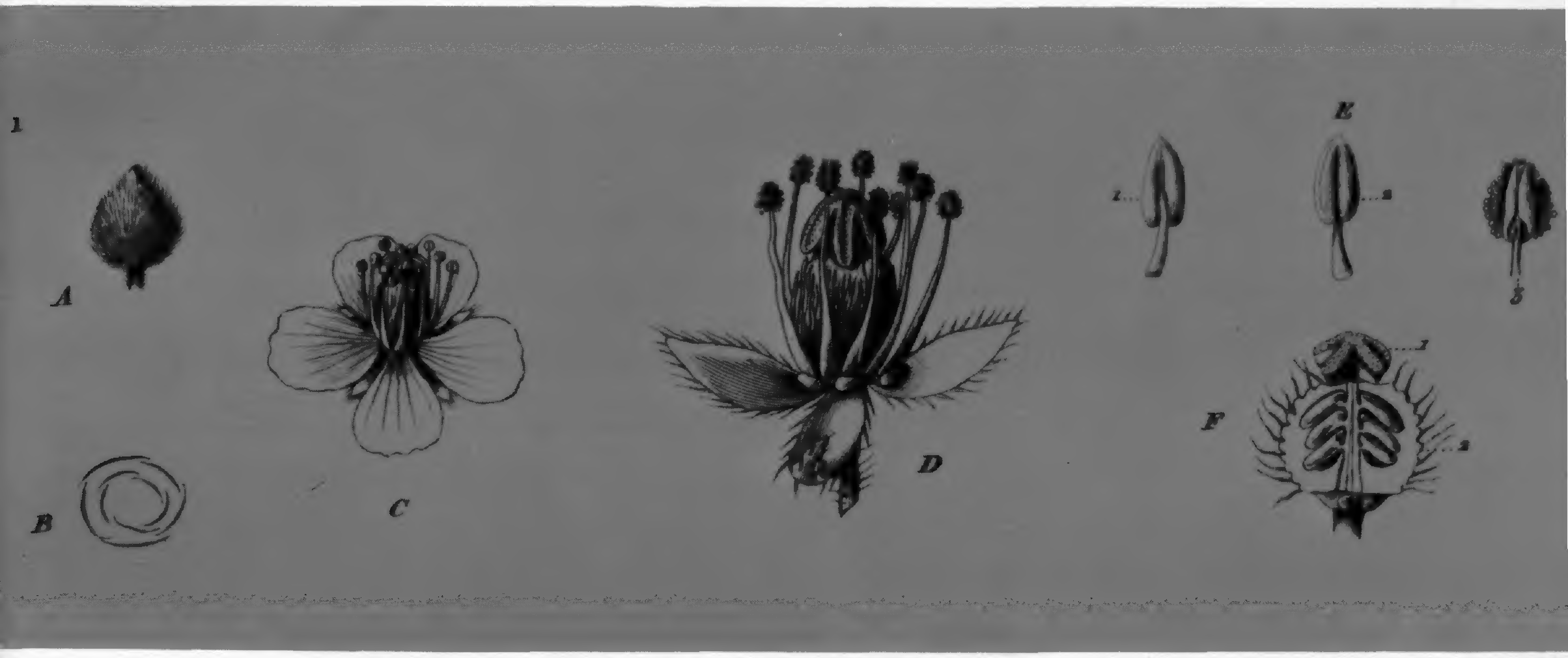

CONTENTS

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ANNALS OF THE

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NOTES ON THE FLORAL GLANDS IN *TRIBULUS* (ZYGOPHYLLACEAE)[1]

DUNCAN M. PORTER[2]

ABSTRACT

Morphology of the intrastaminal floral glands in *Tribulus* has been thought to be species-specific. However, this specificity breaks down in the Galápagos Islands. It is hypothesized that the breakdown there is due to interspecific hybridization between *T. cistoides* and *T. terrestris*.

Tribulus L. is an Old World genus of several dozen species. Most species are weedy occupants of dry disturbed habitats, either natural or man-induced. The yellow-flowered *T. cistoides* L. and *T. terrestris* L. have been distributed around the world by man, their spiny mericarps providing an ideal mechanism for dissemination. *Tribulus cistoides* is native to tropical and subtropical southern Africa.[3] It is now a weed throughout the drier tropics, occurring mainly in maritime habitats. *Tribulus terrestris* is native to the Mediterranean region. It is a wide-spread weed in the warm-temperate areas of the world, occurring on all continents but Antarctica. It has been collected rarely in the tropics, then mostly at higher elevations. The ranges of *Tribulus cistoides* and *T. terrestris* are known to overlap only in two areas. One is in southern Africa; the second is in the Galápagos Islands, Ecuador.

One of the principal diagnostic floral characters distinguishing *Tribulus* from the closely-related genus *Kallstroemia* Scop., with which it is often confused, is the presence of a whorl of five intrastaminal glands at the base of the ovary in *Tribulus*. Intrastaminal glands are lacking in *Kallstroemia*, although both genera

[1] Dr. J. D. Dwyer, Dr. W. H. Lewis, and Mr. W. G. D'Arcy have kindly read and commented upon the manuscript.

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[3] *Tribulus zeyheri* Sond. is the name often used for the species in this area, especially in older works; *T. cistoides* was long considered to be a New World species. However, examination of a large number of specimens from both areas shows the range of morphological variation in the large-flowered *Tribulus* of each to be identical, notwithstanding Launert's (1963) attempt to separate two species in Africa. *Tribulus zeyheri*, therefore, is a synonym of the older name, *T. cistoides*.

ANN. MISSOURI BOT. GARD. 58: 1–5. 1971.

have a whorl of five bilobed *extrastaminal* glands. In *Tribulus* both extrastaminal and intrastaminal glands are located next to or perhaps are continuous with the floral disc.

The disc and the extrastaminal and intrastaminal glands of *Tribulus cistoides* are all nectariferous, with the extrastaminal glands producing most of the nectar (Brown, 1938). The extrastaminal glands in *T. longipetalus* Viv.[4] (as *T. alatus* Del.) and *T. terrestris* are not supplied by vascular bundles, and have been regarded as "stipular in nature" (Nair & Nathawat, 1958: 174). Apparently the intrastaminal glands also lack a vascular supply, as does the disc (*op. cit.* 179). Whether the glands represent reduced stamens or other organs or are organs which have arisen *de novo* is not clear. As floral glands and staminal appendages abound in the Zygophyllaceae, their study should provide a fertile field for anatomical research.

In his admirable study of *Tribulus* in South Africa, Schweikerdt (1937) has indicated the usefulness of the intrastaminal glands as a taxonomic character in the genus. He was the first to point out that the morphology of the intrastaminal glands does not vary within a species. The intrastaminal glands are triangular and free in *T. longipetalus* (as *T. alatus*), *T. macropterus* Boiss., and *T. terrestris* (Schweikerdt, 1937) and connate into a five-lobed urceolate ring surrounding the ovary base in *T. cistoides* (Schweikerdt, 1937, as *T. zeyheri*; Brown, 1938), *T. cristatus* Presl, *T. excrucians* Wawra, *T. pterocarpus* Ehrenb., and *T. pterophorus* Presl (Schweikerdt, 1937). In *Tribulopis solandri* R. Br. (*Tribulus solandri* (R. Br.) F. Muell.), a member of an endemic Australian genus closely allied to *Tribulus*, they are bilobed and basally connate (Porter, 1969).

Following Schweikerdt's lead, others have found this character useful in keys for the identification of *Tribulus* species (Launert, 1963; Schreiber, 1966; Porter, 1967, 1970). Intrastaminal gland morphology seems to be consistent throughout the ranges of most species examined. However, a study of the genus in the Galápagos Islands (Porter, 1971) has revealed a breakdown in the species-specificity of the character. Here, the intrastaminal glands of *T. cistoides* are connate, the usual situation, while those of *T. terrestris* may be either free, as usual, or connate.

The morphology of the intrastaminal glands of those collections of *Tribulus* from the Galápagos Islands cited below has been determined as indicated.

1. *Tribulus cistoides* (intrastaminal glands connate).—Fig. 1.
   LOCALITY UNKNOWN: *Snow 92* (DS).
   ISLA BALTRA: *Howell* 9952 (CAS).
   ISLA CHAMPION: SW slopes of old crater, *Wiggins & Porter 511* (CAS, MO).
   ISLA DAPHNE MAJOR: Dawson, 1964 (DS, MO).
   ISLA ESPANOLA: *Snodgrass & Heller 743* (DS, GH).

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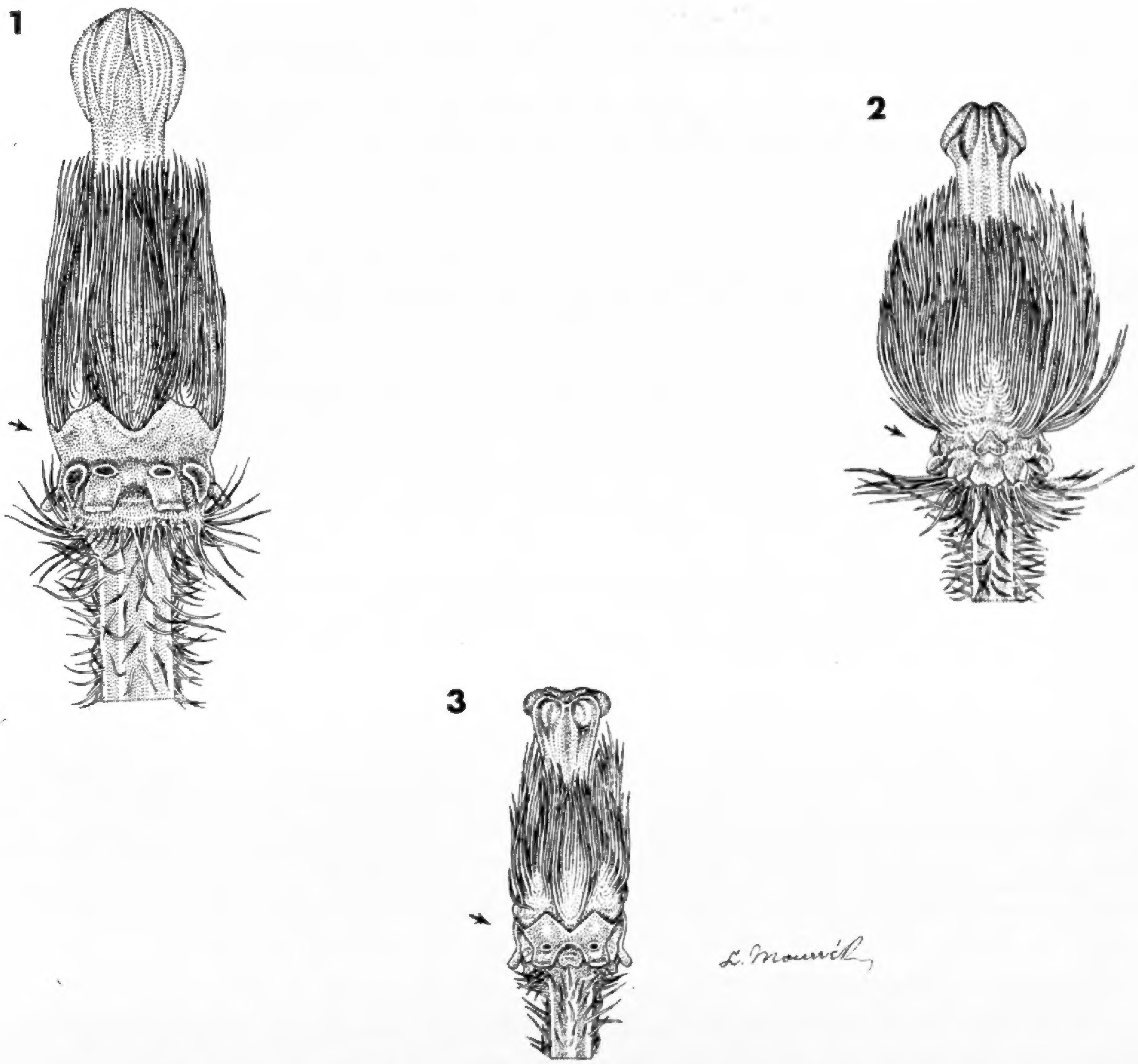
[4] Gruenberg-Fertig and Zohary (1970) have shown that this name takes precedence over the well-known *Tribulus alatus*. Not only is the latter name illegitimate as they indicate, having been published with an older name applicable to a different species in its synonymy, it is also a *nomen nudum*, being published without a description. Accordingly, *T. longipetalus* is the name to be applied to the North African and Middle Eastern species, originally cited by the author as *T. alatus* (Porter, 1967), that has been introduced into Peru.



FIGURES 1–3. Intrastaminal gland morphology in *Tribulus*, × 12½.—1. *T. cistoides* (intrastaminal glands connate).—2. *T. terrestris* (intrastaminal glands free).—3. *T. terrestris* (intrastaminal glands connate). (1. After *Wiggins & Porter 511*. 2. After *Andersson, 1852*. 3. After *Wiggins 18702*. All MO.)

ISLA FLOREANA: Near shore and in open places in vegetation, *Stewart 1725* (CAS); cinder ridge ca. 2 km inland from E end of Post Office Bay, *Wiggins & Porter 543* (CAS, MO); sand dunes at Cormorant Bay, *Wiggins & Porter 561* (CAS, MO).

ISLA GENOVESA: Plateau above "Phillip's steps," *Eisendrath*, 1969 (MO).

ISLA ISABELA: Tagus Cove, near beach on sandy hillsides, *Snodgrass & Heller 165* (DS), in tufaceous soil on tops and sides of hills surrounding cove, *Stewart 1730* (CAS, GH, MO), side of cinder ridge 200 m NE of landing, *Wiggins & Porter 240* (CAS, MO), landing at head of cove, *Wiggins & Porter 241* (CAS, MO); Villamil, *Howell 8935* (CAS, MO), in light ashy soil near sea level, *Stewart 1722* (CAS, GH, MO).

ISLA SAN CRISTOBAL: Punta Pitt, *Snow 255* (DS); Wreck Bay, *Wiggins & Porter 446* (CAS, MO).

ISLA SANTIAGO: Sulivan Bay, *Howell 10023* (CAS).

ISLA SANTA CRUZ: Along trail from Academy Bay to Bella Vista, *Fosberg 44757* (MO, US), *Wiggins 18431* (DS, MO), *Wiggins & Porter 705* (CAS, MO).

ISLA TORTUGA: *Stewart 1723* (CAS, GH).

2. *Tribulus terrestris* (intrastaminal glands free).—Fig. 2.

LOCALITY UNKNOWN: *Andersson*, 1852 (MO).

ISLA ESPANOLA: Gardner Bay, *Howell 8658* (CAS).

ISLA FLOREANA: Post Office Bay, *Howell 8805* (CAS).

3. *Tribulus terrestris* (intrastaminal glands connate).—Fig. 3.
Isla Floreana: Among rocks along shore, *Stewart 1732* (CAS); Black Beach, *Howell 8913* (CAS).
Isla Santa Cruz: Sand dunes 3 miles W of Academy Bay, *Taylor TT100* (CAS); slopes of dunes on lava peninsula along S shore of Tortuga Bay, *Wiggins 18702* (DS, MO).

Nineteen additional collections of *Tribulus cistoides* and one of *T. terrestris* from the archipelago were examined, but these were either sterile or too scrappy to determine as to gland morphology.

The yellow flowers of *Tribulus cistoides* and *T. terrestris* superficially differ mainly in size. Those of *T. cistoides* generally are 20–40 mm in diameter, while those of *T. terrestris* are 5–10 mm in diameter. In the Galápagos Islands, however, the flowers of *T. cistoides* vary from 15–25 mm in diameter. Such wide variation in *T. cistoides* has also been observed in Mexico, where specimens have been collected whose petals vary in size from 8 × 5 mm [Puebla: 5 miles NE of Tehuacán, *Porter 1448* (GH, MEXU, MO)] to 21 × 12 mm [Vera Cruz: Vera Cruz, *Porter 1460* (DS, GH, MEXU)]. A parallel variation exists in the size and the amount of pubescence of the vegetative parts in this species. Plants of *T. cistoides* growing under more extreme ecological circumstances (such as in the open along the edge of a well-traveled road, or in an area subject to the salt spray of the sea) have smaller flowers and leaves, shorter internodes, and are heavily pubescent. Those growing under more favorable circumstances have larger flowers, longer internodes, and less pubescence. Collections of the former type from the Galápagos Islands, the most common phenotype of collections of this species examined from the archipelago, have been described as *Tribulus sericeus* Anderss. Such polymorphism in the genus has led to many problems in specific delimitation (Schweikerdt, 1937; Launert, 1963; Squires, 1969).

Both species in the Galápagos bloom at the same time of year, following the rains. The flowers of *Tribulus cistoides* are protandrous (Robertson & Gooding, 1963), and those of *T. terrestris* are protogynous (Goldsmith & Hafenrichter, 1932). Individual flowers, then, are usually outcrossed; thus the possibility of interspecific hybridization exists. Schweikerdt (1937) has hinted at such hybridization, but so far as I am aware, neither natural nor artificial interspecific hybridization has been demonstrated in *Tribulus*.

Few pollinating insects are known from the Galápagos Islands. Among potential insect pollinators are butterflies, moths, flies, beetles, wasps, an ant, and a bee (Linsley, 1966). However, with one exception, little is known regarding their relationships to pollination. The one exception is *Xylocopa darwini* Cockerell, the endemic Galápagos carpenter bee. *Xylocopa darwini* "is undoubtedly the principal pollen vector associated with plants of the Galapagos flora" (Linsley *et al.*, 1966: 1). It has been observed visiting a wide variety of plants, including 63 species in 28 families (Rick, 1963, 1966; Linsley *et al.*, 1966), for both pollen and nectar. From my personal observation, many of these are yellow-flowered. *Xylocopa darwini* is "common and widely distributed in the archipelago, chiefly at low elevations and along sea beaches" (Linsley, 1966: 226). This describes precisely the habitat of *Tribulus* on the islands, and *X. darwini* has been observed visiting the flowers of *T. cistoides* at Academy Bay, Isla Santa Cruz (Linsley *et al.*, 1966).

In light of the above information, an hypothesis can be proposed to explain the presence of connate intrastaminal glands in several collections of *Tribulus terrestris* from the Galápagos Islands. The condition is the result of gene-exchange between small-flowered individuals of *T. cistoides* and *T. terrestris*, accomplished through pollen carried from one to the other by the carpenter bee, *Xylocopa darwini.* Introgression of genes from *T. terrestris* into *T. cistoides* may also explain the high proportion of small flowers in the latter species as found in the archipelago.

It is interesting to note that in southern Africa, the other area where these two species are known to overlap in range, there is no indication of hybridization between them. Smaller-flowered individuals of *Tribulus cistoides* are rare in southern Africa; they are common in the Galápagos Islands. Accordingly, the opportunities for hybridization in Africa must be few. The presence of a common, wide-ranging pollinator in the Galápagos Islands has increased such opportunities many-fold. Unfortunately, nothing is known of the African pollinators of *Tribulus.*

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A MONOGRAPH OF THE GENUS *AGERATUM* L. (COMPOSITAE-EUPATORIEAE)[1]

MILES F. JOHNSON[2,3]

ABSTRACT

This monograph recognizes 29 species, 2 subspecies, and 14 formae in the Americas. Conventional means have been employed in determining species limits.

The genus is divided into five sections, of which two are described as new. Two species and one forma are described for the first time, and one previously described variety is accorded specific rank. Eleven taxa have been altered in rank, 17 proposed names are reduced to synonymy under other taxa of *Ageratum*, and eleven names are removed from the genus. Chromosome numbers are reported for the first time for four species, three chromosome numbers are confirmed, and corrected determinations are made for vouchers of nine previously published chromosome numbers.

Taxonomic literature, history of cultivation, economic uses, common names, geography, and generic relationships are discussed.

New keys, ecological data, and flowering and fruiting dates are included for the species and the infraspecific taxa. There are 17 distribution maps and illustrations of the new species.

The genus *Ageratum* has not been studied comprehensively since Robinson (1913*b*) published his revision. The lack of collections from Mexico and Central America at that time limited Robinson's work. New taxa have been described since Robinson's revision, but no key includes them. Distribution maps, ecological and chromosome data and times of flowering and fruiting for each species as well as complete descriptions were lacking in most instances. In view of the

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[1] This paper is based on a thesis submitted to the Faculty of the Graduate School of the University of Minnesota, Minneapolis, Minnesota, in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

[2] Department of Biology, Virginia Commonwealth University, Richmond, Virginia 23220.

[3] I am grateful to the curators of various herbaria who have loaned specimens for this study. I am especially grateful to the curators and/or directors of the Botanical Museum and Herbarium, University of Copenhagen, the Herbarium and Library, Royal Botanical Gardens, Kew, the Muséum National d'Histoire Naturelle, Paris, and the Botanisches Museum, Berlin-Dahlem, for allowing me free access to their collections of type specimens for photographing them and study.

Dr. Gerald B. Ownbey, my adviser and major professor, has had an attitude of interest and concern since the outset of this study. My second collecting trip to Mexico was made in his company and would not otherwise have been possible. He has been helpful concerning questions of broad scope as well as those concerning minor detail, and has called upon his background in taxonomy and systematics for the answers on many occasions. These and other aids too numerous to mention, I acknowledge with appreciation.

Bibliographic aid has been freely offered by Dr. John W. Moore. Mrs. Siu-tsun Hsi has been very helpful in cytological aspects of the study. Ronald H. Hofstetter accompanied me to Mexico in 1966 and gave financial aid as well as companionship. Dr. Rogers McVaugh has given information about various type specimens. Dr. Gerald M. Ericson greatly assisted with the Latin portions of this paper. Mrs. Sharon Llewellyn prepared the plates of new species described here. Permission to use copyrighted base maps has been granted by the University of Chicago. To each of them and to my wife, Wilma, who has given much time and effort in translating German, French, and Spanish literature, who acted as interpreter in Mexico and Europe, and who offered much encouragement during the course of this study, I express sincere appreciation.

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ANN. MISSOURI BOT. GARD. 58: 6–88. 1971.

lack of information concerning *Ageratum* and the more abundant collections from Mexico and Central America now available, it was evident that there was need for the preparation of a new monographic treatment of the genus.

The present study of *Ageratum* covers a period of three years. I have studied several species in the field and have grown some from seed in the University of Minnesota greenhouses. However, the main descriptive portions have been drawn from approximately 2,400 specimens borrowed from 18 herbaria in the United States and Europe. I made collecting trips to Mexico in 1964, 1965, and 1966 with extensive collections resulting from the latter. Collections of type specimens have been personally studied and photographed. Chromosome numbers have been determined for several species, and the proper identification determined for numbers previously published.

This monograph treats all species of *Ageratum* over their entire ranges insofar as known, though further information is needed. Data concerning hybridization in the field, degrees of crossability, pollinators, and biological species limits are lacking. It is anticipated that these studies will be carried out later.

Historical Review of Taxonomic Literature

One of the earliest published plant descriptions referring to an *Ageratum* is that of Hermann (1689). That this description does indeed refer to *Ageratum* is recognized from Linnaean publications (1737, 1748, 1753) in which Hermann is cited.

The name was first applied in the generic sense by Linnaeus in *Hortus Cliffortianus* (1737) and as a binomial in *Species Plantarum* (1753) in which *Ageratum* was a part of the Class *Syngenesia Polygamia Aequalis.* (According to Gray (1878), *Ageratum* is an ancient Greek or Latin name applied to some aromatic plant, probably an *Achillea.* The etymology of *Ageratum* is agreed upon by Miller (1768), Lunan (1814), Gray (1878), and L. H. Bailey (1910, 1943), all of whom derive the name from the Greek *a,* not, and *geras,* old age, referring to the long-lasting nature of the flowers. Step (1897) agrees with the etymology but wrote that the name refers to the absence of white pappus bristles so common in some members of the Compositae.)

Ageratum, in the Linnaean sense, included three species: *A. conyzoides, A. ciliare,* and *A. altissimum.* This alignment of species rendered the genus unnatural as *A. altissimum* is now placed with *Eupatorium urticaefolium* Reichard (Robinson, 1906*a*, 1906*b*), and *A. ciliare* was not adequately described for proper determination—its identity is uncertain. However, the plate in Plukenet (1720) which is cited by Linnaeus (1753) as *A. ciliare* shows a laterally compressed achene topped with a capillary pappus, features which exclude this species from *Ageratum.* Thus *A. conyzoides* is the only species remaining in the genus as circumscribed by Linnaeus and is designated the type.

The first major post-Linnaean study of *Ageratum* was that of Candolle (1836). He treated the genus as separate from *Coelestina* though he believed the two genera were distinguished only with difficulty. The genus was comprised of two sections in the Candollean interpretation: *Euageratum* with species having 5 distinct, acuminate, aristate pappus scales and *Pectinellum* including species with 10 distinct, pectinate-ciliate pappus scales. In the former, Candolle placed *A. conyzoides* under which he described four varieties. All are placed in synonymy under *A. conyzoides* in the present paper except var. *mexicanum* which is placed under *A. houstonianum* Miller. Section *Pectinellum* contained *A. melissaefolium* DC., *A. matricarioides* (Spreng.) Less. and *A. domingense* Spreng. Of these, only *A. domingense* is retained in the section; *A. matricarioides* is placed in *Phania* as was done by Robinson (1913*b*), and *A. melissaefolium* is referred to *Trichogoniam* (Robinson, 1913*b*). Species originally described in *Ageratum* but possessing a coroniform pappus were transferred to *Coelestina* Cass. by Candolle.

Bentham and Hooker (1873) included a discussion of the genus and variations in the pappus. Their concept of the genus encompassed species with a cupuliform pappus but excluded *A. adscendens* Sch. Bip. and *A. glanduliferum* Sch. Bip. on the basis of their more numerous pappus scales. These species are now referred to *Oxylobus* Moc. (Robinson, 1913*b*).

The next treatment of the genus was that of Baker (1876). He included *Ageratum* in his tribe Ageratae which was distinguished by 5-ribbed achenes and anthers with apical appendages. The genus *Ageratum* was divided into two subgenera—*Ageratum verum* with elongate, linear, distinct pappus scales and *Coelestina* which included those species with a short, coroniform, 5-dentate pappus. Baker placed *A. conyzoides, A. melissaefolium, A. alternifolium, A. confertum, A. corymbosum, A. campuloclinioides,* and *A. pohlianum* in subgenus *Ageratum verum.* As interpreted today, this arrangement is an unnatural one—all species named above except *A. conyzoides* are removed from *Ageratum* because of the plumose or bristle pappus present in each (Robinson, 1913*b*).

Baker's subgenus *Coelestina* included *A. scorpioideum, A. longifolium, A. micropappum,* and *A. heterolepis.* Of these, *A. longifolium* and *A. heterolepis* lack a pappus and are referred to *Alomia* HBK (Robinson, 1913*b*).

The third major treatment was that of Hemsley (1882) based on specimens at Kew and on a large collection made by Parry and Palmer in San Luis Potosí, Mexico. Hemsley's work was meant to be, in the main, plant geography and not strictly taxonomic. Even so, the taxonomic treatment has some merit.

The genus, in the sense of Hemsley, included 24 species though he enumerated only 20 of them. *Ageratum microcephalum, A. salicifolium,* and *A. strictum* were described as new. He transferred *Coelestina albida, C. latifolia* Benth. *non* Cav., *C. microcarpa, C. paleacea, C. petiolatum, C. scabriuscula, C. tomentosa, Phania arbutifolia,* and *Isocarpha echioides* to *Ageratum.* For the most part, these species have been retained under *Ageratum.* I have reduced *A. salicifolium* to *A. corymbosum* f. *salicifolium* and placed *A. scabriuscula* in the synonymy of *A. petiolatum.* Robinson (1913*b*) synonymized *A. strictum* and *A. latifolium. Ageratum microcephalum* and *A. microcarpum* are placed in *Alomia* (Robinson, 1913*b*). Hemsley had included *A. adscendens, A. arbutifolium,* and *A. glanduliferum* which are now placed in *Oxylobus* Moc. and *A. sessilifolium* which is in *Trichocoronis* (Robinson, 1913*b*).

Kuntze (1891) went to the extreme in applying the principle of priority and transferred all species of *Ageratum* to *Carelia* Moehring (1736).

The most recent major contribution to the taxonomy of *Ageratum* is Robinson's (1913*b*) revision. He limited the genus to species possessing a pappus of 5 distinct scales or a cup-like crown of short, connate scales and excluded those with either a bristle pappus or that lack a pappus. The genus, as he interpreted it, contained two sections: *Euageratum* DC. with the pappus of 5 scales and *Coelestina* (Cass.) Gray with the cup-like pappus. His revision included three species new to science, seven new forms and varieties, one new name and one new combination. Synonymy, brief distribution notes, and citations of specimens were included.

I have followed Robinson's revision to a slight degree but have transferred some species from his section *Euageratum* to section *Coelestina*. I have reinstated *Ageratum domingense* in section *Pectinellum* and have placed *A. stachyofolium* in its own section. Many of Robinson's varieties have been reduced to formae especially under *A. corymbosum*. Though Robinson referred *A. echioides* to *Alomia*, I have reinstated it under *Ageratum*.

The major limitations of Robinson's revision are that it was based solely on herbarium specimens and that in some instances very few plants were available to him. This resulted in describing the same species twice, incorrect determination of individual specimens, inappropriate alliances between species, and describing forms based on corolla color.

Though Robinson (1913*b*) was the authority on *Ageratum* for more than 50 years, his revision was necessarily incomplete. There have been six species, a form, and a subspecies described since 1913 which have not been included in a previous revision of the genus.

Since 1913 the systematic literature concerning *Ageratum* has included distribution data and descriptions of new taxa. More recently, Turner and his associates and Powell and King have published chromosome numbers for several species of *Ageratum*.

History of Cultivation

Ageratum conyzoides is the first species to have been cultivated in Europe. According to Schlectendal (1857–58), it was noted by Hermann in Ghent, Belgium, prior to 1697. The earliest date of cultivation in England is 1714 where it was grown by Mary, Duchess of Beaufort, in her gardens during that year (Dandy, 1958; Miller, 1768; Schkuhr, 1808; Schlectendal, 1857–58; Step, 1897). I believe that cultivation may have begun at least a few years prior to 1714 in England as the Duchess of Beaufort died January 7, 1714 (Dandy, 1958).

Apparently, the cultivation of *Ageratum conyzoides* had spread to Sweden by 1748 as Linnaeus considered it "tame" in his *Hortus Upsaliensis* (Linnaeus, 1748). That *A. conyzoides* was held in high regard by gardeners is apparent from Hooker's (1823) statement that it "is well deserving of a place in every stove," referring to the gardener's hothouses.

Ageratum houstonianum, first collected in 1731 in Vera Cruz, was not cultivated in Europe as an ornamental until 1822 (Step, 1897) or 1823 (Hegi, 1917), though it was known as a weed in hotbeds prior to 1768 (Miller, 1768). By 1860, it was in cultivation in Salzburg (Hegi, 1917). At present *A. houstonianum* is the only species of the genus which is a popular garden plant. The modern horticultural varieties of *A. houstonianum* include tetraploids (personal communication, G. W. Park Seed Co.) and F_1 hybrids, which are derived by selecting progeny from crossed inbred lines of commercial *Ageratum* varieties (personal communications, American Seed Co. and Goldsmith Seeds, Inc.).

Medicinal and Economic Uses

Ageratum conyzoides plays a role in folk medicine over much of its range. Holland (1922) reports *A. conyzoides* as useful externally for treatment of Craw-craw, a contagious, parasitic, pustular skin disease common among Negroes of West Africa, and internally for treatment of fever in Yoruba-land. The same cures are reported by Dalziel (1937) in Nigeria. The plant is also used externally as treatment of Craw-craw and chronic ulcer, and internally as an emetic and for intra-uterine problems, in Sierra Leone (Dalziel, 1937). The juice is an eye medicine in the Gold Coast, an external remedy for pneumonia in children in Liberia, a purgative enema in the Cameroons, and a treatment for sleeping sickness in Portuguese Congo (Dalziel, 1937).

Ageratum conyzoides is highly prized as a remedy for non-menstrual vaginal hemorrhage in South America and as a remedy for prolapsus ani in India (F. M. Bailey, 1906). Leaves scorched over a fire are placed on fresh wounds in Malayasia (Steenis, 1947–48). Natives of Borneo have used leaves on skin boils and wounds due to dog or crocodile bites and as a remedy for stomach ache (Koster, 1935).

Additional medical uses have been culled from herbarium labels. *Ageratum conyzoides* functions as a remedy for stomach ache in Colombia and Venezuela (*Fosberg 19250*, US). The leaves are used medicinally for cuts in the Caroline Islands (*Fosberg 32054*, NY), and an unspecified part of the plant is used as remedy for gonorrhea in El Salvador (*Standley 19220*, US), in an infusion as a syrup for sore throat in Chiapas (*Matuda 16841*, F, NY) and as an anticatarrhal in Colombia (Perez-Arbelaez, 1956). In Canton, China, the whole plant is placed in water, allowed to decay and then fed to small fish which are raised as food (Hu, 1956).

An infusion prepared by boiling *Ageratum echioides* is drunk for malarial treatment in Guatemala (*Steyermark 51500*, NY).

The leaves of *Ageratum gaumeri* are used to check nosebleed in Yucatan (Millspaugh, 1903), and *A. houstonianum* is a remedy for sore throat in Guatemala (*Goll 238*, NY, US).

The value of *Ageratum conyzoides* as a medicinal plant is seemingly due to alkaloids which have a vaso-constrictor action similar to that of ergot (Chevalier, 1910). The medicinal value of *A. echioides, A. gaumeri,* and *A. houstonianum* may be alkaloidal in nature, too, though I am not aware of any studies indicating this.

Ageratum littorale is reported to be used as treatment for unspecified illnesses in Mexico (Martinez, 1933), but Martinez must be referring to some other plant—*A. littorale* does not occur in Mexico.

Common Names

The genus is known as *agerate* in French, *Leberbalsam* in German and by its Latin name among horticulturists and gardeners, though seed packets of *Ageratum houstonianum* are sometimes sold under the name "Floss Flower," the same name applied to *A. conyzoides* in India (Fyson, 1932). There have been numerous names applied to horticultural varieties of *A. houstonianum*, the only species cultivated to any extent in the United States. These names, which are very descriptive, include "Summer Skies," "Blue Blazer," "Blue Mink," "Blue Fox," and "Pure White." Plants sold under the name "Hardy Ageratum," *Ageratum lasseauxii*, and Perennial Ageratum are in the genus *Eupatorium*; those sold as "Golden Ageratum" are *Lonas annua* Vines & Druse (Sims, 1822, and personal communication from F. A. Swink, The Morton Arboretum).

Wild *Ageratum houstonianum* is referred to as "Yerba de Zopilote" (*Kerber 302*, BM, US) and "Flor de Garrapata" (*Kelly 908*, US) in Vera Cruz, its native habitat.

Ageratum corymbosum sens. lat. is known as "Flattop Ageratum" in Texas (Gould, 1962) and in Spanish as "Cielitos" (Robinson, 1913*b*). Reiche (1926) gives "Mota morada" as a common name in Mexico, a name applied to *A. gaumeri* also.

"Frijolito" is the name applied to *A. echioides* (*Steyermark 51500*, NY), "Mota" is used to refer to *A. rugosum* (*Standley 58050*, NY) and "Mejorano" for *A. houstonianum* (*Goll 238*, NY, US) in Guatemala.

Ageratum gaumeri is known as "Tucan" (*Steere 1009*, GH, MICH, US), "bakelus," "Mota," "Mota morada," "Sereno," and "Flor de San Juan" (Millspaugh, 1903) in the Yucatan Peninsula. "Sereno" also refers to *A. houstonianum* in Mexico (*Rovirock 693*, NY).

"Santa Lucia" is the name given to the genus as a whole in Costa Rica (Standley, 1938) and more specifically to *A. oerstedii* (*Holway s.n.*, MIN), *A. conyzoides* (Standley, 1938), and to *A. standleyi* in Honduras (*Molina 14686*, F). This name also refers to species of *Alomia*.

Ageratum standleyi is also known as "Azullilo" in Honduras (*Standley 1498*, F). *Ageratum petiolatum* is referred to as "Conejito" in Nicaragua (*Maxon 7661*, US).

Ageratum conyzoides, a widespread tropical weed, has received names too numerous to list completely. However, I have selected some of the names as examples. "Mejorana" is the name used in El Salvador (Standley, 1928; *Calderon 155*, MO, US; *Standley 19220*, US) and Guatemala (*Cook & Griggs 560*, US), while *A. conyzoides* is known as "Mentrasto" in Brazil (*Macedo 173*, MO; *Blanchet 875*, NY) and Puerto Rico (Cook & Collins, 1903; Stahl, 1937). "Manrubio" is the common name in Colombia (*Daniel 526*, US). Examples of descriptive names include "Hierba del perro" or herb of the dog in El Salvador (*Padilla 249*, US), "Hierba del Zorro" or herb of the fox or cunning fellow in Argentina (*Montes 1797*, US), and "catinga de bode" which is translated as "bad smell of he-goat" in Brazil (Perez-Arbelaez, 1956). The malodorous nature is also the basis for the names "Billy Goat Weed" (Dalziel, 1937; *Russell s.n.*, UC) and "Billygoat Plant" (F. M. Bailey, 1906) in Australia and "Goat Weed" in Ceylon (Cooke, 1908; Trimen, 1895). The Chinese characters for *A. conyzoides*, when translated, read "flower with odor of salty shrimp" (*To, et al. 97L*, UC), again alluding to the disagreeable odor.

Geographic Distribution

Ageratum is restricted to the Americas and adjacent West Indies except for *A. conyzoides* subsp. *conyzoides*, a weed introduced pantropically. Of the 39 taxa recognized in the present paper, the vast majority are in Mexico, Central America, the West Indies, and south Florida. Only four taxa occur in South America, one of these being *A. conyzoides* subsp. *conyzoides*. The genus is widely distributed in Mexico especially in the Temperate Pine-Oak Forest Zone of Leopold (1950). However, the distribution of individual taxa is often localized in a relatively small area. For example, five taxa are localized in Yucatan; *A. oerstedii* is endemic to Costa Rica. Except for *A. conyzoides* subsp. *conyzoides*, ranges of the South American taxa are restricted as well.

Wind is quite probably an important means of dispersal for all species. The fruits are light and easily blown even by gentle air currents from an office fan. Those fruits with a pappus of spreading scales presumably have additional air buoyancy.

Man has played a role in dispersal and introduction of *A. conyzoides* subsp. *conyzoides* at least in the Philippine Islands. Galleons leaving Acapulco and Navidad, Mexico, bound for Manila carried seeds that formed the basis for the plants which are very abundant in the Philippines today (Merrill, 1912). The form of the fruits also aids in their passive dispersal by man, as the fruits are not only small but prismatic. I have often found fruits embedded among the fibers of clothing after a day of studying *Ageratum*. Some are equipped with stiff hairs along the angles which aid in attaching them to clothing. Man's cultivation of crops in the tropics has aided in the spread of this weed as it readily establishes itself in open, worked soil.

Generic-Intergeneric Relationships

Ageratum is placed in the tribe Eupatorieae, characterized by its tubular flowers which are all alike and are never yellow, anthers basally blunt, and style branches terete, clavate, papillate and stigmatic near the base.

Ageratum is apparently closely related to *Alomia* which it closely resembles in habit, habitat, and to a degree in distribution. These genera are distinguished by the lack of a pappus in *Alomia*. Heretofore, *Ageratum* was considered to be closely related to *Oxylobus*, but study of data gathered from chromosome numbers, morphology, and ecology suggests a more distant relationship.

Species Concept

Species and lower taxa are delimited primarily on morphological bases. Geographical distribution and chromosome numbers have been employed to supplement morphology when appropriate.

For the most part, the species are very distinct morphologically. Introgression and consequent blurring of species limits, if it is occurring, is not evident in this genus. Though cytodemes of tetraploid plants do occur, these have not been recognized nomenclaturally unless morphological differentiation accompanies the polyploidy.

The major morphological subunits of the species which have a distinct geographic area and between which there is little or no chance of transfer of germ plasm are referred to here as subspecies. Only two subspecies, between which the barrier to transfer of germ plasm is genetic, are recognized in this paper—*A. conyzoides* subsp. *conyzoides* and *A. conyzoides* subsp. *latifolium*. The first is a tetraploid, while the latter is a diploid.

Formae are recognized when consistent, minor, vegetative variations which do not have a distinct geographic area occur. Formae based on corolla color have not been maintained. This character is extremely variable, and it becomes exceedingly arbitrary and subjective if the varying shades are given names. No deterrent to gene exchange between formae of a single species is implied by a form name.

Chromosome Numbers

The basic chromosome number for the genus is $x = 10$. Natural tetraploids, $n = 20$, are reported for nine taxa. A triploid, $3n = 30$, is reported for the first time for the genus.

It is common to find polyploid chromosome races within a normally diploid species of *Ageratum*. Usually, in *Ageratum*, the diploids and polyploids are so similar that they are indistinguishable by means other than actually counting chromosomes. I have measured pollen grains, stomatal guard cells, and other morphological characters on specimens for which the ploidy level is known. For the most part, there is no difference between features from $2n$ and $4n$ plants, and thus the polyploids can be termed "semi-cryptic" (Davis & Heywood, 1963). Due to the similarities between polyploids and diploids, no attempt is made to set apart chromosome races within a taxon except in *A. conyzoides sens. lat.*

Ageratum conyzoides subsp. *conyzoides*, a tropical, tetraploid weed, is very similar to *A. conyzoides* subsp. *latifolium* which is diploid. The main gross morphological character that distinguishes these taxa is the setiferous pappus scales of *A. conyzoides* versus truncated scales in subsp. *latifolium*. Though not always consistent, known references to chromosome numbers indicate that the tetraploid plants produce a setiferous pappus and that the $2n$ plants have a truncated one.

Systematic Treatment

Ageratum L., Sp. Pl. 2: 839. 1753.

Carelia Adans., Fam. Pl. 2: 123. 1763.

Annual *herbs* and perennial *shrubs* 0.45–24 dm tall; *roots* fibrous or a taproot, at times adventitious; *stems* woody or herbaceous, rarely succulent, erect, repent, decumbent, simple or branched, puberulous, pilose, scabrous, glandular-villous or glabrous, glandular-atomiferous to eglandular, sap watery; *leaves* opposite or alternate, petioled or sessile, firm or more or less membranaceous, ovate, elliptic, lanceolate, linear, deltoid, orbicular or cordate, 0.5–10(–13) cm

TABLE 1. Haploid chromosome numbers reported for the genus *Ageratum*.

Taxon	Haploid number	Locality and voucher	Source
A. *albidum*	$n = 20$	MEXICO. OAXACA: Monte Alban, *King 3490* (DS, MICH, NY, TEX, UC, US).	Turner, Ellison & King, 1961.
A. *conyzoides* subsp. *conyzoides*	$n = 10$	None given.	Ishikawa, 1911, 1916.
	$n = 10$	None given.	Mehra *et al.*, 1966.
	$n = 20$	PANAMA. Concepción, *King 5286* (TEX, UC, US).	Turner & King, 1964.
	$n = 20$	PANAMA. COCLE: El Valle, *King 5327* (TEX, UC, US).	Turner & King, 1964.
	$n = ca.\ 20$	PANAMA. Cerro Azul, *King 5248* (TEX, US).	Turner & King, 1964.
	$n = 20$	UGANDA. *Lewis 6028* (TEX).	Turner & Lewis, 1965.
	$n = 20$	TANGANYIKA. *Lewis 6060* (MO, TEX).	Turner & Lewis, 1965.
	$n = 20$	KENYA. *Lewis 5912* (MO, TEX).	Turner & Lewis, 1965.
	$n = 20$	SIERRA LEONE. *Harvey 104* (K).	Löve, 1966.
	$n = 20$	DOMINICA.	Powell & King, 1969.
A. *corymbosum* f. *corymbosum*	$n = 20$	MEXICO. MICHOACAN: *King 3644* (DS, MICH, NY, TEX, UC, US).	Turner, Ellison & King, 1961.[c]
	$n = 11$	MEXICO. MICHOACAN: E of Jiquilpan, *King & Soderstrom 4901* (MICH, TEX, UC, US).	Unpublished, data from herbarium labels.
	$n = 10$	MEXICO. OAXACA: NE of Huajuapan, *King 3544* (MICH, TEX).	Turner, Powell & King, 1962.[d]
	$n = 10$	MEXICO. PUEBLA: W of Izucar de Matamoros, *King 2933* (MICH, TEX).	Turner, Powell & King, 1962.
	$n = 10$	GUATEMALA. E of Chiantla, *Ownbey & Muggli 3971* (MIN).	Author.
	$n = 15$	MEXICO. MICHOACAN: E of Morelia, *Owenbey & Muggli 3948* (MIN).	Author.
A. *corymbosum* f. *albiflorum*	$n = 10$	MEXICO. CHIAPAS: SE of Comitan, *King 3045* (TEX).	Turner, Powell & King, 1962.[e]
	$n = 20$	PERU. *Wurdack 443* (NY, TEX, US).	Unpublished, data from herbarium labels.
	$n = ca.\ 17$	GUATEMALA. *King 3153* (TEX).	Unpublished, data from herbarium labels.
	$n = 20$	THAILAND. *King 5528* (TEX), *5537* (TEX, UC), *5574* (TEX), *5577* (TEX, UC), *5584* (TEX).	Unpublished, data from herbarium labels.

TABLE 1. Haploid chromosome numbers reported for the genus *Ageratum*. (Continued from page 14)

Taxon	Haploid number	Locality and voucher	Source
A. conyzoides subsp. *latifolium*	$n = 10$	MEXICO. HIDALGO: *King 4226* (F, MICH, NY, TEX, UC).	Turner, Powell & King, 1962.[a]
	$n = 10$	MEXICO. PUEBLA: *King 4140* (MICH, NY, TEX, UC).	Turner, Powell & King, 1962.
A. corymbosum f. *euryphyllum*	$n = 20$	MEXICO. SAN LUIS POTOSI: La Capilla, *Rock 456* (TEX).	Turner, Beaman & Rock, 1961.[b]
	$n = 10$	MEXICO. OAXACA: S of Tehuacan, *Powell & Edmondson 666* (F, MICH, TEX).	Powell & Turner, 1963.[f]
	$n = 10$	MEXICO. JALISCO: W of Sahuayo, *Powell & Edmondson 841* (TEX).	Powell & Turner, 1963.[g]
	$n = 10$	MEXICO. DURANGO: W of Revolcaderos, *Ownbey & Muggli 3927* (MIN).	Author.
A. corymbosum f. *salicifolium*	$n = 10$	MEXICO. JALISCO: W of Guadalajara, *Powell & Edmondson 866* (F, MICH, TEX).	Powell & Turner, 1963.[h]
	$n = 20$	MEXICO. DURANGO: N of Durango, *King 3750* (DS, MICH, NY, TEX, UC, US).	Unpublished, data from herbarium labels.
A. echioides	$n = 20$	MEXICO. CHIAPAS: SE of San Cristobal de las Casas, *Ownbey & Muggli 3986* (MIN).	Author.
A. elassocarpum	$n = 11 \pm 1$	MEXICO. CHIAPAS: SE of Las Cruces, *King 3112* (DS, MICH, NY, TEX, UC, US).	Turner, Powell & King, 1962.[i]
A. guatemalense	$n = 10$	GUATEMALA: S of Huehuetenango, *Ownbey & Muggli 3972* (MIN).	Author.
A. houstonianum	$n = 10$	None given.	Cooper & Mahoney, 1935.
	$n = 20$	None given.	Morrison & Rajhathy, 1960.
	$n = 10$	MEXICO. VERA CRUZ: W of Cordoba, *King 2360* (MICH, TEX).	Turner, Ellison & King, 1961.
	$n = 10$	MEXICO. MORELOS: S of Cuernevaca, *King 4160* (MICH, TEX, UC).	Turner, Powell & King, 1962.
	$n = 10$	GUATEMALA. S of Goban, *King 3311* (DS, MICH, TEX, UC).	Turner, Powell & King, 1962.
A. houstonianum f. *isochroum*	$n = 10$	MEXICO. CHIAPAS: San Quintin, *Breedlove 9135* (MICH).	Unpublished, data from herbarium labels.

TABLE 1. Haploid chromosome numbers reported for the genus *Ageratum*.
(Continued from page 15)

Taxon	Haploid number	Locality and voucher	Source
A. nelsonii	$n = 10$	MEXICO. CHIAPAS: E of Oaxaca-Chiapas border along Rte. 190, *King 2981* (MICH, TEX).	Turner, Powell & King, 1962.[j]
	$n = 10$	MEXICO. CHIAPAS: E of Oaxaca-Chiapas border along Rte. 190, *King 2751* (MICH, TEX).	Turner, Powell & King, 1962.[k]
A. petiolatum	$n = 10$	PANAMA. N of Concepción, *King 5289* (TEX, UC).	Turner & King, 1964.[l]
A. platypodum	$n = 20$	MEXICO. JALISCO: E of Tapalpa, *Ownbey & Muggli 3941* (MIN).	Author.
A. rugosum	$n = 20$	GUATEMALA. N of Salama, *King 3291* (TEX.)	Turner, Ellison & King, 1961.[m]
	$n = 20$	GUATEMALA. N of Palen, *Ownbey & Muggli 3976* (MIN).	Author.
A. tomentosum	$n = 10$	MEXICO. PUEBLA: N of Puebla-Oaxaca border, *King 3548* (NY, TEX, UC, US).	Turner, Ellison & King, 1961.

[a] Published as *A. latifolium* Cav.
[b] Published as *A. corymbosum* Zuccag.
[c] Published as *A.* cf. *lucidum* Robins.
[d] Plus fragments.
[e] Published as *A. corymbosum* Zuccag.
[f] Published as *A. albidum* (DC.) Hemsl.
[g] Published as *A.* cf. *corymbosum* Zuccag.
[h] Published as *A. salicifolium* Hemsl.
[i] Published as *A.* cf. *paleaceum* (Gay) Hemsl. var. *paleaceum*.
[j] Published as *A.* cf. *tomentosum*.
[k] With fragments, published as *A. paleaceum* (Gay) Hemsl. var. *nelsonii* Rob.
[l] Published as *A. corymbosum* Zuccag.
[m] Published as *A. corymbosum* Zuccag.

long, 0.25–9 cm wide, base obtuse, cordate, truncate, apex acute to acuminate, margin revolute or plane, crenate, dentate or shallowly lobed to entire, ciliate, scabrous or glabrous, upper surface usually green to dark green or brown, pilose, scabrous, glandular-punctate and/or atomiferous or eglandular to glabrous, at times rugulose, lower surface pale green to gray, densely to sparingly pilose, glandular punctate and/or atomiferous to eglandular, 3-veined or the venation reticulate, rarely palmate; stomatal apparatus on the lower leaf surface of the paracytic type (Essau, 1960); *petioles* 0.2–3(–6) cm long, pilose, glandular-atomiferous to glabrous, at times narrowly winged distally; *inflorescences* in compact to open corymbiform clusters, in heads borne singly or in an irregular panicle, the 3–10(–30 or more) heads borne on pilose, glandular or eglandular, bracteate peduncles 0.3–8.5(–15) cm long; *involucres* campanulate, hemispherical or turbinate, bracts bi- or less commonly triseriate, firm or membranaceous, 2- or 4-ribbed or smooth and merely nerved, lanceolate, lanceolate-oblong, ovate or spatulate, 2–6.85 mm long, outer bracts 0.5–1.55 (0.4–1.35) mm wide, green to variously tinged with red or purple, pilose and glandular-atomiferous to glabrous, margin green to scarious, entire to variously erose apically, ciliate, scabrous or glabrous, apex acuminate, acute or rounded, ciliate or glabrous; *receptacle* conical, naked or less commonly paleaceous, paleae resembling involucral bracts; *corollas* funnelform or tubular, 1.1–3.75 mm long, pilose, puberulent, scabrous, glandular-atomiferous or glabrous, tube and narrow throat pale green or white, the 5 erect or spreading deltoid lobes lavender, lilac, mauve, violet, blue, gray or white; *style* branches bifurcate, terete, clavate, papillate, stigmatic area near base, same color as corolla lobes; *anthers* apically appendaged; *pollen* spheroidal, echinate, tectate, tricolporate or rarely tetracolporate; *achenes* 5-angled, prismatic, dark brown to black, 1–2.75 mm long, glabrous or scabrous on angles or throughout, with whitish carpopodium at base or carpopodium lacking; *pappus* of 5–6 free, membranous, flattened, elongate, oblong scales 0.23–3.5 mm long, with or without setae, or pappus coroniform or cup-shaped and 0.1–0.55 mm long, margin entire, undulate or setiferous; recorded chromosome numbers $n = 10$, $n = 20$, $3n = 30$.

Type species: *Ageratum conyzoides* L.

KEY TO SECTIONS OF *AGERATUM*

1. Stems erect or decumbent; leaves opposite or alternate, variously shaped but not orbiculate-cordate; involucral bracts 2- or 4-ribbed or 5-nerved; corolla tube very gradually expanded toward the throat; achenes with whitish carpopodium or the carpopodium lacking; pollen grain wall thin, ca. 2–3 μ thick 2
   2. Leaves alternate, short petiolate; involucral bracts 4-ribbed; achenes glabrous, basally sharp-pointed, carpopodium lacking; pappus coroniform .... Section IV. *Stachyofolium*
   2. Leaves opposite, short or long petiolate; involucral bracts 2-ribbed or 5-nerved; achenes glabrous or scabrous throughout or at least on the angles, carpopodium conspicuous or inconspicuous; pappus of 5 or rarely 6 basally free, usually setiferous scales or the pappus coroniform 3
      3. Annual or perennial herbs; pappus of 5 to 6 basally free, usually apically setiferous scales; achenes scabrous at least on the angles or throughout; carpopodium conspicuous or inconspicuous; receptacle naked or paleaceous 4
         4. Achenes scabrous only along the angles, or if on the sides, the hairs not yellow; carpopodium conspicuous; involucral bracts firm, 2-ribbed, narrowly lanceolate, lanceolate or oblong, the apex acute; receptacle naked .... Section I. *Ageratum*
         4. Achenes scabrous throughout, the hairs conspicuously yellow and pointed upward; carpopodium inconspicuous, involucral bracts membranaceous, 5-nerved, widely ovate, the apex broadly rounded; receptacle paleaceous .... Section V. *Perplexans*
      3. Woody or herbaceous perennials; pappus coroniform, cup-like or if the margin setiferous, the setae basally connate; achenes glabrous, carpopodium conspicuous; receptacle paleaceous or naked .... Section II. *Coelestina*
1. Stems repent; leaves opposite, orbiculate-cordate on vertically elongate petioles; involucral bracts unribbed; corolla tube abruptly expanded toward the throat; achenes lacking a carpopodium; pollen grain wall ca. 5 μ thick .... Section III. *Pectinellum*

Section 1. **Ageratum**

Euageratum DC., Prod. 5: 108. 1836.
Ageratum verum Baker *in* Martius, Fl. Bras. 6 (2): 194. 1876.

Annual or perennial *herbs*; *roots* fibrous, at times adventitious; *leaves* opposite, ovate, elliptic, linear, lanceolate, oblong or deltoid, variously pubescent to glabrous; *inflorescences* grouped in corymbiform clusters or borne singly; *involucral* bracts 2- or 3-seriate, narrowly lanceolate, lanceolate or oblong, apex gradually or abruptly contracted, margin entire or apically erose or fimbriate, stipitate-glandular to glabrous; *receptacles* naked; *corollas* tubular, varying shades of blue and lavender or white; *achenes* scabrous on angles; *carpopodium* conspicuous; *pappus* of 5, rarely 6, scales basally free and usually setiferous.

Type species: *Ageratum conyzoides* L.

Species in this section occur in British Honduras, the Yucatan Peninsula, northern South America, southern Mexico, Central America, and the West Indies. One species is a pan-tropic weed. Flowering and fruiting occur year around as local conditions permit.

KEY TO SPECIES IN SECTION *AGERATUM*

1. Heads 3–18, grouped in a terminal corymbiform cluster; peduncles less than 4 cm long; leaves firm, at least not membranous, ovate, elliptic, linear, lanceolate, oblong or deltoid; pappus scales abruptly contracted apically to a scabrous or pectinate, coarse seta or the pappus scales truncated and variously pectinate to entire 2
   2. Plants erect; leaves elliptic or linear 3
      3. Leaves elliptic, 3–6 cm long, 0.8–2 cm wide; plants 3–5 dm tall; generally pubescent throughout; coastal regions, British Honduras .... 1. *Ageratum ellipticum*
      3. Leaves linear, 2.3–5 cm long, 0.25–0.5 cm wide; plants 2–5 dm tall, generally glabrous throughout; tropical pinelands, British Honduras .... 3. *Ageratum peckii*
   2. Plants erect or decumbent-repent; leaves ovate, lanceolate, oblong or deltoid 4
      4. Plants decumbent-repent, less commonly erect; leaves lanceolate to oblong, 4.5–6.7 cm long, 0.5–1.4 cm wide, glabrous; involucral bracts 3-seriate, firm, glabrous; stem glabrous or sparingly pilose-puberulent at nodes; wet areas and fresh water ponds, British Honduras .... 2. *Ageratum radicans*
      4. Plants erect, less commonly decumbent; leaves ovate to deltoid, pilose and glandular; involucral bracts biseriate, less firm, pilose or sparingly so to stipitate-glandular; stems decidedly puberulous-pilose to lanate-woolly especially above; Mexico, Central America, northern South America or a pan-tropic weed 5
         5. Leaves ovate to deltoid, the base cordate to truncate; involucral bracts narrowly lanceolate, the apex long-acuminate, entire, conspicuously pilose, and stipitate-glandular; southern Mexico, British Honduras, Guatemala, West Indies .... 4. *Ageratum houstonianum*
         5. Leaves ovate, the base obtuse, never cordate or truncate; involucral bracts wide, oblong, sparingly pilose to glabrous, eglandular, the apex abruptly contracted to less commonly gradually acuminate, the margin erose to variously fimbriate, rarely entire .... 5. *Ageratum conyzoides*
1. Head single, terminal; peduncles 4.5–15 cm long; leaves thin, ovate; pappus scales blunt, variously fimbriolate apically, rarely with a fine apical seta or pappus minute and appearing coroniform .... 6. *Ageratum gaumeri*

1. **Ageratum ellipticum** Robins., Contr. Gray Herb. 90: 5. 1930.

Holotype: BRITISH HONDURAS: Honey Camp, *Lundell 512* (GH); isotypes, DS, F, K, MO, NY.

Annual, 3–5 dm tall; roots fibrous; *stems* erect, branched, short pilose, at least at nodes, to nearly glabrous; *leaves* elliptic, becoming lanceolate near inflorescences, (3.1–)3.5–4.5(–6) cm long, (0.8–)1.1–1.8(–2) cm wide, apex acute, base more or less gradually attenuate to the petiole, margin revolute, entire to remotely crenate, ciliate to rarely glabrous, both surfaces pilose to nearly glabrous, the 3 longitudinal veins prominent; *petioles* 0.5–2 cm long, marginally pilose; *inflorescences* of 3–5(–6) heads borne on bracteolate, short puberulent-pilose peduncles ca. 1 cm long; *involucres* campanulate, bracts triseriate, lanceolate, 3–3.5(–4) mm high, 0.5–0.75 mm wide, green, glabrous, prominently 2-ribbed, margin entire, at times minutely ciliate; *corollas* tubular, 1.65–2 mm long, glabrous to minutely scabrous, tube and narrow throat pale green to white, 5 lobes acute, erect, blue to lilac; *achenes* dark brown to black, 1–1.15(–1.25) mm long, white puberulent-scabrous on angles and sides; *pappus* of 5, rarely 6, lanceolate, pale tan scales, apex tapering to a scabrous elongate seta, margin entire to variously fimbriate, entire scale 1.4–1.9 mm long.

Ageratum ellipticum is a distinct, apparently rare, endemic species in British Honduras. Robinson (1930), in describing the species, called attention to its similarities to *A. radicans.* Though indeed similar and seemingly closely related, these taxa are readily distinguishable. The widely elliptic, pilose leaves, pilose stems and shorter achenes are constant features of *A. ellipticum* that set it apart from *A. radicans. Ageratum ellipticum* is similar to *A. peckii* in the achenes, pappus and corollas but is distinguishable by the general pubescence, the larger elliptic leaves and larger size of the former.

This species is endemic to the coastal area of British Honduras. Specimens studied were collected in August and September; buds, flowers, and fruits were present.

BRITISH HONDURAS. Monkey River, near Jenkins Creek, *Gentle 4135* (F, GH, MICH, MO, NY); vicinity of Tower Hill, *Karling 31* (F, GH, US); Honey Camp, *Lundell 512* (DS, F, GH, K, MO, NY); Pine Ridge, near Honey Camp, *Meyer 127* (F, K).

2. **Ageratum radicans** Robins., Proc. Amer. Acad. Arts 47: 192. 1911.

Holotype: BRITISH HONDURAS: Pond near Manatee Lagoon, *Peck 99* (GH); isotype, K; photograph, MIN.

Annual, 2.7–7 dm tall; *roots* fibrous, adventitious at lower nodes if stem repent; *stem* branched, erect or procumbent to repent, glabrous to sparingly pilose-puberulent at nodes and near inflorescences; *leaves* glabrous to sparingly pilose at least on veins, lanceolate to oblong, 3.4–6.2(–8) cm long, (0.4–)0.61–1.7(–1.9) cm wide, tip acute, base gradually attenuate to a narrowly winged petiole, margin revolute, entire to remotely crenate on distal two-thirds, veins longitudinal, mid-vein conspicuous as seen from beneath; *petioles* ca. 1.3 mm long, glabrous to pilose; *inflorescences* of 3–5 heads borne on puberulent bracteolate peduncles 0.5–1 cm long; *bracteoles* alternate, subulate, glabrous to ciliate along margin; *involucres* campanulate, bracts firm, triseriate, prominently 2-ribbed, lanceolate (2.5–)3–4(–4.5) mm high, (0.4–)0.5–0.85 mm wide, green, glabrous, margin herbaceous to scarious, entire, glabrous to minutely ciliate, apex acute; *corollas* tubular to narrowly funnelform, 1.8–2.25(–2.45) mm long, glabrous throughout, the 5 obtuse lobes purplish-lavender to bright blue; *achenes* dark brown to black, (1.0–)1.15–1.35(–1.5) mm long, puberulent on angles, carpopodium white; *pappus* of 5 (rarely 6) whitish, lanceolate scales, (1.45–)1.75–2.05(–2.35) mm long, margin of scales fimbriate, apex gradually attenuate to an elongate scabrous seta.

Robinson (1911) described this species as "*prostratum reptans*" from seeing only one specimen. After having seen a number of collections, it is evident that Robinson drew attention to an uncommon growth habit; the usual form is a conspicuously upright stem. Some plants, however, may become prostrate and form roots at the lower nodes.

Ageratum radicans is undoubtedly closely related to *A. ellipticum* as both species are very similar in gross morphology, distribution, and ecology. These species are commonly confused by collectors and herbarium curators as is evident from the number of misapplied names on herbarium labels. However, *A. radicans* is distinguished from *A. ellipticum* by the overall glabrous condition and the lanceolate to oblong leaves of the former. The lanceolate leaves are also the best means to distinguish *A. radicans* from *A. peckii*, in which the leaves are linear.

Ageratum radicans is endemic to British Honduras in wet areas and fresh water ponds. Flowers and fruits are present in December, January, and February; and again in July and August.

BRITISH HONDURAS. Butcher Burn, Sibun River, *Bartlett 11389* (GH, K, MICH, US); Mondes, *Campbell 58* (K); Bakers, near Belize River, 18 miles from Belize, *Espat 46* (F); Maskall Pine Ridge, *Gentle 1355* (K, MICH, MO, NY, TEX, US); Gracie Rock, Sibun River, *Gentle 1757* (K, MICH, MO, NY, US); Augustine, *Hunt 43* (BM, US); Mountain Pine Ridge, *Lamb 132* (K); Orange Walk, *Lundell 70* (F); Baker's Pine Ridge, *Lundell 3821* (MICH, US), *4705* (NY, UC, US); pond near Manatee Lagoon, *Peck 99* (GH, K); All Pines, *Schipp 611* (BM, F, GH, K, MICH, MO, UC).

3. **Ageratum peckii** Robins., Proc. Amer. Acad. Arts 47: 192. 1911.

Holotype: BRITISH HONDURAS: Pine Ridge near Manatee Lagoon, *Peck 80* (GH); isotype, K.

Annual or *perennial*, ca. 2–5 dm tall; *roots* fibrous; *stems* erect, branching, glabrous, woody at base, bark dark red; *leaves* numerous, glabrous, linear-oblong, (2.3–)3–5 cm long, (0.25–)0.3–0.5 cm wide, tip rounded to acute, base long attenuate to the slightly winged petiole, margin entire to remotely crenate (under 15× magnification), lower surface with (1–)3–5 longitudinal veins, mid-vein more or less conspicuous; *inflorescences* corymbiform, the 3–5 heads borne on glabrous to sparingly puberulent bracteolate pedicels 0.3–2 cm long; *bracteoles* alternate, subulate, 1.5–3 mm long, merging with involucral bracts; *involucre* campanulate, biseriate, bracts prominently 2-ribbed, green to brown, glabrous, lanceolate to linear, (3.1–)3.6–3.8 mm high, (0.45–)0.55–0.65 mm wide, tip gradually acuminate, margins entire; *corollas* tubular or gradually expanded upward, (1.7–)2.2–2.3 mm long, glabrous, the obtuse lobes purple to blue; *achenes* dark brown to black, 1–1.25(–1.45) mm long, glabrous to sparingly puberulent; *pappus* of 5 upright, lanceolate, tawny scales, 1.5–2.2 mm long, margin variously fimbriolate, apex abruptly tapered to an elongate scabrous seta.

Ageratum peckii is one of the lesser known species in the genus. I have seen only three collections during the course of this study. However, even with few data upon which to base a decision, the plants designated *Ageratum peckii* comprise a good species. The glabrous, elongate, nearly entire leaves and the erect habit serve to distinguish this species from all other taxa. See also the discussion under *A. ellipticum* and *A. radicans*.

This species is endemic to British Honduras in tropical pine lands. Flowers and fruits are present in February, July, and August.

BRITISH HONDURAS. El Cayo District, Mountain Pine Ridge, *Bartlett 11696* (GH, K, MICH, US); 12 miles N of Belize, Pine Ridge, *O'Neill 8383* (F, GH, NY, UC); Pine Ridge near Manatee Lagoon, *Peck 80* (GH, K).

4. **Ageratum houstonianum** Miller, Gard. Dict. Ed. 8. 1768.

Holotype: MEXICO: Vera Cruz, *William Houston s.n.* (BM, not seen); photographs, MIN, NY, UC.

Annual, (2.5–)3–7(–9) dm tall; *roots* fibrous, adventitious at lower nodes if stem decumbent; *stems* simple or branched, especially above, erect or decumbent, reddish to green, glandular-villous to lanate above, hairs white to yellowish; *leaves* opposite, at times alternate above, ovate to deltoid, 2.4–8.6(–9.5) cm long, (1.7–)2.9–6.5(–8) cm wide, apex rounded or acute, base cordate to truncate, margin crenate or rarely dentate, more or less ciliate, upper surface dark green, pilose, hairs scattered or dense, especially over the veins, lower surface pale green, penninerved, densely pilose, especially over veins, to nearly glabrous; *petioles* 0.6–3.5 mm long, densely white pilose, especially on upper ones; *inflorescences* terminal, the 5–15 heads borne in tight or open cymose clusters on densely pilose-puberulent (at times glandular) bracteolate peduncles; *involucres* campanulate, bracts biseriate, narrowly lanceolate, (3.75–)4–5 mm high, outer ones 0.5–0.75(–0.95) mm wide, green or brownish, 2-ribbed, densely pilose to nearly glabrous, apex acuminate, glandular-ciliate, at times deep red, margin entire, herbaceous to scarious, glandular-ciliate especially above; *corolla* (2.15–) 2.5–3.5 mm long, funnelform, tube white, glandular to glabrous, throat blue, lilac, lavender, rarely white, the 5 lobes upright or spreading, acute, externally puberulous, pigmented as the throat; *achenes* 5-angled, black, (1.15–)1.5–1.75 mm long, scabrous on angles, carpopodium white, prominent; *pappus* of 5 free oblong, scarious scales (1.5–)2–3(–3.4) mm long, margin pectinate, apex setiferous, setae scabrous, at times the scales apically truncate and without setae, then scales 0.1–0.15 mm long.

Published cytological studies give the chromosome number $n = 10$ (Cooper & Mahoney, 1935; Turner, Ellison & King, 1961, for collections from Vera Cruz; Turner, Powell & King, 1962, for collections from Guatemala and Morelos). Morrison and Rajhathy (1960) disagree with the other authors; they report 40 chromosomes. As *Ageratum conyzoides* is tetraploid, $n = 20$, and similar in appearance to *A. houstonianum,* one wonders if Morrison and Rajhathy may have misidentified their material.

Ageratum houstonianum is closely related to *A. conyzoides* as is evidenced from the similarities of habit, achenes, pappus, corollas and the malodorous nature when fresh. The relationship is also indicated through the presence of the same alkaloid (Chevalier, 1910) and the presence of the heterocyclic compound, ageratochromene, isolated from the plants' essential oils (Alertson, 1955; Hegnauer, 1964). *Ageratum houstonianum* is often confused in herbaria, botanical gardens, and in the field with *A. conyzoides.* However, the combination of ovate leaves with cordate bases, and narrowly lanceolate, conspicuously pilose involucral bracts with stipitate glandular pubescence on the gradually acuminate apex distinguishes *A. houstonianum* from similar species.

Ageratum houstonianum is divided into formae based on characters of the pappus and involucre.

1. Pappus scales oblong, pectinate, apically setiferous, scale (1.5–)2–3(–3.4) mm long; involucral bracts stipitate-glandular, ciliate ..... 4a. *Ageratum houstonianum* f. *houstonianum*

1. Pappus scales oblong, pectinate, apically truncate, not setiferous, 0.1–0.15 mm long; involucral bracts with or without stipitate glands .... 4b. *Ageratum houstonianum* f. *isochroum*

4a. **Ageratum houstonianum** Miller forma **houstonianum**.

Ageratum conizoides Lam., Ill. Gen. Pl. Bot. 248. *Pl. 672.* 1823. (Holotype: op. cit. *pl. 672.*)

Ageratum mexicanum Sims, Bot. Mag. 52: 2524. 1825, fide Robinson (1913*b*). (Holotype: op. cit. *pl. 2524*; plant raised from seeds sent by Bullock from Mexico.)

Ageratum mexicanum Sweet, Brit. Fl. Gard. 1. *t. 89.* 1825, fide Robinson (1913*b*). (Holotype: op. cit. *t. 89*; plant raised from seeds sent by Bullock from Mexico.)

Ageratum conyzoides L. var. *mexicanum* DC., Prod. 5: 108. 1836, fide Robinson (1913*b*). (Holotype: based upon Sims (1825) and Sweet (1825).)

Carelia houstoniana (Miller) Kuntze, Rev. Gen. Pl. 1: 325. 1891, fide Robinson (1913*b*).

Ageratum mexicanum Hort. *ex* Vilm., Fl. Pl. Terre. Ed. 4. 43. 1894.

Ageratum mexicanum Hort. *ex* Vilm. var. *nanum* Vilm., Fl. Pl. Terre. Ed. 4. 44. 1894.

Ageratum mexicanum Hort. *ex* Vilm. var *nanum* Vilm. forma *imperiale* Vilm., Fl. Pl. Terre. Ed. 4. 44. 1894.

Ageratum mexicanum Hort. *ex* Vilm. var. *nanum* Vilm. forma *azureum* Vilm., Fl. Pl. Terre. Ed. 4. 44. 1894.

Ageratum mexicanum Hort. *ex* Vilm. var. *nanum* Vilm. forma *multiflorum* Vilm., Fl. Pl. Terre. Ed. 4. 44. 1894.

Ageratum wendlandii Vilm., Fl. Pl. Terre. Ed. 4. 1894. (Holotype: unnumbered figure, op. cit., p. 2.)

Ageratum wendlandii Vilm. var. *albis* Vilm., Suppl. Fl. Pl. Terre. 2. 1884.

Ageratum mexicanum Hort. *ex* Vilm. forma *albiflorum* Vilm., Blumengärtnerei 2: 445. 1896.

Ageratum mexicanum Sims var. *majus* Vilm., Blumengärtnerei 2: 445. 1896.

Ageratum mexicanum Sims forma *lasseauxii* (Carr.) Vilm., Blumengärtnerei 2: 445. 1896.

Ageratum mexicanum Sims forma *wendlandii* Vilm., Blumengärtnerei 2: 445. 1896.

Ageratum mexicanum Sims var. *majus* Vilm. forma *coeruleum* Vilm., Blumengärtnerei 2: 445. 1896.

Ageratum mexicanum Sims var. *nanum* Vilm., Blumengärtnerei 2: 445. 1896.

Ageratum houstonianum Miller var. *typicum* Robins., Contr. Gray Herb. 68: 5. 1923. *Nom. inval.*

Ageratum houstonianum Miller var. *typicum* Robins. forma *normale* Robins., Contr. Gray Herb. 68: 5. 1923. *Nom. inval.*

Ageratum houstonianum Miller var. *angustatum* Robins., Contr. Gray Herb. 68: 6. 1923. (Holotype: FRANCE. Naturalized in maritime Alps, Menton, *Walther s.n.* (Z, not seen); tracing and small fragment, GH.)

Ageratum houstonianum Miller var. *typicum* Robins. forma *niveum* Robins., Contr. Gray Herb. 68: 6. 1923. (Holotype: UNITED STATES. Founded on material purchased from Joseph Breck and Sons Corporation, grown for the Department of Agriculture at Glen Echo, Maryland, *Freeman 5074* (US); isotype, GH.)

Ageratum houstonianum Miller var. *typicum* Robins. forma *luteum* Robins., Contr. Gray Herb. 68: 6. 1923. (Holotype: UNITED STATES. Founded on material supplied by the Joseph Breck and Sons Corporation and cultivated at Glen Echo for the Department of Agriculture, *Freeman 5084*, in part (US); isotype, GH.)

Pappus scales apically setiferous, (1.5–)2–3(–3.4) mm long; involucral bracts narrowly lanceolate, ciliate, stipitate-glandular.

Though no type is cited by Miller (1768), his description included Houston's handwritten note "Eupatorium herbaceum melissae folio villosum flore coeruleo," which accompanied Houston's specimen collected in Vera Cruz. As it would appear that this is the only specimen upon which Miller based his description, I am designating it as the lectotype.

In his discussion, Miller states that the species "was found growing naturally at La Vera Cruz by the late Dr. William Houston." Seeds were sent to Europe and grown, the plants becoming weedy in the hot-beds of the nurseries.

Hegi (1917) states that this plant has been known in Europe since 1823, and shortly thereafter Sims (1825) described *Ageratum mexicanum* based on plants grown from seeds brought from Mexico to the Sloane Street Nursery in London by a Mr. Bullock. There is no question but that the plant Sims described and illustrated is identical to Miller's *A. houstonianum.* The ovate-deltoid, pilose, cordate-based leaf, the pubescent petiole and the red tipped phyllaries illustrated in color and described all point to the previously described species. Sweet (1825) described *A. mexicanum* basing his illustration, too, on plants grown from Bullock's seeds at the Sloane Street Nursery in London.

Candolle (1836) reduced *Ageratum mexicanum* Sims to one of four varieties under *A. conyzoides* L. The only specimen studied bearing this varietal name (microfisch, MIN) shows deltoid, cordate leaves densely pilose on the lower surface. The microfisch does not show the stem to be markedly pilose though Candolle describes it as "hirtello" (shaggy, rough). Candolle gives *A. mexicanum* of Sims and Sweet in synonymy so it is obvious that he referred to the same plant as did the earlier writers.

Ageratum houstonianum has been cultivated as an ornamental for nearly 150 years (Hegi, 1917). The variations observed in the cultivars led Vilmorin (1884, 1894, 1896) and Robinson (1923) to propose several new taxa. Both authors used height of stems and colors of the corollas as well as size and number of leaves and flowers as distinguishing characters. Vilmorin (1884, 1894) included plates of his taxa, and from these it is quite evident that he referred exclusively to *A. houstonianum sens. lat.*

Robinson's varieties and formae were described so that botanists could give "uniformity of listing when these plants are found in the wild as escapes" (Robinson, 1923). *Ageratum houstonianum* var. *typicum* and *A. houstonianum* var. *typicum* f. *normale* are names applied to plants having blue corollas and style branches. In my opinion, such names are superfluous, as this is the usual situation, and they are invalid under Art. 24 of the *Code.*

Ageratum houstonianum var. *angustatum,* described as having been found naturalized in the maritime Alps of France, suggests a graden escape. Though technical characters of the involucre, corolla, achenes, and pappus place this plant with *A. houstonianum,* the leaves are in whorls of 3 or alternate and are generally obtuse at the base. No idea of the pubescence can be gathered from the tracing (GH), though the fragment (GH) seen does suggest a general scabrous-pilose condition. Robinson's variety may well be a teratological form of the species and such should not be set apart without more data.

Ageratum conizoides Lam. appears to be *A. houstonianum.* The plate shows ovate leaves with more or less cordate bases and a more densely pubescent stem than is commonly seen in *A. conyzoides.* Lamarck also shows the involucral bracts as narrowly lanceolate, rather than abruptly contracted apically as in *A. conyzoides.*

Due to the considerable color variations of the corolla in this species, those names applied to plants with white corollas are placed in synonymy.

This forma is native in central and southern Mexico and extends into adjacent Guatemala and British Honduras (Fig. 1), usually in damp habitats in shade or

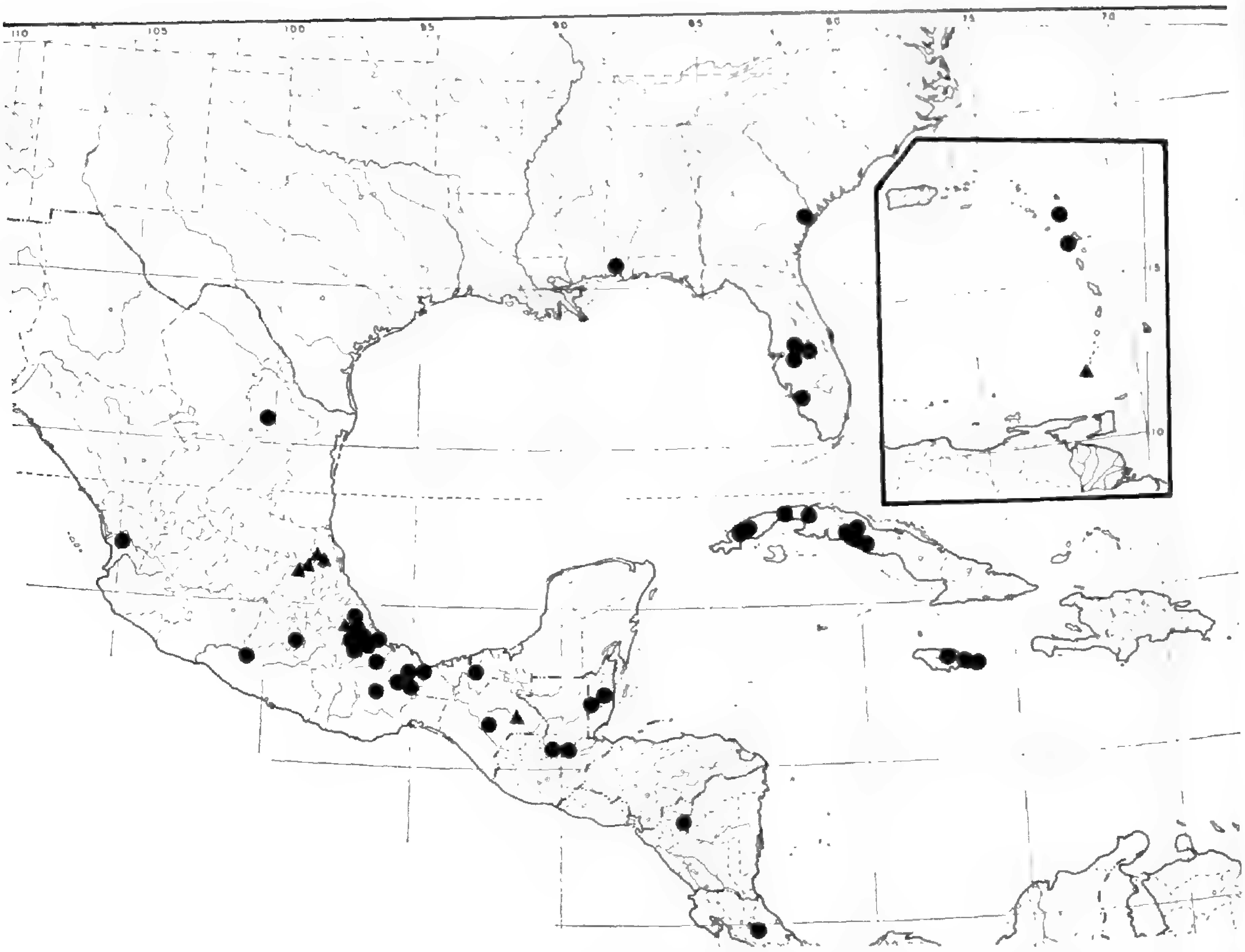


FIGURE 1. The distribution of *Ageratum houstonianum*. — Solid circle, forma *houstonianum*; triangle, forma *isochroum*. (Base map copyright University of Chicago.)

full sun from about 200–1700 m elevation, escaping from gardens and becoming established in central Florida, Cuba, Jamaica, and Hawaii. I have seen specimens from Africa, China, India, France, Java, Okinawa, the Philippines, and North Viet Nam, all of which are escapes from cultivation. The report of establishment in Alabama (Mohr, 1901) is probably based on errors in identification. Buds, flowers, and fruits are present from January through April and again from July through September but may be present throughout the year, depending on local conditions.

ANTIGUA. *Liebmann 148* (GH, K, US).

BRITISH HONDURAS. El Cayo, *Bartlett 12098* (GH, MICH); Gracie Rock, Sibun River, *Gentle 1792* (A, K, MICH, MO, NY).

COLOMBIA. Cundinamarca, *Dugand & Jaramillo 3880* (US).

CUBA. SANTA CLARA: Lomas de Banno, *Ekman 16296* (A, GH, NY); San Blas, *Jack 8206* (GH, NY, US).

GUATEMALA. Fields along National Route 5, ca. 4 miles S of Coban, *King 3311* (MICH, NY, TEX, UC, US); ca. 2 miles W of Santa Cruz Verapaz, *King 3336* (MICH, NY, TEX, UC, US); Fallabon, *Lundell 2196* (MICH).

JAMAICA. Morce's Gap, *Nichols 33* (F, GH, MO, NY, US).

MEXICO. CHIAPAS: Municipio de Tenejapa, *Breedlove 6211* (DS, MICH); grassy swamp near Coapinala, *Wonderly 28* (MICH). GUERRERO: Coyuca, *Hinton 5537* (BM, GH, MO, US). MORELOS: About 11 miles S of Cuernevaca, *King 4160* (F, MICH, NY, TEX, UC, US). NAYARIT: Road along river in swampy area near Tepic, *Mexia 501* (A, BM, F, GH, MICH, MO, NY, UC, US). NUEVO LEON: Près Monterrey, *Obbon s.n.* (K). OAXACA: Yaveo, *Mexia 9177* (F, GH, MO, NY, UC). TABASCO: Villahermosa, *Juzepczuk 1923* (US). VERA CRUZ:

Grassy slopes among scattered shrubs, Orizaba, *Balls B4308* (K, UC, US); Vallée de Cordoba, *Bourgeau 1537* (F, GH, K, MSC, US); 5.5 miles S of Xalapa, *Johnson & Hofstetter 2004* (MIN); Jalapa, *Pringle 8065* (BM, F, GH, MIN, MSC, NY, UC, US); Mt. Orizaba, *Seaton 55* (F, GH, NY, US).

PERU. LIMA: Cascadas de Barranco, cera de Lima, *Ferreyra 6331* (US).

Reported in Sumatra and Java (Koster, 1935), Jamaica (Fawcett & Rendle, 1936), and Madiera, Porto Santo, and Desertas (Lowe, 1868).

4b. **Ageratum houstonianum** Miller forma **isochroum** (Robins.) M. F. Johnson, comb. nov.

Ageratum houstonianum Miller var. *muticescens* Robins. forma *isochroum* Robins., Contr. Gray Herb. 68: 6. 1923. (Holotype: MEXICO. Prov. Huasteca: Wartenberg, near Tantoyuca, *Ervendberg 100* (GH); isotype, F.)

Ageratum houstonianum Miller var. *muticescens* Robins., Proc. Amer. Acad. Arts 51: 532. 1916.

Ageratum houstonianum Miller var. *muticescens* Robins. forma *versicolor* Robins., Contr. Gray Herb. 68: 6. 1923. (Holotype: Founded on material sold by the Joseph Breck and Sons Corporation and grown at Glen Echo, Maryland, for study at the Department of Agriculture at Washington, *Freeman 5084*, in part (US); isotype, GH.)

Very similar to *Ageratum houstonianum* f. *houstonianum*, differing in the presence of truncate pappus scales 0.1–0.15 mm long and the involucral bracts, which at times lack stipitate glands.

The type location as recorded on the label is inaccurate as "Prov. Huasteca" is unknown from Mexico. Smith (1899) does not include Huasteca in his index to maps, but rather Huatusco, a canton in Vera Cruz, in which the village of Tantoyuca is located. Ervendberg's collection is thus assumed to have originated in Vera Cruz.

Robinson's variety is similar to *A. houstonianum* f. *houstonianum* in leaf shape, pilose pubescence, and shape of involucral bracts, as well as having the same chromosome number, $n = 10$ (*Breedlove 9135*, MICH). However, forma *isochroum* is aberrant in two respects—general lack of gland tipped pubescence on the involucral bracts and the presence of very short pappus scales which have slightly spreading, blunt, pectinate lobes. Plants with these characters are not geographically separated from the typical members of the species; therefore the status of forma is maintained, and the available form name *isochroum* is applied.

This forma is found in Mexico, Central America, and the West Indies (Fig. 1) in habitats similar to that of forma *houstonianum*. I have seen specimens from Germany and Texas; both are garden escapes. Buds, flowers, and fruits are present as in forma *houstonianum*.

GRENADA. *Linden 1157* (MO, NY).

MEXICO. CHIAPAS: Savannah near airport of San Quintin, along the Río Jatate, *Breedlove 9135* (DS, MICH). HIDALGO: 4 miles SW of Chapulhuacan on road to Jacala, *Graham & Johnston 4732* (MICH, TEX); 12.7 miles SW of Hidalgo-San Luis Potosí state boundary, *Johnson & Hofstetter 2009* (MIN); pastured roadside sod 2.2 miles W of Santa Ana on Route 85, *Johnson & Ownbey 1960* (MIN). PUEBLA: Roadside bank 3 miles E of María Andrea, *McGregor 16463* (MSC). VERA CRUZ: C. de Tantoyuca, *Cardenas 273* (F, GH); Wartenberg, near Tantoyuca, *Ervendberg 100* (F, GH).

NICARAGUA. Moist grassy opening in a forest, Jinotega, *Grant 1307* (F, MICH).

UNITED STATES. MARYLAND: Cultivated at Glen Echo, *Freeman 5084* (GH).

5. **Ageratum conyzoides** L., Sp. Pl. 2: 839. 1753.

Type: Three specimens in the Linnaean Herbarium labeled *Ageratum conyzoides* (in Linnaeus' handwriting?) are presumably type specimens (not seen); microfisch photographs, MIN. King and Robinson (1969) have come to the same conclusion.

Annuals or sub-shrubs where growing conditions are suitable, (1.45–)2–10(–15) dm tall, malodorous when fresh; *roots* fibrous, adventitious at base if stem decumbent; *stems* erect, less commonly decumbent, branching; stems and branches reddish, becoming green above, striate, puberulous-white pilose, especially at nodes and on upper stem, to nearly glabrous; *leaves* opposite, at times alternate above, petioled, thin, ovate below, ovate to elliptic-oblong above, lower (0.7–)3–10 cm long, (0.4–)1.9–7 cm wide, upper progressively smaller, base obtuse, rarely oblique, apex acute, less commonly rounded, margin crenate, ciliate or glabrous, upper surface pilose, especially on veins, to nearly glabrous, lower surface abundantly pilose, yellow or amber glandular-punctate, less commonly nearly glabrous and eglandular-punctate; *petioles* (0.4–)1–3.3(–7.5) cm long, sparsely to abundantly white pilose, especially on upper leaves; *inflorescences* of (1–3)4–18 heads borne in terminal cymose clusters; *peduncles* bracteolate, puberulent-pilose, 0.5–1.6 cm long; *involucres* campanulate to hemispheric, bracts biseriate, oblong to lanceolate-oblong, 3–4.75(–5) mm high, outer ones 0.5–1.5(–1.75) mm wide, 2-ribbed, sparsely pilose to glabrous, green to reddish or apically and marginally tinged with red-purple, apex abruptly to less commonly gradually acuminate, puberulous, margin basally entire, apically erose to variously fimbriate, rarely entire, minutely to conspicuously ciliate-scabrate; *corolla* tubular to funnelform, 1.5–2.5(–3) mm long, glabrous to sparsely puberulent apically, tube and throat greenish to white, lobes mauve, heliotrope, blue, lavender to white, acute, erect or spreading; *achenes* 5-angled, black, 1.25–1.75(–2) mm long, scabrous on angles, carpopodium brownish or white; *pappus* of 5, rarely 6, membranous, tawny to reddish-brown oblong scales all abruptly tapering to a scabrous seta or some scales truncate, entire scale (0.4–)1.5–3 mm long in subsp. *conyzoides* or pappus 0.25–0.9 mm long, all scales oblong, apically truncate to obscurely acuminate, variously laciniate but not setiferous in subsp. *latifolium*.

The species can be divided into two subspecies based on the characters in the following key.

1. Pappus scales 1.5–3 mm long, apically tapering to a scabrous seta at least in some heads .... 5a. *Ageratum conyzoides* subsp. *conyzoides*
1. Pappus scales 0.25–0.9 mm long, apically truncate to obscurely acuminate, variously laciniate but not setiferous .... 5b. *A. conyzoides* subsp. *latifolium*

5a. **Ageratum conyzoides** L. subsp. **conyzoides.**

Ageratum hirtum Lam., Ency. Méth. 1: 53. *Pl. 672, f. 2.* 1783, fide Robinson (1913*b*). (Holotype: op. cit. *Pl. 672, f. 2.*)
Ageratum humile Salisb., Prod. 188. 1796.
Ageratum hirsutum Lam. *in* Poiret, Ency. Méth. Bot. Suppl. 1: 242. 1810, fide Robinson (1913*b*). (Holotype: *Pl. 672, f. 2. in* Lam., Illustr. 1783.)
Ageratum album Willd. *ex* Steud., *Nomen.* 18. 1821.
Cacalia mentrasto Vell., Fl. Flum. 8. *t.* 69. 1825, fide Baker *ex* Martius (1876). (Holotype: op. cit. *t. 69.*)
Ageratum cordifolium Roxb., Fl. Ind. 3: 415. 1832.

Ageratum conyzoides L. var. *hirtum* (Lam.) DC., Prod. 5: 108. 1836, fide Robinson (1913*b*).
Ageratum suffruticosum Regel, Gartenflora 3: 389. *t. 108.* 1854. (Holotype: op. cit. *t. 108*; plate of plant growing in a garden.)
Ageratum nanum Hort. *ex* Sch. Bip. *in* Kock & Fint., Wochenschr. 1: 26. 1858.
Ageratum odoratum Vilm., Fl. Pl. Terre. Ed. 2. 42. 1866, fide Robinson (1913*b*).
Carelia conysodes (L.) Kuntze, Rev. Gen. Pl. 1: 325. 1891, fide Robinson (1913*b*).
Carelia conysodes (L.) Kuntze α *robusta* Kuntze, Rev. Gen. Pl. 1: 325. 1891, fide Robinson (1913*b*).
Carelia conysodes (L.) Kuntze α *robusta* Kuntze var. *alba* Kuntze Rev. Gen. Pl. 1: 325. 1891, fide Robinson (1913*b*).
Carelia conysodes (L.) Kuntze β *umbrosa* Kuntze, Rev. Gen. Pl. 1: 325. 1891, fide Robinson (1913*b*).
Carelia conysodes (L.) Kuntze β *umbrosa* Kuntze var. *coerulea* Kuntze, Rev. Gen. Pl. 1: 325. 1891, fide Robinson (1913*b*).
Carelia conysodes (L.) Kuntze γ *pusilla* Kuntze, Rev. Gen. Pl. 1: 325. 1891, fide Robinson (1913*b*).
Carelia conysodes (L.) Kuntze γ *pusilla* Kuntze var. *alba* Kuntze, Rev. Gen. Pl. 1: 325. 1891, fide Robinson (1913*b*).
Ageratum conyzoides L. var. *inaequipaleaceum* Hieron., Bot. Jahrb. 19: 44. 1895. (Holotype: COLOMBIA. Crescit prope Papayan, *Lehmann 4666* (GH); isotype, NY.)
Ageratum conyzoides L. forma *album* (Willd.) Robins., Contr. Gray Herb. 42: 462. 1913. (Holotype: PUERTO RICO. In graminosis ad "Cocoa," *Sintenis 5874*, not seen.)
Ageratum humile Larr., Escritos 406. 1922.
Ageratum arsenii Robins., Contr. Gray Herb. 64: 3. 1922. (Holotype: MEXICO. Nuevo Leon: Cercado près Monterrey, *Arsène s.n.* (K); sketch, GH.)

Annuals or sub-shrubs, 0.45–15 dm tall; *leaves* (0.7–)3–10 cm long, (0.4–)1.9–7 cm wide, base obtuse, rarely oblique; *petioles* (0.4–)1–3.3(–7.5) cm long; *inflorescences* terminal, the (1–)4–18 heads in cymose clusters; *peduncles* 0.5–1.5 cm long; *involucres* campanulate, bracts oblong 3–5 mm high, outer ones 0.5–1.75 mm wide, apex abruptly acuminate, margin basally entire, apically erose to variously fimbriate; *corolla* 1.5–3 mm long; *achenes* 1.25–2 mm long, scabrous; *pappus* of 5, rarely 6, membranous scales (0.4–)1.5–3 mm long, basally free and all or some abruptly tapering to a scabrous seta.

The oldest synonym is *Ageratum hirtum* Lam. (1783), a name applied to "an *Ageratum conyzoides* Lin." (Lamarck, 1783: 53). Lamarck's later name, *Ageratum hirsutum*, as represented in the plate (Lamarck, 1823), is clearly applied to *Ageratum conyzoides.*

Vellozo (1825) applied a vernacular name as the specific epithet in his *Carelia mentrasto.* The accompanying plate suggests *Ageratum conyzoides,* though the leaves are illustrated as rather thick and fleshy.

Candolle (1836) reduced Lamarck's *Ageratum hirtum* to varietal rank under *Ageratum conyzoides* L. Roxburgh (1832) described *Ageratum cordifolium* from Bengal, India. The description undoubtedly places his species with *Ageratum conyzoides,* and an *Ageratum* species collected in India must be *Ageratum conyzoides* as this is the only taxon found beyond the limits of the Western Hemisphere. Vilmorin (1866) applied the name *Ageratum odoratum* to *Ageratum conyzoides,* apparently used as garden ornamentals, giving the name *A. conyzoides* as the Latin synonym.

Kuntze (1891) removed all recognized species from *Ageratum* L. transferring them to *Carelia* Moehr. applying the rule of priority in the strictest sense. He described a series of varieties under *Carelia conysodes* (Kuntze's spelling) using size of plants and leaves, their pubescence and corolla color as bases for his taxa. As these varieties are quite probably merely local responses to ecological conditions, they cannot be accorded taxonomic rank.

Hieronymus (1895) described *A. conyzoides* L. var. *inaequipaleaceum* to include those plants which have blunted as well as setaceous pappus scales in the same head. This character, while noticeable, is not consistent as florets bearing fully setaceous scales are often adjacent to florets with blunt scales. The plants with the aberrant pappus occupy the same geographic range as plants with a setiferous pappus; thus the status of variety cannot be maintained. Due to the inconsistent nature of this pappus character, Hieronymus' varietal name is placed in synonymy.

Ageratum arsenii Robins. (1922) is a somewhat decumbent perennial which possesses a pappus similar to that described above. These characters, which Robinson interpreted as delimiting this species, are widespread in *A. conyzoides*, and the description applies readily to this taxon. Thus the name, *A. arsenii*, must be listed in synonymy. Arsène collected the type specimen at Monterrey, Mexico, which is about 300 miles from the nearest station in Vera Cruz. It is assumed that Arsène's single collection represents a cultivar or a garden escape.

Giving taxonomic recognition to white flowered plants in this species is quite superfluous. White corollas are known to be mixed with blue ones on a single plant, the usual purplish color fades toward white with increasing age in the living plant, and the colors tend to fade on herbarium specimens so that distinguishing corolla color becomes meaningless. For these reasons, varietal and forma names alluding to white corollas are placed in synonymy.

Ageratum conyzoides subsp. *conyzoides* exhibits considerable variation, as is expected in a wide-spread taxon. Subshrubs to 10 dm tall as well as ephemeral annuals a mere 4.5 cm tall are known. These extremes indicate the plasticity of this subspecies to varying ecological conditions; tall and robust in the more optimum tropics to very dwarfed in more rigorous environments of ecological stresses. Variations in size of achenes and length of pappus, width of involucral bracts and length and width of leaves is also evident. Those specimens from South America, in many instances, possess structures at the upper limits of the size range. Plants from the Philippine Islands are quite consistent in having involucral bracts at the lower end of the size range. Pubescence on the South American plants is often longer than the pubescence of plants from other areas. Other examples of size variation are not as sharply restricted geographically and are more difficult to cite. In all cases, however, the plants possess the key features of *A. conyzoides* subsp. *conyzoides*, and it is most desirable to treat this widespread subspecies as in the past, *i.e.*, as one variable taxon.

Ageratum conyzoides subsp. *conyzoides* is a tetraploid, $2n = 40$ (Turner & King, 1964; Turner & Lewis, 1965; Powell & King, 1969; Löve, 1966) which may account in part, for its widespread weediness (*cf.* Baker, 1965). The tetraploidy is consistent over the wide geographic range from which chromosome counts are known. The only published chromosome number indicating otherwise is that of Ishikawa (1916) and Mehra *et al.* (1966) in which the number $n = 10$ is recorded. As no voucher for this number is given in either paper, one cannot ascertain if a correct determination of the authors' material was made and if this number applies here.

Ageratum conyzoides subsp. *conyzoides* is distinguished from *A. conyzoides* subsp. *latifolium* by the characters listed in the key to subspecies and by the different ploidy levels of these taxa. *Ageratum conyzoides sens. lat.* is similar to *A. houstonianum sens. lat.* but is readily distinguished as discussed under the latter species.

This subspecies is native in South and Central America (Fig. 2); adventive and common as a pantropic weed extending about 20° north and south of the equator from sea level to *ca.* 2500 m elevation (Fig. 3). It is reported from southeastern United States (Chapman, 1883); these are records of cultivars. Flowers and fruits are present during the entire year, depending somewhat on location and local conditions.

ANTIGUA. Tyrells, *Box 1122* (US).

ARGENTINA. 25 km E of Jujuy, Río Zapala, *Eyerdam & Beatle 22370* (GH, MO, UC).

AUSTRALIA. QUEENSLAND: Rock Hampton, *Russell, Jr. s.n.* (UC).

BAHAMA ISLANDS. Eleuthera, *E. G. Britton 6375* (F, NY, US).

BELGIAN CONGO. [Republic of the Congo.] Catuba, *Quarro 3217* (MO).

BOLIVIA. Yucachaca, *Steinbach 9680* (GH, MO, NY, UC).

BRAZIL. Vicosa, *Mexia 4718* (GH, K, MO, NY, UC); Itapiranga, *Smith & Reitz 12629* (GH, MO, WIS).

BURMA. Haka, *Dickason 7711* (A).

CAMEROON. Without locality, *Braun 14* (NY).

CHILE. Santiago, *Claude-Joseph 1604* (US).

CHINA. Yeung Ling shan, *Lau 183* (GH, MICH, MO, NY, UC); Shiu Chau, *To et al. 97L* (UC).

COLOMBIA. Bucaramanga, *Fassett 25587* (MICH, WIS); SE of Quetame, *Pennell 1796* (GH, NY).

COSTA RICA. Cartago, *Cooper 5824* (NY, US).

DOMINICA. Without locality, *Cooper 77* (GH, MICH, MO, NY, UC, US).

DOMINICAN REPUBLIC. Loma Bajita, *Valeur 922* (K, MO, NY, US).

ECUADOR. Canyon of the Río Chanchan, near Huigra, *Camp E-3161* (GH, K, MO, NY, UC, US); Banos, *Landeman 4* (BM, K); Galápagos Islands, Indefatigable Island, *Stevenson 212* (UC).

EGYPT. Lougier, *Kralik s.n.* (DS, GH).

EL SALVADOR. Volcan de San Salvador, *Standley 22871* (GH, US).

FORMOSA. Tomita-cho, Taihoku-shi, *Tanaka & Shimada 11194* (MICH, MO, NY, UC).

GUATEMALA. Gualan, *Deam 330* (GH, MICH, MO, NY, US); Santa Rosa, *Heyde & Lux 3781* (F, GH, NY, US); between Escuintla and Santa Lucia Cotz, *Standley 63459* (F).

BRITISH GUIANA. Moruka River, Pomeroon District, *de la Cruz 2545* (GH, MO, NY, US).

FRENCH GUIANA. Cayene, *Broadway 20* (GH, NY, US).

HAITI. Pennery, *Ekman 2490* (A, US).

HONDURAS. Vicinity of El Zamorano, *Standley 24646* (F, GH, NY, US); along Río Choluteca at Ojo de Agua, *Williams 17312* (F); vicinity of La Ceiba, *Yunker et al. 8239* (F, GH, K, MICH, MO, NY, US).

INDIA. Barapani, Khasi Hills, *Koelz 22968* (MICH).

KENYA. 8 miles NE of Runyerjes, cytological voucher, *Lewis 5912* (MO, TEX).

LAOS. Chochinchina, *Gandoger s.n.* (MO).

LIBERIA. 3 miles NE of Suacoco, Gbarnga, *Okeke 12* (MO, UC).

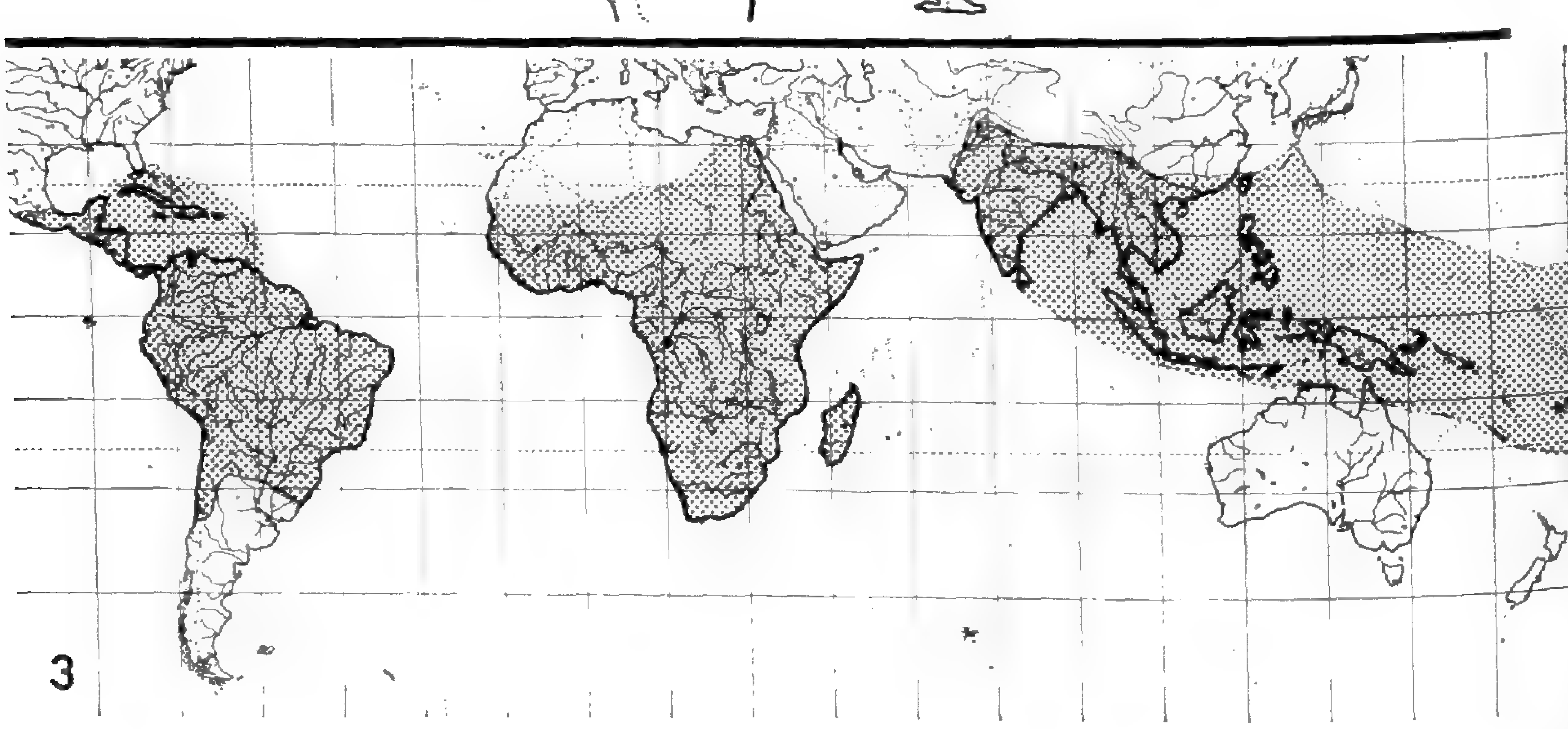
MEXICO. CHIAPAS: Tapachula,, *Fischer 35427* (F). NAYARIT: Tepic, *Palmer 1850* (F, GH). PUEBLA: 6 miles SW of Puebla-Vera Cruz state border, *King 4140* (F). VERA CRUZ: Chontla, C. de Tantoyuca, *Cardenas 433* (F).

MOZAMBIQUE. Sabi River, Merinqua district, *Chase 2595* (NY).

NEPAL. 6 miles N of Hitaura, *Brydon 29* (DS).

NICARAGUA. Chinandego, *Baker 2021* (GH, K, MO, MSC, NY, UC, US); Cerro Sialci, sierra SW of Jinotega, *Standley 10598* (F).


2


3

FIGURES 2–3. — 2. The distribution of *Ageratum conyzoides* in the New World. Solid circle, subsp. *conyzoides*; triangle, subsp. *latifolium*. — 3. The pantropical distribution of *Ageratum conyzoides* subsp. *conyzoides*.

NIGERIA. Baba Eko, Ijebu Prov., *Ross 297* (MO, NY).
NORTHERN RHODESIA. [Zambia.] Kitwe, Ndola district, *Linley 162* (MO).
PANAMA. Concepción, cytological voucher, *King 5286* (TEX, UC, US); El Valle, cytological voucher, *King 5327* (TEX, UC, US).
PERU. Zepalacio, *Klug 3470* (GH, MO, NY, US).
PHILIPPINE ISLANDS. Manila, *Merrill 35* (GH, MO, NY).
PUERTO RICO. 2 miles W of Ponce, *Heller 6143* (GH, MO, NY, US); Gaguas, *Millspaugh 208* (NY).
RUANDA. Minuli, *Troupin II 639* (MIN, MO).
ST. CROIX. *Ricksecker 430* (DS, GH, MIN, MO, NY, UC, US).
SINGAPORE. Bord des routes, Singapore, *Debeaux s.n.* (NY).
SOUTH AFRICA. Durban, *Schlechter 2934* (MO).
SOUTHERN RHODESIA. [Rhodesia.] Belingew, *West 2772* (MO).
SUDAN. Katire, *Jackson 381* (MO).
SURINAM. Paramaribo, *Samuels 192* (GH, NY).
TANGANYIKA. [Tanzania.] 4 miles W of Tanga, *Lewis 6060* (MO, TEX).
THAILAND. 11 km S of Khas Yai Forest Station and 105 km E of Saraburi, cytological voucher, *King 5537* (GH, TEX, UC); 16 km NNE of Ranong, cytological voucher, *King 5577* (TEX, UC).
UNITED STATES. HAWAII: Kawaihapai, *Degener 11034* (GH, MICH, MO, NY, WIS).
VENEZUELA. Tovar, *Pittier 9362* (GH, NY, US).
UGANDA. Mabira Forest, *Loveridge 19* (A, MO).
VIET NAM. Tourane, *Clemens 3082* (MICH, MO, MSC, NY, UC).

5b. **Ageratum conyzoides** L. subsp. **latifolium** (Cav.) M. F. Johnson, comb. et stat. nov.

Ageratum latifolium Cav., Ic. 4. *t. 357.* 1797. (Holotype: PERU: Prope Liman, *Nee s.n.* (MA, not seen); photograph, MIN.)
Ageratum brachystephanum Regel, Gartenflora 3: 245. *tab. 108, fig. c.* 1854, fide Robinson (1913*b*). (Holotype: op. cit. *tab. 108, fig. c.*)
Ageratum muticum Griseb., Fl. Brit. W. Ind. 356. 1861, fide Robinson (1913*b*).
Ageratum maritimum Sch. Bip. *ex* Griseb., Fl. Brit. W. Ind. 356. 1861, *non* HBK (1820), fide Robinson (1913*b*).
Calea densiflora Klatt, Leopoldina 20: 96. 1884, fide Robinson (1913*b*).
Carelia brachystephana (Regel) Kuntze, Rev. Gen. 1: 325. 1891, fide Robinson (1913*b*).
Carelia mutica (Griseb.) Kuntze, Rev. Gen. 1: 325. 1891, fide Robinson (1913*b*).

Annuals, 2–8 dm tall; *leaves* ovate, (1.5–)3–6.5(–7.4) cm long, 2–5(–5.7) cm wide, base obtuse to truncate, rarely cordate; *petioles* 0.8–3 cm long; *inflorescences* terminal, 3–12 heads grouped in corymbose clusters; *peduncles* 0.5–1.6 cm long; *involucres* hemispheric to less commonly campanulate, bracts lanceolate-oblong, 3.5–5 mm high, outer ones (0.5–)0.65–1.4(–1.5) mm wide, apex gradually or abruptly tapering to a scabrous apex, margin entire or variously erose to fimbriate apically; *corollas* 1.5–2.5 mm long; *achenes* (1.25–)1.5–1.85(–2) mm long, scabrous; *pappus* of 5 free membranous, oblong, tawny scales 0.25–0.7 mm long, margin entire to variously erose, apex truncate to obscurely acuminate, not setiferous.

The synonym *Ageratum brachystephanum* Regel (1854) is clearly a name applied to this taxon as is evidenced from the figure, labeled *A. brachystephanum*, of an achene with a pappus of short scales accompanying the plate of *A. suffruticosum* Regel (Regel, 1854). *Ageratum muticum* Griseb. (1861) was the name applied to this subspecies in the West Indies and referred to plants with some setiferous pappus scales in each inflorescence. *Ageratum maritimum* Sch. Bip. *ex* Griseb. (1861) *non* HBK (1820) was applied to plants of the West Indies and Peru which possessed a pappus of free, awnless scales. The description in

Grisebach (1861) indicates that Schultze's name is a synonym for the older *A. latifolium* Cav. Klatt's description of *Calea densiflora* (1884) indicates that his name is synonymous with *A. conyzoides* subsp. *latifolium*. Kuntze's names under *Carelia*, fall automatically into synonymy. See the discussion under *A. conyzoides* subsp. *conyzoides* as well. *Ageratum latifolium* Cav. var. *galapageium* Robins. (Robinson, 1913*b*) possesses achenes which lack a pappus and should be referred to the epappose genus *Alomia*.

Cavanilles (1797), when he described *Ageratum latifolium*, was well aware of the similarities between it and *A. conyzoides*. He went to considerable length to point out that *A. conyzoides* has pappus scales drawn out apically into a long seta and that his species was notably different because its pappus scales are always short and without setae. After studying numerous specimens of *A. latifolium*, it is evident to me that the pappus character is not sufficient to separate *A. latifolium* from *A. conyzoides*. The pappus of *A. conyzoides* subsp. *conyzoides* has, at times, setiferous scales as well as truncated ones on the same fruit. The distinguishing feature of both species as conceived by earlier authors is combined in one head, or even one flower.

Other morphological characters which are of high taxonomic value elsewhere in this genus are of little value in distinguishing *Ageratum conyzoides* and *A. latifolium* as separate species. The involucral bracts are the same size, shape, and of the same texture; the bract margins are similarly erose or fimbriate. Achenes and corollas are identical in both taxa. Leaves are of the same shape and texture in both taxa, though those of subsp. *latifolium* tend to be slightly shorter and wider at the base than in subsp. *conyzoides*. Pollen grains have been studied in both taxa. The grains are extremely similar in size and wall sculpture, though subsp. *latifolium* tends to have grains with echinae slightly longer than grains of subsp. *conyzoides*. However, this is not a consistent feature and cannot be used as a taxonomic character. Studies of plastic peels showing guard cells from the lower leaf surface revealed no characters of taxonomic merit.

An apparently consistent morphological character distinguishing these subspecies is present only in the pappus scales as given in the key—non-setiferous ones in subsp. *latifolium versus* at least some setiferous scales in subsp. *conyzoides*. This feature, in combination with diploidy, $2n = 20$ in subsp. *latifolium* (Turner, Powell & King, 1962), and tetraploidy, $2n = 40$ in subsp. *conyzoides* (Turner & King, 1964; Turner & Lewis, 1965; Löve, 1966; Powell & King, 1969), serves to distinguish these otherwise very similar taxa.

Though the taxa considered here have been recognized as species for nearly 200 years, I have reduced them to subspecies under the older name *A. conyzoides* L. The reduction cannot be carried further because the difference in ploidy level quite certainly hinders gene exchange between them. Any hybrid progeny would be triploid and, if viable, probably sterile. Thus the designation of subspecies.

Ageratum conyzoides subsp. *latifolium* is native in western South America and Central America, occurring in moist grasslands and on mountain slopes and in forests, less commonly as a weed in waste places and villages, from sea level to *ca.* 2500 m elevation (Fig. 2). It is in flower and fruit during the entire year, but most commonly from November through April.

BAHAMA ISLANDS. Little Harbor Cay, *Britton & Millspaugh 2240* (F, NY, US).
COLOMBIA. Near Río San Joaquin, *Killip 7812* (GH, NY, US); Villavicencio, *Pennell 1597* (GH, NY); Bogotá, *Triana 1157* (BM, NY, P, US).
COSTA RICA. Potrero at Pejivalle Farm, above Río Pejivalle, *Dodge & Thomas 4336* (GH, MO, US).
CUBA. Vedado, *Baker 1411* (F, NY).
DOMINICAN REPUBLIC. Paradis, *Fuertes 458* (NY, US).
ECUADOR. Cumbaco, *Mille 532* (GH, K, MO, NY, US); Galápagos Islands, San Cristobal, *Schimpff 147* (BM, MO, NY, P).
HAITI. Vicinity of Mission, Fonds Varettes, *Leonard 3644* (GH, NY, US).
HONDURAS. San Juan del Rancho, N of Cerro de Uyuca, *Standley 15149* (F).
JAMAICA. Peckham, Upper Clarendon, *Harris 12825* (BM, GH, NY).
MEXICO. HIDALGO: 12 miles SW of Hidalgo-San Luis Potosí state border, cytological voucher, *King 4226* (F, MICH, NY, TEX, UC). NAYARIT: 9 miles N of Compostela, *McVaugh & Koelz 556* (MICH).
NICARAGUA. Jinotega, *Grant 7307* (GH).
PERU. 40 km S of Lima, *Grant 7503* (GH); 2–6 km from Oconeque, *Metcalf 30601* (GH, MO, UC, US).
VENEZUELA. Between La Sabana de las Piedras and Cerro Negro, *Steyermark 61833* (US).

6. **Ageratum gaumeri** Robins., Proc. Amer. Acad. Arts 47: 191. 1911.

Holotype: MEXICO. Yucatan: Izamal, *Gaumer 395* (GH); isotypes, DS, K, MICH, MO, NY, P, UC, US.

Annual, 1.5–4 dm tall; *roots* fibrous, rarely adventitious at basal nodes; *stem* erect, abundantly branched, generally pilose at nodes, internodes sparsely pilose to glabrous; *leaves opposite* or rarely alternate above, thin, ovate to less commonly deltoid, (0.6–)2.3–6.5(–8) cm long, (0.3–)1.6–4.1(–6.4) cm wide, base obtuse, apex acute, margin crenate-dentate, sparsely strigose, upper surface pale green to brown, smooth, sparingly pilose to glabrous, lower surface similar, venation inconspicuous; *petioles* 1–3(–3.5) cm long, pilose or glabrous; *inflorescences* borne singly on glabrous to sparingly pilose bracteolate peduncles (2.1–)4.5–13.5(–15) cm long; *involucres* campanulate, bracts biseriate, lanceolate, 2–3 mm high, 0.4–0.75(–1) mm wide, prominently 2-ribbed, glabrous to sparsely pilose, green to rose-colored apically, margin scarious, entire to slightly erose to scabrous, apex gradually to abruptly acuminate; *corollas* funnelform, 1.3–2.2 mm long, tube pale green to white, glabrous, the 5 lobes blue, lilac or lavender, glabrous to marginally puberulent; *achenes* brown, (1.1–)1.25–1.7 mm long, sparsely scabrous on angles, slightly curved toward the oblique white carpopodium; *pappus* of 5 white or rose-colored, membranaceous, blunt scales (0.05–)1.05–1.8(–2.05) mm long, apex variously fimbriate, at times finely setiferous or minute and coroniform.

Ageratum gaumeri may be divided into formae based on characters of the pappus and tomentum of the leaves.

1. Pappus of 5 scales; leaves pilose .... 6a. *Ageratum gaumeri* forma *gaumeri*
1. Pappus coroniform, minute; leaves generally glabrous .... 6b. *Ageratum gaumeri* forma *fallax*

6a. **Ageratum gaumeri** Robins. forma **gaumeri**.

Ageratum intermedium sensu Millspaugh, Field Columbian Mus. Publ. Bot. Ser. 3: 90. 1904, *non* Hemsley (1887), fide Robinson (1913*b*).

Leaves sparingly pilose; pappus of scales 0.35–1.85(–2.05) mm long.

The original *Ageratum gaumeri*, which is included in this forma, was distributed as *A. corymbosum* Zuccag. and *A. intermedium* Hemsley. This forma is readily distinguished from *A. corymbosum* by its annual habit, its ovate, thin leaves, its pappus of laciniate to setiferous scales and its inflorescences of a single head; from *A. intermedium* (*i.e.*, *A. maritimum* HBK) by its inflorescences, pappus, thin leaves, more numerous bracts on the peduncle and upright habit. The long bracteolate peduncle bearing a single head is the most constant characteristic of *A. gaumeri* and serves to set it apart from all other taxa.

This forma occurs in Yucatan and northern Guatemala at 15–30 m elevation. Buds, flowers, and mature fruits are generally present from December through March (occasionally in May, June, August).

GUATEMALA. PETEN: Arroyo (Río) Petexbatum S of Sayaxcho, *Steyermark 46184* (F, MICH); Sayaxche, *Steyermark 46252* (F).

MEXICO. YUCATAN: Izamal, *Armour 72* (F), *Coulter 72* (F); Valladolid, *Crockett 86* (MICH); Izamal, *Gaumer 395* (BM, DS, GH, K, MICH, MO, NY, P, UC, US); San Anselmo, *Gaumer 1735* (BM, F, GH, MO, US); Chichankanab, *Gaumer 2508* (F), *Gaumer s.n.* (F, K); Xnococ, *Gaumer & Sons 23482* (BM, GH, K, MO, NY, US); Izamal, *Greenman 374* (F); Chichen Itza, *Goldman 564* (F, US), *Lundell & Lundell 7859* (MICH), *Steere 1009* (GH, MICH, US); Merida, *Schott 208* (F); without locality, *Valdez 13* (F, GH, MICH, MO, NY, US); without locality or collector, *3925* (F, GH).

6b. **Ageratum gaumeri** Robins. forma **fallax** Robins., Contr. Gray Herb. 104: 4. 1934.

Holotype: MEXICO. Yucatan: Muna, *Steere 2125* (GH); isotype (MICH).

Leaves glabrous; pappus coroniform, minute, 0.05–0.1 mm long, margin undulate.

Robinson (1934) described *Ageratum gaumeri* f. *fallax* as distinct because the achenes possess a very minute coroniform pappus which, in association with the more glabrous leaves, set this taxon apart.

Forma *fallax* occurs in Yucatan and on Cozumel Island. Flowers and fruits are present in July and August.

MEXICO. QUINTANA ROO: Savannah N of Lake Coba, *Lundell & Lundell 7782* (MICH); low forest, San Miguel, Cozumel Island, *Steere 2633* (GH, MICH). YUCATAN: Hills S of Muna, along roadside, *Lundell & Lundell 8172* (GH, MICH, US); Muna, on rocks, on high ridge, *Steere 2125* (GH, MICH).

Section II. **Coelestina** (Cass.) Gray, Syn. Fl. 1(2): 93. 1884.

Coelestina Cass., Bull. Soc. Philom. Par. 1817: 10. 1817.
Caelestina Cass., Dict. Sci. Nat. 16: 10. 1820.
Coelestinia Endl., Gen. 366. 1838.
Ageratum subgenus *Coelestina* (Cass.) Baker *in* Mart., Fl. Bras. 6(2): 197. 1876.

Woody or herbaceous *perennials*; *roots* fibrous, or rarely a taproot; *leaves* opposite, lanceolate, ovate, deltoid, elliptic or linear, variously pubescent and glandular-atomiferous to glabrous; *inflorescences* grouped in tight or loose corymbiform clusters or borne in an irregular panicle; *involucral bracts* 2-seriate, lanceolate, linear-lanceolate, apex gradually acuminate, acute or rounded, margin entire, glabrous or ciliate; *receptacles* naked or paleaceous; *corollas* tubular to funnelform, varying shades of lavender and blue to white; *achenes* glabrous; *carpopodium* conspicuous; *pappus* coroniform, rarely bearing marginal subulate setae.

Lectotype: *Ageratum corymbosum* Zuccag.

Species in this section are found in the pine-oak forest zones of Mexico and extend through Central America to Panama; less common occurrences are in extreme southern Florida and the West Indies. Flowering and fruiting occur, in the main, from June through January; local conditions may favor year around blooming.

KEY TO SPECIES IN SECTION *COELESTINA*

1. Heads not clustered, borne in an irregular panicle; plants generally glabrous throughout; leaves lanceolate, sessile or very short petioled; British Guiana .... 26. *Ageratum scorpioideum*
1. Heads in an open or tight corymbiform cluster; plants with tomentum and glandular-atoms; leaves ovate, deltoid, elliptic or lanceolate; petioles evident; widespread in Mexico, Central America, and South America 2
   2. Receptacles of all heads paleaceous 3
      3. Heads small, the involucral bracts (3.0–)3.25–4 mm long 4
         4. Paleae linear, firm, indurate apically; Mexico 5
            5. Leaves thin, ovate to lanceolate, 5.5–9.5 cm long, 2.4–3.6 cm wide, both surfaces glabrous or puberulous over the venation, lower surface conspicuously glandular-atomiferous .... 12. *Ageratum elassocarpum*
            5. Leaves more or less firm, lanceolate, (2.4–)5–12(–12.5) cm long, (1.4–)3.3–5 cm wide, both surfaces white pilose to densely so beneath, lower surface glandular-atomiferous .... 11. *Ageratum nelsonii*
         4. Paleae spatulate, lax, erose apically; Brazil .... 10. *Ageratum micropappum*
      3. Heads larger, involucral bracts 4–5(–6) mm long 6
         6. Leaves deltoid, rarely ovate, base truncate, lower surface densely white woolly, eglandular; root a taproot ...... 15b. *Ageratum tomentosum* f. *bracteatum*
         6. Leaves ovate, elliptic, lanceolate to linear, base cuneate, lower surface white pilose, glandular-atomiferous; roots fibrous 7
            7. Leaves ovate to elliptic 8
               8. Lower leaf surface conspicuously covered with amber to yellow-colored glandular-atoms; corolla lobes violet, glandular-atomiferous; pappus 0.2–0.5 mm high; flowering in October, rarely earlier .... 8. *Ageratum paleaceum*
               8. Lower leaf surface with few, if any, yellow glandular-atoms; corolla lobes white, eglandular; pappus 0.4–0.5(–0.7) mm high; flowering in July and August .... 7. *Ageratum albidum*
            7. Leaves lanceolate to linear .... 9. *Ageratum echioides*
   2. Receptacles of all heads naked or paleae few and sporadic in a single head 9
      9. Perennial herbs, stems decumbent to repent, rarely erect; leaves succulent or thin; plants of seashore habitat 10
         10. Pappus coroniform but deeply laciniate; leaves succulent, ovate, borne on petioles 0.3–1(–2) mm long; stems, petioles, and peduncles sparingly white pilose .... 19. *Ageratum maritimum*
         10. Pappus coroniform, margin entire or at times setiferous, but not deeply laciniate; leaves thin, ovate or deltoid, borne on petioles 1–3.6 cm long; stems, petioles, and peduncles glabrous to very sparingly tomentose .... 20. *Ageratum littorale*
      9. Shrubs, stems woody, erect, only very rarely decumbent at the base; leaves not succulent, but if thin, plants not of seashore habitat 11
         11. Heads large, (0.6–)0.8–1 cm in diameter; leaves shiny on both surfaces, upper bright green and orange glandular punctate, lower surface pale green, densely glandular punctate .... 25. *Ageratum lucidum*
         11. Heads small, not greater than 5 mm in diameter; both leaf surfaces never shiny or only the upper surface shiny 12
            12. Involucral bracts lanceolate (0.85–)1–1.35 mm wide, glabrous to sparingly pilose, margin entire, ciliate at least apically, to glabrous 13

13. Leaves ovate, 4–9.5 cm long, 3–6 cm wide, upper surface yellow-green, margin crenate, venation on the lower surface conspicuous, often red; petioles slightly winged; involucral bracts green to reddish, 5.25–6.5 mm long, (0.85–)1–1.35 mm wide, prominently 2-ribbed basally .... 21. *Ageratum platypodum*

13. Leaves lanceolate, 1.1–8 cm long, 0.7–2.9 cm wide, upper surface bright green, margin sharply dentate, venation inconspicuous, not red; petioles not winged; involucral bracts green to reddish, 4.2–6.85 mm long, (0.7–)1–1.3 mm wide, 2-ribbed, the ribs conspicuous .... 22. *Ageratum riparium*

12. Involucral bracts lanceolate to linear-lanceolate, less than 1 mm wide, more abundantly pilose, rarely glabrous, margin entire, glabrous, rarely ciliate apically 14

14. Leaves remote from the inflorescences, somewhat thick, fleshy and velvety; stems white pilose, hairs *ca.* 0.75 mm long .... 18. *Ageratum guatemalense*

14. Leaves not conspicuously remote from the inflorescences, not thick, fleshy and velvety; stem, if pilose, with shorter hairs 15

15. Leaves thin, semi-membranous, borne on elongate petioles 16

16. Leaves broadly ovate, 7–9 cm long, 6.5–9 cm wide, upper surface bright green, lower surface pale green, abundantly dotted with yellow glandular atoms; venation palmate, conspicuous, pilose; petioles 2.5–4 cm long, white pilose, narrowly winged; involucral bracts pale brownish to pale green, glabrous .... 23. *Ageratum oerstedii*

16. Leaves narrowly ovate, 3–6.6 cm long, 1.4–4.15 cm wide, upper surface shiny green, lower surface dull, gray to off-green, less conspicuously dotted with glandular atoms; venation reticulate, conspicuous, sparingly pilose; petioles 1.2–3 cm long, pilose-puberulous, not winged; involucral bracts pale green to reddish, pilose basally .... 24. *Ageratum petiolatum*

15. Leaves not semi-membranous, petioles not elongate 17

17. Leaves rigid, lanceolate to ovate, margin entire, lower surface densely covered with pale gray to silvery indument 18

18. Leaves lanceolate, (3.5–)4–6 cm long, *ca.* 1.7 cm wide, upper surface scabrous to scabrous-puberulent, eglandular-punctate, lower surface densely white-tomentose, eglandular; petioles 0.7–0.8 cm long; involucral bracts 4.75–5 mm long, 0.55–0.6 mm wide, dark green, white pilose and eglandular throughout .... 17. *Ageratum chortianum*

18. Leaves ovate, 2–3.5 cm long, 1–2 cm wide, upper surface scabrous to puberulent, amber glandular-punctate, lower surface densely white to gray tomentose with scattered amber glandular-atoms; petioles 0.1–0.4 cm long; involucral bracts 3.5–4.5 mm long, 0.5–0.65 mm wide, green to deep reddish, puberulous and glandular-atomiferous .... 16. *Ageratum standleyi*

17. Leaves not rigid, ovate, lanceolate, elliptic or deltoid, margin crenate or dentate, at times remotely so, not entire, lower surface variously covered with white pubescence or scabrous 19

19. Leaves deltoid, rarely lanceolate, 1.6–3.5(–6.5) cm long, lower surface densely white tomentose; plants shrubby, small, to 4.5 dm tall; root a taproot .... 15a. *Ageratum tomentosum* f. *tomentosum*

19. Leaves not deltoid, larger than above, lower surface pilose to scabrous; plants shrubby, larger, to 24 dm tall; roots fibrous 20
    20. Leaves ovate, upper surface conspicuously dark green or brown, lower surface abundantly white tomentose at least over the prominent primary venation; involucral bracts conspicuously pilose; extreme southern Mexico and Central America, rare northward .... 14. *Ageratum rugosum*
    20. Leaves ovate, ovate-lanceolate, triangular-lanceolate, narrowly lanceolate or elliptic-lanceolate, upper surface green, at times shiny green but not conspicuously dark green or brown, lower surface densely to sparingly pilose or scabrous, primary venation conspicuous and white or inconspicuous; involucral bracts pilose, rarely densely so; common in Mexico .... 13. *Ageratum corymbosum*

7. **Ageratum albidum** (DC.) Hemsl., Biol. Centr. Amer. Bot. 2: 81. 1881.

Coelestina albida DC., Prod. 5: 107. 1836. (Holotype: MEXICO. Oaxaca: Inter Oaxaca et Mitla, *Andrieux 548* (DC-G, not seen), photograph, MIN; isotype, K, photographs, F, GH, US, fide Robinson (1913*b*).)
Carelia albida (DC.) Kuntze, Rev. Gen. 1: 325. 1891, fide Robinson (1913*b*).

Herbs 4–6.5 dm tall from perennial roots; *roots* fibrous, woody, coarse; *stems* erect, simple, branching only near summit, herbaceous and reddish, becoming woody and gray toward base, puberulent-pilose throughout to glabrous basally; *leaves* opposite, petioled, thickened, ovate to elliptic, (2.7–)3–5(–6.9) cm long, 1.2–2.5(–3.5) cm long, base obtuse to cuneate, margin crenate, revolute, scabrous, apex widely acute, upper surface dark green, more or less rugulose, conspicuously white, long pilose and scabrous, lower surface paler green, densely long, white pilose to less densely covered, at times, with scattered yellow glanduliferous atoms, the 3–5 veins white, prominent; *petioles* 1–4 mm long, densely white pilose; *inflorescences* terminal, the 5–20 heads in a convex corymbose cluster; *peduncles* less than 5 mm long, densely white puberulous-pilose, bracteolate; *bracteoles* linear, green, puberulous and pilose, about 3 mm long; *involucres* campanulate, bracts bi- or tri-seriate, firm, 2-ribbed, green, apically white or reddish, lanceolate, 4–5(–5.5) mm high, outer ones 0.8–0.9(–1) mm wide, margin entire, green or scarious, at times ciliate, apex acute, surface white pilose; *receptacle* paleaceous, paleae firm, linear, 4–5(–5.2) mm long, apex acute, white; *corollas* narrowly funnelform, 2.25–3 mm long, white throughout, tube and throat white-pilose, lobes glabrous; *achenes* black, (1.35–)1.5–2.25 mm long, glabrous, slightly tapered toward white carpopodium; *pappus* coroniform, 0.4–0.5(–0.7) mm long, margin undulate, irregular.

Ageratum albidum is related to *A. paleaceum* as evidenced from similar receptacle paleae and general morphology in both. However, the species are readily separable as indicated in Table 2. From this summary, it is evident that though these species may be sympatric in at least part of their ranges, reproductive isolation operating through different blooming times may maintain their distinctness.

TABLE 2. A comparison of *Ageratum albidum* and *A. paleaceum*.

Character	*A. albidum*	*A. paleaceum*
Corolla color.	White.	Violet.
Glands.	Few to none.	Numerous amber to yellow atomiferous glands on the lower leaf surfaces, peduncles, bracteoles, and corollas.
Growth habit.	Perennial herbs.	Woody, perennial shrubs.
Flowering and fruiting.	July to September.	October to December.

Ageratum albidum is distinguished from *A. elassocarpum*, another paleaceous species, by the lavender corollas, the more glabrous leaves, shorter pappus, and a more southern distribution of the latter species.

Robinson (1913*b*) described *Ageratum albidum* (DC.) Hemsl. var. *nelsonii* based on *Nelson 2822a* (GH). In the description, he states that this variety is similar in involucre, paleae, pappus, etc. to *A. albidum*, differing in wider leaves on longer petioles and a more leafy stem. Comparisons of morphological measurements of leaves, involucral bracts, paleae, and pappus quickly shows these taxa to be quite different as summarized in Table 3.

It is my opinion that the plants previously determined as *Ageratum albidum* var. *nelsonii* cannot be treated in this way. The combination of characters found in these plants, densely pilose leaves on long petioles and small heads with receptacle paleae, is found nowhere else in the genus. Thus it is more logical to treat these plants as a separate species, *Ageratum nelsonii* (Robins.) M. F. Johnson.

Ageratum albidum occurs locally in Oaxaca, Mexico, in open sun in association with oaks and leguminous shrubs in rocky clay-loam soil from *ca.* 1700–2500 m elevation. Flowers are present in July and August; fruits are present in September and dispersed in October.

MEXICO. OAXACA: Valley of Etla, *Alvarez 751* (GH); between Oaxaca and Milta, *Andrieux 548* (K); steep slope with *Quercus* and *Pinus* 3 km E of Istlan de Juarez, *Breedlove 12225* (MICH); Cerro de San Felipe, *Conzatti & Gonzales 542* (GH); vicinity of Cerro Zempoaltepetl, near Tlahuitoltepec, *Hallberg 955* (MICH, US); ruins of Monte Alban, *Johnson*

TABLE 3. A comparison of *Ageratum albidum* and *A. nelsonii*.

Character	*A. albidum*	*A. nelsonii*
Leaves.	Ovate to elliptic, 2.7–6.9 cm long, 1.2–3.5 cm wide.	Lanceolate, 2.4–12.5 cm long, (1.4–)3.3–4 cm wide.
Petioles.	1–4 mm long.	(0.2–)1–2.5 cm long.
Involucre.	4–5.5 mm high, outer bracts 0.8–0.9(–1) mm wide.	3.25–4 mm high, outer bracts 0.5–0.85(–1) mm wide.
Paleae.	4–5.2 mm high.	3.3–3.75 mm high.
Pappus.	0.4–0.5(–0.7) mm high.	(0.1–)0.15–0.3 mm high.

& *Hofstetter 1997* (MIN), *Kenoyer 1523* (GH), *King 3490* (DS, MICH, NY, TEX, UC, US); mountains along route 175 *ca.* 24 miles N of the junction with route 190, *King 3502* (TEX); valley of Oaxaca, *Nelson 1208* (GH, US); hills above Oaxaca, *Pringle 4816* (BM, F, GH, K, MICH, MIN, MO, MSC, NY, P, UC, US); Monte Alban, *C. L. Smith 365* (MO, UC, US); Las Sedas, *C. L. Smith 366* (F, NY); Tenango, *L. C. Smith 424* (GH).

8. **Ageratum paleaceum** (DC.) Hemsl., Biol. Centr. Amer. Bot. 2: 83. 1881.

Coelestina paleacea Gay *ex* DC., Prod. 5: 107. 1836. (Holotype: MEXICO. Oaxaca: Circa Oaxaca, *Andrieux 287* (DC-G, not seen), photographs, GH, US; isotype, P. fide Robinson (1913*b*).)

Carelia paleacea (DC.) Kuntze, Rev. Gen. 1: 325. 1891, fide Robinson (1913*b*).

Ageratum rhytidophyllum Robins., Proc. Amer. Acad. Arts 36: 476. 1901. (Holotype: MEXICO. Oaxaca: Sierra de San Filipe, *Pringle 5675* (GH), photograph, MIN.)

Perennial *shrubs* 4–7.5(–12) dm tall; *roots* fibrous; *stems* erect, simple or branched from an enlarged woody caudex, younger parts deep red, puberulous-tomentose to pilose, densely so toward inflorescences, older parts brownish-gray, puberulous-tomentose to glabrous; *leaves* opposite, petioled, thickened, lower ones ovate, 3.9–5.7(–6) cm long, 1–2 cm wide, upper ones ovate-lanceolate to lanceolate, base of blade obtuse, rarely oblique, apex acute, margin revolute, very shallowly crenate to entire, upper surface dull to bright green, at times partially purple or bluish, rugose, scabrous, lower surface pale green, conspicuously reticulate-veined, densely covered with white pilose hairs and amber or yellow atomiferous glands; *petioles* 0.3–0.6(–0.9) cm long, puberulous-tomentose to pilose with scattered yellow or amber atomiferous glands; *inflorescences* terminal, the 20–30 or more heads grouped into dense corymbose clusters; *peduncles* coarse, bracteolate, usually less than 5 mm long, puberulous with scattered yellow or amber and/or black atomiferous glands; *bracteoles* alternate, less than 3 mm long, green to tawny, puberulous-tomentose with scattered atomiferous glands, merging with involucral bracts; *involucre* campanulate, bracts triseriate, more or less firm, lanceolate to linear, inner bracts 4–5(–6) mm long, 0.5–0.8 mm wide, outer bracts about one half as long, green to purple, white pilose to sparingly so, 2-ribbed, margin entire, at times ciliate and/or scarious, apex acute, slightly thickened, white; *receptacle* paleaceous, paleae linear, 3.25–5 mm long, pale green to purplish, apex acute, white, minutely scabrous; *corollas* funnelform, 2.2–3(–3.2) mm long, sparingly puberulous and glandular-atomiferous on tube or at least on lobes to glabrous, tube and narrow throat pale green, the 5 acute lobes and exerted style branches violet to pale violet; *achenes* 5-angled, shiny brown to black, 1.4–1.9(–2.25) mm long, glabrous, tapering toward small carpopodium; *pappus* coroniform, whitish, 0.2–0.3 mm high, margin entire or obscurely dentate.

Ageratum paleaceum (DC.) Hemsl. was described by Candolle (1836) based upon C. Gay's unpublished, but proposed, name for *Andrieux 287*. It was placed in the genus *Coelestina* Cass. and transferred to *Ageratum* by Hemsley (1881). Robinson (1901) was apparently unaware of Gay's earlier name when *A. rhytidophyllum* was published. This oversight was corrected in Robinson's revision of 1913.

Ageratum paleaceum is similar to *A. albidum* but is readily distinguished from it and other species by the short-petioled, thick, ovate leaves which are white pilose and conspicuously dotted with orange glanduliferous atoms beneath. See discussion under A. *albidum* as well.

The chromosome number $n = 11 \pm 1$ reported by Turner, Powell & King (1962) for "*Ageratum* cf. *paleaceum* (Gay) Hemsl. var. *paleaceum*" is taken from *King 3112*. Personal study of this specimen indicates it cannot be referred to A. *paleaceum* but rather to A. *elassocarpum*.

This species occurs in Oaxaca, Michoacán, and Puebla from *ca.* 1500–2800 m elevation. Buds and flowers are present in October, rarely before; fruits are present in November and December.

MEXICO. MICHOACAN: 1 km S of Jacona, *Cutler 4058* (US). OAXACA: 3 km E of Ixtlan de Juros, *Breedlove 12230* (MICH); Ixtlan de Juarez, *Krueger & Gillespi 2* (GH, MO); valley of Oaxaca, *Nelson 1439* (US); *Nelson 1446* (GH, US); Sierra de San Felipe, *Pringle 5675* (GH); *Pringle 6177* (F, GH, MIN, MO, MSC, NY, P, UC, US); Cerro Verde, *Purpus 4424* (UC); Cerro Espino, *Reko 3538* (US); Las Sedas, *C. L. Smith 364* (NY, UC); Sierra de San Felipe, *C. L. Smith 594* (F, MO, UC, US); San Juan del Estado, *L. C. Smith 277* (GH). PUEBLA: Moria, *Nicolas s.n.* (F).

9. **Ageratum echioides** (Less.) Hemsl., Biol. Centr. Amer. Bot. 2: 81. 1881.

Isocarpha echioides Less., Linnaea 5: 141. *t. 2, fig. 14–16.* 1830. (Holotype: MEXICO. Vera Cruz: In graminosis prope Hacienda de la Laguna, *Schiede 304* (B, not seen), photograph, GH.
Carelia echioides (Less.) Kuntze, Rev. Gen. 1: 325. 1891.
Alomia echioides (Less.) Robins., Contr. Gray Herb. 42: 449. 1913.

Perennial *herbs* 3.5–6.5 dm tall from a gnarled woody caudex; *roots* coarse, fibrous; *stems* erect, simple to sparingly branched near summit, leafy on lower half, upper half naked or with 1 or 2 pairs of reduced leaves, surface deep red to tan, densely white pilose-puberulent basally and toward midregion to nearly glabrous, pilose hairs up to 0.1 mm long; *leaves* opposite, somewhat firm, elliptic-lanceolate to nearly linear, 5–7.5(–13.5) cm long, 0.8–1.5(–2.6) cm wide, base long attenuate-cuneate, apex acute to broadly so, margin revolute, scabrous, remotely and shallowly crenate, upper surface dull, dark green, white pilose to scabrous, pubescent over the 3 longitudinal veins, lower surface pale green, yellow glandular-punctate, white pilose, at times densely so over the 3 prominent white veins, to glabrous; *petioles ca.* 0.2–1.2 cm long, slightly winged, densely white pilose to glabrous; *inflorescences* terminal, the 5–11 or more heads grouped in tight corymbose clusters; *peduncles* less than 5 mm long, puberulous to pilose-puberulous; *involucres* campanulate, bracts triseriate, lanceolate-oblong, 4–4.5(–5) mm high, 0.65–1.05 mm wide, green, becoming red apically, surface with scattered pilose hairs, prominently 2-ribbed basally, margin herbaceous to scarious, entire, pilose, apex acute, white, subindurate; *corollas* tubular to narrowly funnelform, 2.2–2.75 mm long, tube and throat pale green, short pilose to glabrous, lobes acute, erect or spreading, pale blue to bluish-purple, sparingly pilose to glabrous; *receptacle* conical, paleaceous, paleae light green, apically red, linear to spatulate, 3.75–5 mm long, 0.3–0.5 mm wide, 1-ribbed, margin entire, at times scarious, apex acute, indurate, white, minutely scabrous; *achenes* black (1.35–) 1.45–1.8 mm long, glabrous, basally tipped with inconspicuous carpopodium; *pappus* coroniform, tawny, 0.05–0.25(–0.55) mm high, margin dentate to variously coarsely pectinate.

The type specimen of *Ageratum echioides* is quite probably not extant as the collection of Compositae held at Berlin (B) was destroyed during World War II. At least, I was unable to find the type when I visited Berlin in 1966.

Robinson (1913*b*) and Candolle (1836) recognized this species as belonging with the epappose genus *Alomia* HBK. However, the plants at hand do possess a coroniform pappus, though in certain instances a very small one, and thus are here referred to section *Coelestina* of *Ageratum*. I have seen some specimens Robinson annotated as *Alomia echioides*, and even these show the pappus.

This species appears most closely related to *Ageratum guatemalense*. See the discussion under that species. *Ageratum echioides* also resembles *A. ellipticum* in general habit, leaf shape and size, pubescence, and in the corollas which are glabrous or nearly so. These species differ markedly in the pappus, setiferous scales in *A. ellipticum* and coroniform in *A. echioides*. The presence of receptacle paleae in *A. echioides* also serves to distinguish these species. *Ageratum echioides* is similar to the paleaceous species *A. albidum* in size and shape of corollas, achenes, and involucral bracts but differs in the bluish corollas, shorter pappus and the distinctive elliptic-lanceolate to linear, tri-veined, somewhat firm leaves generally borne on the lower half of the stem. These characters separate *A. echioides* from other paleaceous species as well.

Ageratum echioides is found in eastern and southern Mexico and adjacent Guatemala in association with *Quercus* and *Pinus* and in moist pastures and fields and on slopes from *ca.* 1600–1950 m elevation. Flowering occurs in June–August and September, less commonly later; fruits are mature and dispersed in October.

GUATEMALA. Near Jacaltenango, *Nelson 3561a* (US); between Guatemala and San Raimundo, *Standley 62978* (MICH); below Miramar, *Steyermark 51500* (F, GH, NY).

MEXICO. CHIAPAS: Steep slope along road to Mal Paso, *Breedlove 10343* (MICH); pasture at NW edge of Teopisca along Mexican Highway 190, *Breedlove 10533* (MICH); 4 miles N of Jitotol on road to Pueblo Neuvo Solistahuacan, *Breedlove 12057* (MICH); 17 miles E of La Trinitaria along road to the Lagos de Montebello, *Breedlove & Raven 13028* (MICH); between Mazapa and Motozintla, *Matuda 4867* (MO); Comitan, *Matuda 15798* (F); *ca.* 13 miles SE of San Cristobal de las Casas, *Ownbey & Muggli 3986* (MIN). GUERRERO: Acapulco, *Hancock 36* (F). JALISCO: Guadalajara, *Holway 511* (NY). VERA CRUZ: Orizaba, *Botteri 408* (BM), *Botteri 623* (GH); region d'Orizaba, *Bourgeau 2393* (GH, P); region of San Andreas Tuxtla, *Dressler & Jones 251* (GH, US); between Fortin and Coscomatepec, *Langman 3614* (US); Zacuapan, *Purpus 1854* (MO), *Purpus 2199* (F, GH, US); without definite location, *Bourgeau 3207* (GH, P), *Sartorius s.n.* (GH).

10. **Ageratum micropappum** Baker *in* Mart., Fl. Bras. 6(2): 198. 1876.

Holotype: BRAZIL. Bahía Province, *Blanchet 3700* (K, not seen); isotypes, C, GH, P; photographs, GH, TEX, P, US.

Shrub, height unknown; *roots* unknown; *stem* conspicuously ribbed longitudinally, deep red to brown, white puberulent with scattered yellow glandular atoms, becoming tomentose near inflorescences; *leaves* opposite, petioled, subcoriaceous, ovate to lanceolate, 6–7.8 cm long, 2.9–3.8 cm wide, base cuneate, slightly decurrent along petiole, apex broadly rounded, margin slightly revolute, dentate, teeth thickened, cuspidate, upper surface glabrous or with widely scattered yellow glandular atoms, the reticulate venation inconspicuous, lower surface conspicuously white to tan tomentose with yellow glanduliferous atoms over surface and prominent reticulate veins; *petioles* winged, *ca.* 0.7–1.5 cm long, tomentose and glandular atomiferous beneath, glabrous above; *inflorescences* terminal, heads grouped into a dense corymbose cluster; *peduncles* white-tomentose, glandular atomiferous, bracteolate; *bracteoles* linear, tomentose; *involucres* campanulate, bracts biseriate, firm, 2-ribbed, oblong, *ca.* 3.25 mm long, *ca.* 0.8–0.85 mm wide, margin entire, ciliate toward apex, apex rounded, variously ciliate or erose; *receptacle* paleaceous, paleae flattened, spatulate to lanceolate, *ca.* 4–4.25 mm long, 0.5–0.65 mm wide, 2-ribbed, margin entire, glabrous to sparingly ciliate, apex rounded, obtuse, ciliate or more or less erose; *corollas* narrowly funnelform, *ca.* 2–2.25 mm long, tube and throat white, glandular to glabrous, lobes glabrous, lavender (?); *achenes* black, 1.85–2.05 mm long, glabrous, slightly tapered toward white carpopodium; *pappus* coroniform, 0.1–0.15 mm high, margin undulate to minutely dentate.

Ageratum micropappum is distinguished by the oblong, ciliate, 2-ribbed receptacle paleae, the involucral bracts with rounded apices, the firm, ovate leaves with cuspidate teeth, the lower surfaces of the leaves with dense tomentum and the prominent, reticulate venation. Only one other species of *Ageratum* is present in Brazil, the weedy *A. conyzoides* with which *A. micropappum* cannot be confused.

This species is known only from the type locality. Flowering and fruiting data are not known.

BRAZIL. BAHIA: *Blanchet 3700* (C, GH, P); Mt. Taboa, Boanfin, *Curran 201* (GH, US).

11. **Ageratum nelsonii** (Robins.) M. F. Johnson, stat. et comb. nov.

Ageratum albidum (DC.) Hemsl. var. *nelsonii* Robins., Contr. Gray Herb. 42: 471. 1913. (Holotype: MEXICO. Chiapas: Between Zanatepec and Tapana, *Nelson 2822a* (GH), photograph, MIN.)

Perennials, 4–5 dm tall; *roots* fibrous, coarse, from a woody caudex; *stem* erect, woody, simple or branched, bark brown to deep red, pilose-puberulent to densely white pilose; *leaves* opposite, petioled, lanceolate, (2.4–)5–12(–12.5) cm long, (1.4–)3.3–5 cm wide, base obtuse, apex acute, margin revolute, crenate or dentate, scabrous, upper surface dull dark green to brownish green, at times mixed with deep red, abundantly white pilose to scabrous, venation reticulate, inconspicuous, lower surface pale green, yellow to amber glandular atomiferous, densely white pilose, at times becoming so dense as to obscure surface, venation reticulate, the 3 principal veins prominent; *petioles* (0.2–)1–2.5 cm long, white scabrous as well as pilose; *inflorescences* terminal, the 20 or more heads grouped in a tight, convex corymbiform cluster; *peduncles ca.* 5–7 mm long, white pilose and amber glandular atomiferous, at times densely pilose, bracteolate; *bracteoles* alternate, subulate, white pilose, green to reddish; *involucres* campanulate, bracts biseriate, lanceolate, 3.25–4 mm long, outer ones 0.5–0.85(–1) mm wide, 2-ribbed though at times obscurely so, surface green, white pilose and at times glandular atomiferous, margin entire, green to scarious, at times apically ciliate, apex acute, becoming white and more or less indurate; *receptacle* conical, paleaceous, paleae linear, 3.3–3.75 mm long, 1-ribbed, pilose to glabrous, green to reddish, becoming white and indurate apically, margin entire, apex acute; *corollas* funnelform, 2–2.5(–2.75) mm long, tube and narrow throat white to pale blue or lavender, glabrous to sparingly dotted with yellow glandular atoms, lobes acute, blue to lavender, glabrous; *achenes* dull black, (1.15–)1.3–1.55 mm long, slightly tapered toward white carpopodium; *pappus* coroniform, (0.1–)0.15–0.3 mm high, margin 5-dentate or merely undulate.

Ageratum nelsonii was first described as a variety of *A. albidum* as noted in the discussion of the latter. However, the pilose stem and involucral bracts, and the larger densely pilose leaves suggest affinities elsewhere. The relatively large, pilose leaves with dark green upper surfaces are similar to leaves of *A. rugosum* from which it can be distinguished by means of the paleaceous receptacles, smaller heads and short pappus. Receptacle paleae borne in small heads and the presence of lanceolate leaves on elongate petioles suggest an affinity with *A. elassocarpum.* However, the glabrous to nearly glabrous leaves of *A. elassocarpum* and the densely pilose ones of *A. nelsonii* serve well to distinguish these species. The combination of lanceolate, rather densely pilose leaves on elongate petioles, receptacle paleae and small heads are features unique to *A. nelsonii.*

Turner, Powell & King (1962) published the chromosome number $n = 10$ for *King 2981* which was reported as *Ageratum* cf. *tomentosum* (Benth.) Hemsl. and for *King 2751* which was reported as *A. paleaceum* (Gay) Hemsl. var. *nelsonii* Rob. Personal study of these vouchers indicates beyond question that they should be referred to *A. nelsonii* and the number, $n = 10$, to this species.

Ageratum nelsonii occurs in the states of Mexico, Oaxaca, and Chiapas in association with *Pinus* and *Quercus* in rocky, gravelly soil from near sea level to *ca.* 2000 m elevation. It flowers from June to September (–October); fruits are present from July to December.

MEXICO. CHIAPAS: 1 km NW of Aguacatenango, *Breedlove 7891* (DS, MICH); 11 miles S of La Trinitaria, *Breedlove & Raven 13269* (MICH); 2 miles S of Tuxtla Gutierrez, *Breedlove & Raven 13349* (MICH); 15 miles SE of Tapanatepec, *Breedlove & Raven 13722* (MICH); 7 miles E of the Chiapas-Oaxaca border, *King 2751* (MICH, TEX); 10 miles E of the Chiapas-Oaxaca border, cytological voucher, *King 2981* (MICH, TEX); Monserrate, *Purpus 10233* (GH, US), *Purpus 9104* (F, GH, MO, NY, US). MEXICO: Tlalpam, *Rose & Hay 5496* (US). OAXACA: Mountains about Yalalag, *Nelson 971* (US); between Zanatepec and Tapana, *Nelson 2821* (US), *Nelson 2822a* (GH).

12. **Ageratum elassocarpum** Blake, Contr. U. S. Natl. Herb. 22: 588. 1924.

Holotype: MEXICO. Chiapas: Sierra de Tonala, *Purpus 6628* (US); isotypes, B, BM, F, MO, NY, UC. Type distributed as *Ageratum corymbosum* Zuccag.

Perennial *shrubs* (2–)4–7 dm tall; *roots* fibrous; *stems* erect to lax above, branched, herbaceous above, woody below, bark reddish on young stems to, at times, gray-brown on older parts, densely white puberulous over-all to glabrous toward base; *leaves* thin, opposite, rarely alternate above, petioled, ovate to lanceolate above, 5.5–9.5 cm long, 2.4–3.6 cm wide, base cuneate, apex acute to broadly so, margin shallowly crenate to subentire, upper surface dark green, puberulous to scabrous, lower surface green, glabrous to puberulous over veins, conspicuously (15× magnification) glandular-atomiferous, glands shiny to dull yellow or amber, at times mixed with black atoms; *petioles* (0.5–)1–1.8 cm long, channeled adaxially, puberulous-tomentose; *inflorescences* terminal, 12–20 or more heads grouped in dense corymbose clusters; *peduncles ca.* 5 mm long, bracteolate, densely puberulous with scattered yellow, amber or rarely black glandular atoms; *bracteoles* alternate, green, *ca.* 2–3 mm long, puberulous-glandular atomiferous over both surfaces; *involucres* campanulate, bracts biseriate, firm, 2-ribbed, lanceolate, 2–3.75(–4) mm high, outer ones 0.5–0.75(–0.85) mm wide, green throughout to tinged with red, apically white, surface white puberulous with scattered yellow or black atomiferous glands, margin entire, apex acute, minutely scabrous; *receptacle* paleaceous, paleae linear, 2–2.75 mm long, firm, pale green below to apically white, glabrous to scabrous-ciliate, glandular-atomiferous apically, margin entire, apex acute; *corollas* tubular to narrowly funnelform, (1.5–)2–2.25 mm long, glabrous to minutely puberulous with scattered yellow or black atomiferous glands, tube and throat pale green to white, the 5 acute lobes and exerted style branches blue to bluish-lavender; *achenes* 5-angled, dull black, 1.25–1.5(–1.8) mm long, glabrous, tapering toward white carpopodium; *pappus* coroniform, 0.2–0.3 cm high, light tan, margin denticulate, projections extending *ca.* 0.05 mm above the ribs of the achene.

Ageratum elassocarpum shows affinities with *A. corymbosum sens. lat.* and especially to forma *elachycarpum* in leaf shape and size, overall external morphology, and habitat preference. Both *A. elassocarpum* and *A. corymbosum* f. *elachycarpum* have small heads with involucral bracts less than 4 mm high. The pappus is 2–3 mm high in both taxa which is shorter than in the bulk of *A. corymbosum sens. lat.* Though often determined as *A. paleaceum* or *A. corymbosum*, *A. elassocarpum* is distinct from similar species and formae. The combination of small heads with receptacle paleae and thin ovate-lanceolate leaves that are quite glabrous on the lower surface serves well to separate this species from those with which it may be confused.

The chromosome number $n = 11 \pm 1$, voucher *King 3112* (DS, MICH, NY, TEX, UC, US), was reported for *Ageratum* cf. *paleaceum* (Gay) Hemsl. var. *paleaceum* by Turner, Powell & King (1962). From study of this voucher I am convinced that *King 3112* should be referred to *A. elassocarpum* as it has the thin ovate-lanceolate nearly glabrous leaves and small heads associated with *A. elassocarpum* and never found on *A. paleaceum*. The collection of the voucher in Chiapas also indicates that it cannot be *A. paleaceum* as the range of the latter is farther north.

This species is restricted to Chiapas and adjacent Oaxaca in association with *Quercus* and *Pinus*, in full sun or partial shade *ca.* 500–1960 m elevation. It flowers from late June through October; fruits are present in September and mainly dispersed by December.

MEXICO. CHIAPAS: Pan-American Highway, 23 miles W of Ocozocautla, *Cronquist 9680* (MICH, MO, MSC, NY, TEX, US); low hills along route 195, about 36 miles S of Tuxtla Gutierrez, *King 3107* (DS, MICH, NY, TEX, UC, US); 22 miles S of Las Cruces, cytological voucher, *King 3112* (DS, MICH, NY, TEX, UC, US); Sierra de Tonala, *Purpus 6628* (BM, F, MO, NY, UC, US); steep, moist roadside slope covered with *Pinus* and grasses, 19 km N of Arriaga on highway 195, *Roe et al. 862* (WIS). OAXACA: Grazed areas 28 km NW of La Ventosa along the Trans-Isthmian highway, *King 632* (MICH, US); grazed areas 2 km E of Zanatepec, *King 1953* (MICH, NY, TEX, UC, US).

13. **Ageratum corymbosum** Zuccag. *ex* Pers., Syn. 2: 420. 1807, *non* Benth. (1852).

Neotype: MEXICO. Jalisco: 4.5 miles W of Tizapan on S shore of Laguna de Chapala, *Johnson & Hofstetter 1981* (MIN).

Shrubs to sub-shrubs (1.5–)3.5–20 dm tall; *roots* fibrous, coarse, rarely adventitious on lower stem; *stems* woody, erect and usually clumped from a woody caudex, simple or branched, bark deep red to purplish distally, becoming brown to gray toward base, pilose-puberulent throughout to short puberulent toward inflorescences to nearly glabrous on older parts, rarely rhizomatous; *leaves* opposite, at times alternate near inflorescences, petioled, extremely variable in dimensions and shape (see key to formae below), base cuneate to truncate, margin revolute, crenate to dentate to shallowly lobed to subentire, scabrous to pilose, apex acute, upper surface smooth, dull green, scabrous to scabrous-puberulous to sericeous, lower surface dull, pale green, dotted with yellow to amber glanduliferous atoms, abundantly white pilose to puberulous at least over the reticulate venation; *petioles* variable in length (see below), channelled adaxially, puberulent-pilose; *inflorescences* terminal on stems and branches, the numerous heads grouped into dense or less commonly open corymbiform clusters; *peduncles* 0.5–4 cm long, white pilose-puberulous, bracteolate; *bracteoles* (2.5–)3–4.5 mm long, subulate, green to red-purple, white puberulous to velutinous; *involucres* campanulate to hemispherical, bracts firm, biseriate, greenish to apically red, 2-ribbed, linear-lanceolate to lanceolate, (2–)2.75–7 mm high, outer ones 0.45–1(–1.1) mm wide, margin entire, herbaceous or scarious, at times ciliate apically, apex acute, reddish, minutely scabrous, submucronate, surface white pilose, at times densely so, at times dotted with yellow or amber glanduliferous atoms; *receptacle* naked or rarely 1 head of plant sparingly paleaceous; *corollas* narrowly funnelform, (1.75–)2–3.75(–4.25) mm long, tube greenish to white, short pilose, throat white, pilose, yellow or amber atomiferous to subglabrous, lobes acute, spreading, short pilose to glabrous, blue to bluish, gray-blue, lavender-purple, mauve or white; *achenes* 5-angled, dark brown to black, glabrous, (1.1–)1.3–3(–3.5) mm long, slightly tapered toward inconspicuous basal carpopodium; *pappus* coroniform, white to tawny, 0.2–0.85 mm high, margin entire to lobed to variously finely pectinate, at times setiferous, setae subulate, firm, connate basally, entire pappus then 1.1–3.2 mm long.

Zuccagni (*ex* Persoon, 1807) did not cite any specimens, and citations of specimens are lacking in the list of synonyms as well. Thus I have chosen a personal collection as neotype, as I feel it best exemplifies the taxon as originally described.

This variable species is separated into formae based on the following key characters.

1. Involucral bracts (2.05–)2.4–3.5(–4) mm high, achenes 1.2–1.65(–1.75) mm long, leaves ovate to lanceolate; Guatemala and Honduras, rarely Mexico .... 13f. *A. corymbosum* f. *elachycarpum*
1. Involucral bracts higher and achenes longer, leaves widely ovate, ovate-lanceolate, triangular-lanceolate, narrowly lanceolate, elliptic-lanceolate; widespread in Mexico 2
   2. Leaves narrowly lanceolate, 3.3–10 cm long, 0.5–1.8(–2.4) cm wide, margin subentire to remotely crenate-dentate .... 13b. *A. corymbosum* f. *salicifolium*

2. Leaves not narrowly lanceolate or if so, the margin grossly and coarsely dentate to lobed, not sub-entire 3
   3. Leaves elliptic-lanceolate, 4.2–8.5 cm long, 1.5–3.3 cm wide, margin coarsely and conspicuously crenate-dentate, teeth at times becoming large and lobe-like, upper surface bright, shiny green, rarely dull green, venation reticulate, white and conspicuous on both surfaces .... 13c. *A. corymbosum* f. *lactiflorum*
   3. Leaves not elliptic-lanceolate, margin not lobed, upper surface usually dull green, venation not conspicuous at least on the upper surface 4
      4. Leaves ovate to ovate-lanceolate, 4–7 cm long, (1.5–)2–3.5 cm wide, margin crenate to dentate, upper surface scabrous to pilose, lower surface sparingly white pilose to scabrous; abundant in Mexico .... 13a. *A. corymbosum* f. *corymbosum*
      4. Leaves ovate to widely so, to triangular-lanceolate, margin crenate to dentate, upper surface pilose to scabrous, lower surface densely pilose 5
         5. Leaves ovate to triangular-lanceolate, 4.5–8(–11.3) cm long, 2.3–4.5 (–5.9) cm wide, margin crenate to dentate to subentire, petioles to 2.6 cm long .... 13d. *A. corymbosum* f. *albiflorum*
         5. Leaves widely ovate, (3–)4.2–7 cm long, (1.5–)3–4.5 cm wide, margin crenate to less commonly dentate, teeth coarse, petioles shorter .... 13e. *A. corymbosum* f. *euryphyllum*

13a. **Ageratum corymbosum** Zuccag. *ex* Pers. forma **corymbosum.**

Sparganophorus ageratoides Lag., Elench. Hort. Matr. 25. 1815, fide Robinson (1913*b*).
Ageratum coelestinum Sims, Bot. Mag. *t. 1730.* 1815, fide Robinson (1913*b*). (Holotype: loc. cit. *t. 1730.*)
Coelestina coerulea Cass., Dict. 6. Suppl. 8. 1817, fide Robinson (1913*b*).
Coelestina corymbosa (Zuccag.) DC., Prod. 5: 108. 1836, fide Robinson (1913*b*).
Coelestina suffruticosa Sweet, Hort. Brit. 229. 1826, fide Robinson (1913*b*).
Coelestinia lessingiana Klotzsch *ex* Walp., Rep. 2: 545. 1843, fide Robinson (1913*b*).
Coelestinia lessingiana (Klotzsch) Hemsl., Biol. Cent. Amer. Bot. 2: 81. 1881, fide Robinson (1913*b*).
Carelia corymbosa (Zuccag.) Kuntze, Rev. Gen. 1: 325. 1891, fide Robinson (1913*b*).
Ageratum corymbosum Zuccag. forma *album* Robins., Contr. Gray Herb. 42: 475. 1913. (Holotype: MEXICO. Jalisco: Near Huejuquilla, *Rose* 2538 (GH); isotype, US; photograph, MIN.)
Coelestina sclerophylla Wooton & Standl., Contr. U. S. Natl. Herb. 16: 176. 1913. (Holotype: MEXICO. Sonora: Guadalupe Canyon, *Merton 2031* (US).)

Shrubs to 20 dm tall; *leaves* ovate to ovate-lanceolate, 4–7 cm long, (1.5–)2–3.5 cm wide, base obtuse, apex acute, margin revolute, scabrous, crenate to dentate, upper surface shiny to dull green, scabrous, lower surface pale green, sparingly white pilose to scabrous, dotted with yellow to amber glanduliferous atoms; *inflorescences* grouped in flat-topped, congested corymbiform clusters; *involucral bracts* 2-ribbed, narrowly lanceolate, 4.5–6.5 mm long, 0.5–0.8 mm wide, margin entire, green to scarious, apex acute, white pilose and at times dotted with glanduliferous atoms; *corollas* tubular to narrowly funnelform, 2.5–3.5 mm long, tube and narrow throat pale green to white, pilose and/or glandular atomiferous, lobes acute, pilose to glabrous, blue, lavender, mauve to white; *achenes* (1.6–)2–2.6 mm long, dark brown to black, slightly tapered toward inconspicuous white carpopodium; pappus coroniform, 0.25–0.6(–0.7) mm high, margin finely and variously fimbriate to dentate, rarely, if ever, setiferous.

Robinson (1913*b*) described forma *album* to include those plants with white corollas. Corolla color ranges from purples to pale lavenders and to white in what might be termed a color continuum. To select one of these shades and give it taxonomic rank is quite meaningless. Problems also arise due to fading of corollas on herbarium sheets. Thus names alluding to corolla color are placed in synonymy.

Wooton and Standley (1913) described *Coelestina sclerophylla* from Sonora, considering it distinct from *A. corymbosum* f. *corymbosum* because of leaf shape, pubescence, inflorescences, and a northern location. The holotype, *Merton 2031*, is beyond question *A. corymbosum* f. *corymbosum*. As there are no discontinuities in any of the above listed characters between Wooton and Standley's proposed species and *A. corymbosum* f. *corymbosum*, the name is placed in synonymy.

The chromosome number $n = 10$ is reported (Turner, Powell & King, 1962), vouchers *King 2923* and *King 3544*. An apparently unpublished record listed on *King & Soderstrom 4901* is $n = 11$. A tetraploid race, $2n = 40$, is recorded for a Michoacán collection, voucher *King 3644* (Turner, Ellison & King, 1961).

A triploid metaphase configuration varying from 10 groups of trivalents to 10 groups of univalents and 10 bivalents was seen in a preparation made from buds collected by G. B. Ownbey and J. Muggli in Michoacán. The voucher, *Ownbey & Muggli 3948* (MIN), is *A. corymbosum* f. *corymbosum* and gives no indication it might be triploid. A triploid plant would be expected to produce a high percentage of sterile pollen grains and a low percentage of viable ones. Staining the pollen with cotton blue, however, showed 95–100% good staining grains, indicating that the pollen was viable and probably not of triploid parentage. Seeds from these plants (*Ownbey & Muggli 3948*) germinated easily and quickly, also suggesting that no genetic imbalance was present. No chromosome counts from somatic cells of these plants were made, however. Measurements of the gross morphology also does not give an indication that this particular plant is triploid. It seems, then, that the buds collected in the immediate vicinity of the voucher and used for the chromosome counts came from a triploid plant, but that the voucher is from different plants which are diploid. A mixed population of diploid and tetraploid plants at this locality is suspected.

Ageratum corymbosum f. *corymbosum*, a common form of the most common species of *Ageratum* in Mexico, is distinguished by the combination of shrubby habit, heads borne in congested clusters, short petioled, ovate to ovate-lanceolate leaves with sparingly pilose upper surfaces and scabrous lower surfaces.

This forma occurs throughout Mexico with the possible exception of the Yucatan Peninsula. It extends into western Guatemala often in association with *Quercus* and *Pinus* and along roadsides and in grazed land from near sea level to *ca.* 2800 m elevation (Fig. 6). This form is reported from Texas (Gould, 1962), New Mexico and Arizona (Wooton & Standley, 1913; Tidestrom & Kittell, 1941), though I have not seen specimens collected in the United States. Flowers and fruits are present from July through December.

GUATEMALA. 13 miles S of Huehuetenango, *King 3389* (DS, MICH, NY, TEX, UC, US); 1.6 miles E of Chiantla, cytological voucher, *Ownbey & Muggli 3971* (MIN).

MEXICO. AGUASCALIENTES: 20.4 miles W of Aguascalientes, *Johnson & Hofstetter 1964* (MIN). CHIHUAHUA: Chihuahua, *LeSueur 70* (F, GH, MO, TEX); 35 km S of Ciudad Chihuahua, *Weber & Charette 11638* (MICH, WIS). COAHUILA: San Lorenzo Canyon, 6 miles SE of Saltillo, *Palmer 387* (F, GH, MO, NY, US). DISTRITO FEDERAL: Pedregal, *Balls B5592* (BM, GH, K, UC, US); Lomas, *Lyonnet 196* (BM, GH, K, MO, NY, US). DURANGO:

20 miles W of Durango, *Johnson & Johnson 1768* (MIN). GUANAJUATO: Sierra de Guanajuato, *Guillemin-Tarayre 1872* (GH). GUERRERO: 25 km WSW de Camotla, *Rzedowski 18110* (MICH). HIDALGO: El Chico, near Pachuca, *Purpus 1565* (F, GH, UC). JALISCO: Cerro de Talcozagua, 3–2 km E of Tapalpa, *Iltis et al. 733* (MICH, TEX, WIS); 4.5 miles E of Tizapan on S shore of Laguna de Chapala, *Johnson & Hofstetter 1981* (MIN); Guadalajara, *Palmer 290* (MICH, MO, NY, US). MEXICO: La Junta, Santo Tomas, *Matuda 29363* (NY, US). MICHOACAN: E of Zapota, *Arsène 2678* (BM, GH, K, MO, NY, US); 21 miles E of Jiquilpan, cytological voucher, *King 3644* (DS, MICH, NY, TEX, UC, US); *ca.* 22 km S of Uruapan, cytological voucher, *King & Soderstrom 4901* (MICH, TEX, UC, US); 3.6 miles E of Morelia, cytological voucher, *Ownbey & Muggli 3948* (MIN). MORELOS: Hillsides above Cuernevaca, *Pringle 6234* (BM, F, GH, MICH, MIN, MSC, MO, NY, P, UC, US). NAYARIT: On road to San Blas, 1.6 miles from junction with Mexico 15, *Johnson & Hofstetter 1977* (MIN). OAXACA: 15 miles NE of Huajuapan de Leon, cytological voucher, *King 3544* (MICH, TEX). PUEBLA: Cerro Chiquihuite, near Totomehuacan, *Arsène 2171* (GH, MO, US); 4 miles W of Izucar de Matamoros, cytological voucher, *King 2923* (TEX). QUERETARO: 2 miles E of Querétaro, *Johnson & Ownbey 1934* (MIN). SAN LUIS POTOSI: 33 km E of San Luis Potosí, *Roe et al. 114* (MIN). SINALOA: Culiacan, *Brandegee s.n.* (GH). SONORA: Guadalupe Canyon, *Merton 2031* (US); 18 miles SE of Magdalena, *Wiggins 7149* (DS, MO, TEX, US). VERA CRUZ: 5.5 miles W of Xalapa, *Johnson & Hofstetter 2005* (MIN).

13b. **Ageratum corymbosum** Zuccag. forma **salicifolium** (Hemsl.) M. F. Johnson, stat. et comb. nov.

Ageratum salicifolium Hemsl., Biol. Contr. Amer. Bot. 2: 83. 1881. (Holotype: MEXICO. Nayarit: Between San Blas and Tepic, *Sinclair s.n.* (K), photographs, GH, MICH.)
Ageratum strictum Hemsl., Biol. Centr. Amer. Bot. 2: 83. 1881.
Coelestina corymbosa Benth., Bot. Sulph. 111. 1844.
Carelia salicifolia (Hemsl.) Kuntze, Rev. Gen. 1: 325. 1891.
Carelia stricta (Hemsl.) Kuntze, Rev. Gen. 1: 325. 1891.
Ageratum salicifolium Hemsl. subsp. *annectens* Blake, Contr. U. S. Natl. Herb. 22: 588. 1924. (Holotype: MEXICO. Morelos: Cuernevaca, *Pringle 9045* (US); isotype, MICH.)

Shrubs 4.5–15 dm tall; *leaves* narrowly lanceolate, 3.3–10 cm long, 0.5–1.8(–2.4) cm wide, firm, base cuneate, apex acute, margin somewhat revolute, entire to remotely crenate-dentate, scabrous, upper surface bright and shiny green to dark green, scabrous to sparingly white pilose, lower surface paler green, sparingly white pilose to more or less abundantly so at least over the 3 rather inconspicuous primary veins and reticulate secondary venation and dotted with amber to yellow glanduliferous atoms; in characters of involucre, corollas, achenes and pappus very similar to forma *corymbosum*.

This narrow-leaved form has been unquestionably accepted as a distinct species since its description by Hemsley (1881). Robinson (1913*b*) suggested that it may be a variety of *Ageratum corymbosum* but retained it in the rank of species. From observation in the field, especially in the type locality, I have seen forma *salicifolium* in the immediate vicinity of forma *corymbosum*. Except for the more narrow leaves of the former, the plants appear to be identical. This conspicuous similarity is noted too from herbarium specimens. Similarities are noted also in chromosome numbers, distribution and habitat, blooming time, stem and leaf pubescence, and size and shape of corollas, pappus and achenes. After studying a number of specimens, it became very evident that narrow leaves alone are not an acceptable means of distinguishing this species; variation in leaf dimensions in this species is continuous with forma *salicifolium* at the narrow extreme and forma *albiflorum* at the opposite extreme (Fig. 4). As there is no readily discernable discontinuity in morphology between the narrow-leaved pop-

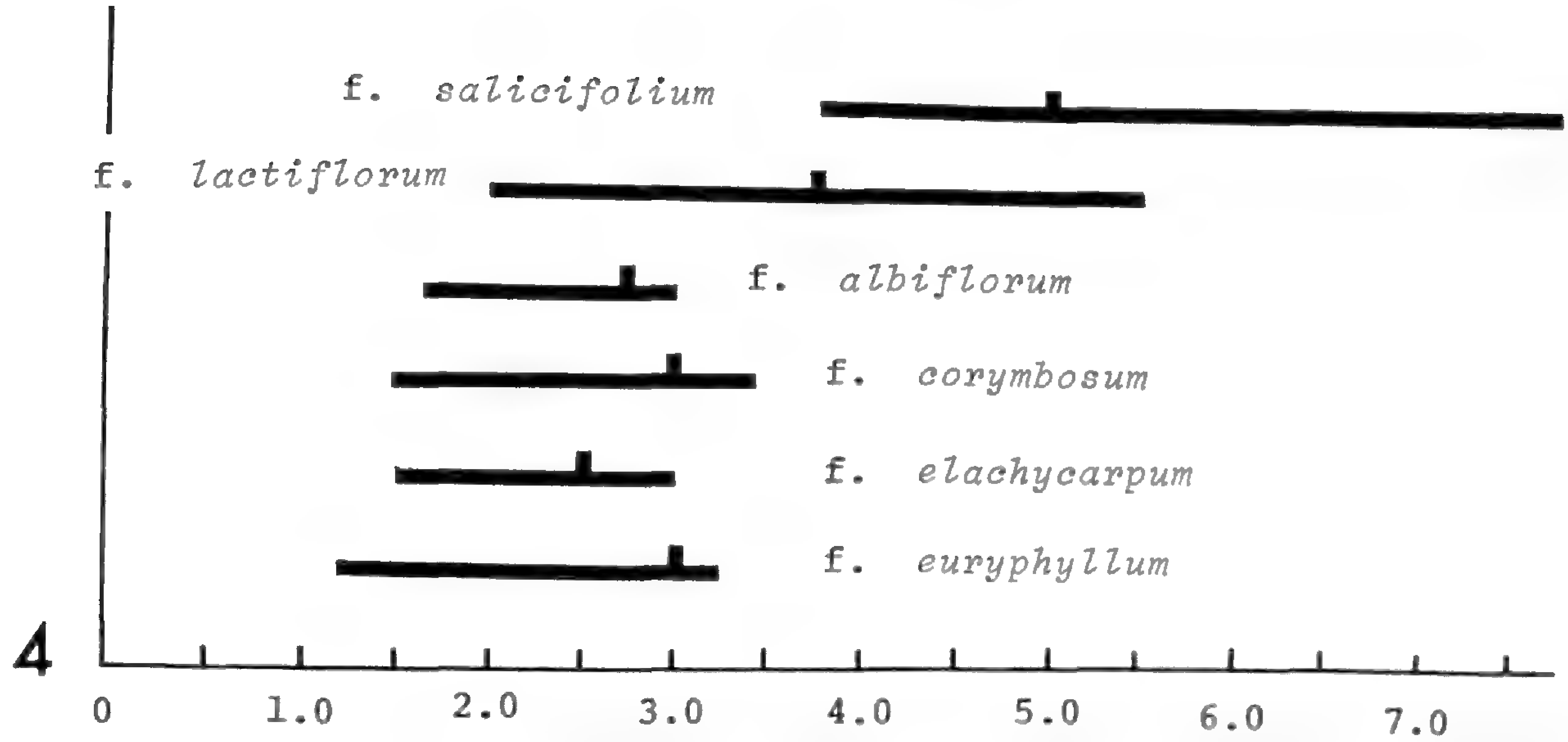


FIGURE 4. Variation in leaf length/leaf width ratio in formae of *Ageratum corymbosum* Zuccag. The median is indicated.

ulations and the remainder of the species, it is logical to consider *A. salicifolium* Hemsl. a forma of *A. corymbosum* Zuccag.

Blake (1924) saw an unusual specimen (*Pringle 9045*) on which he noted a single head bearing a very few receptacle paleae around the outer margin and from this described a new subspecies, implying that this plant provided a link between paleaceous and non-paleaceous species of section *Coelestina*. It is my opinion that Blake placed excessive importance upon the paleaceous nature of the receptacle which is present rarely and sporadically among other formae of this species as well.

Blake (1924) stated that the plant bearing the same collection number at the Gray Herbarium lacks any visible traces of receptacle paleae. I have observed this to be true on the same number at Michigan. Thus it is obvious that paleae

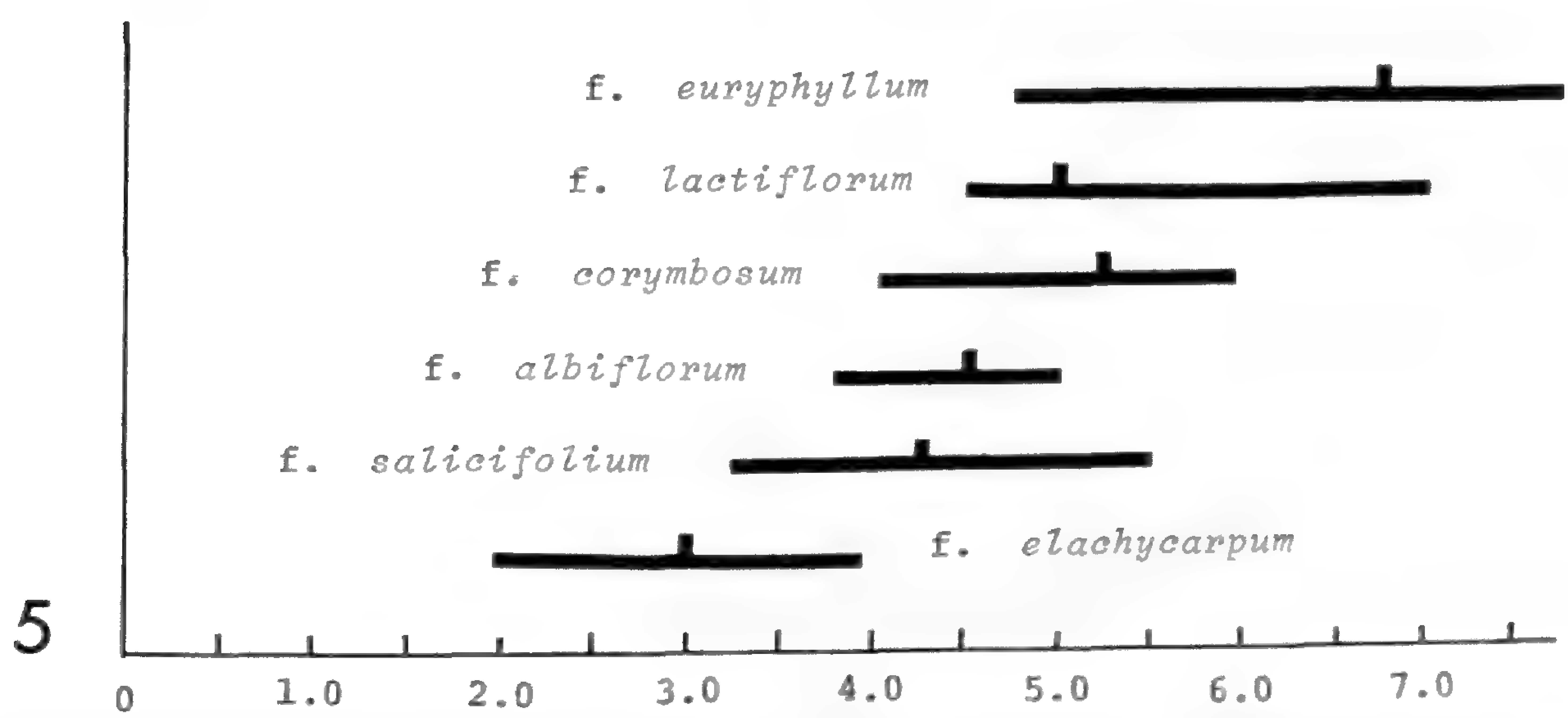
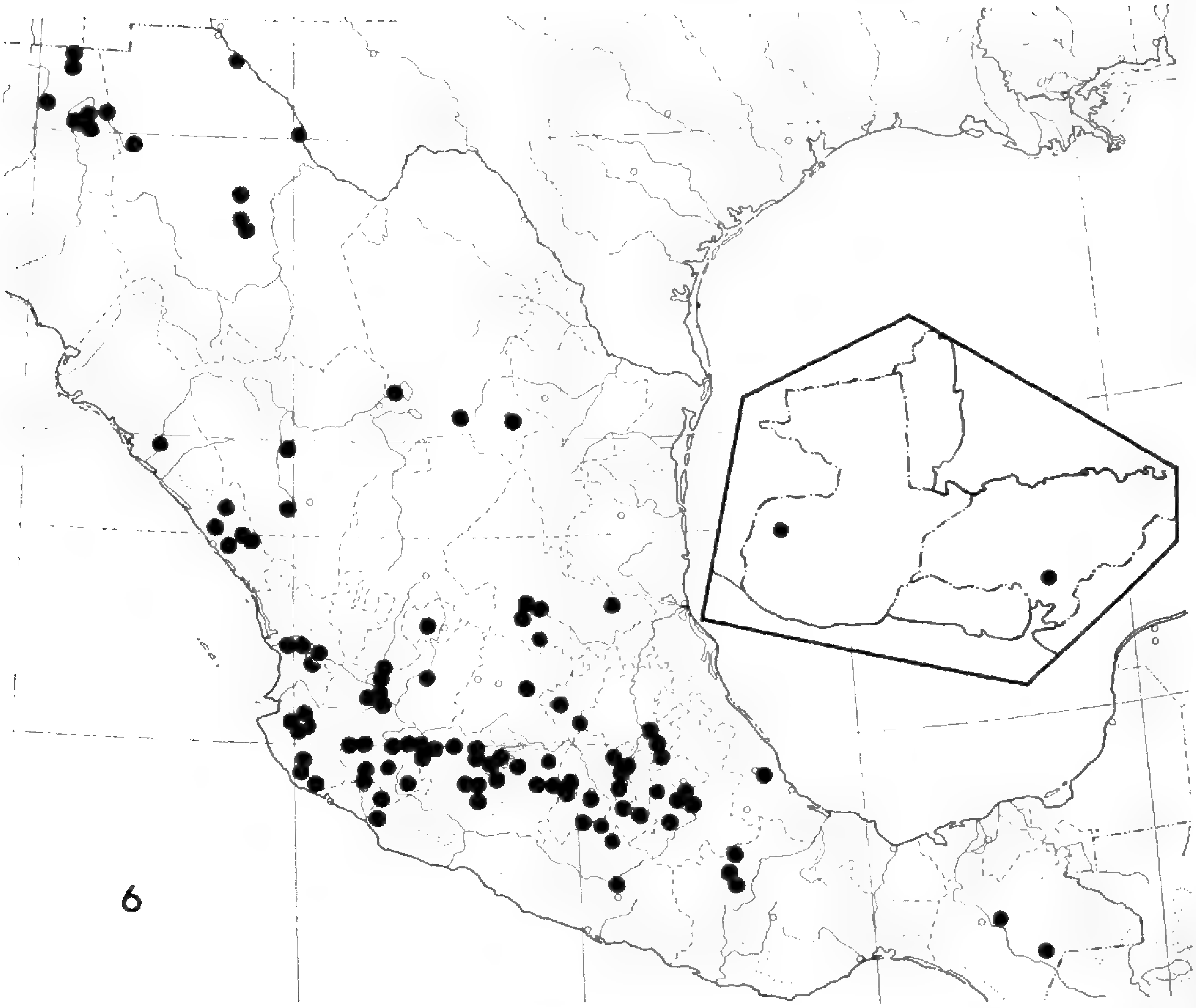


FIGURE 5. Variation in length of involucral bracts in formae of *Ageratum corymbosum* Zuccag. Length is expressed in mm, and the median is indicated.



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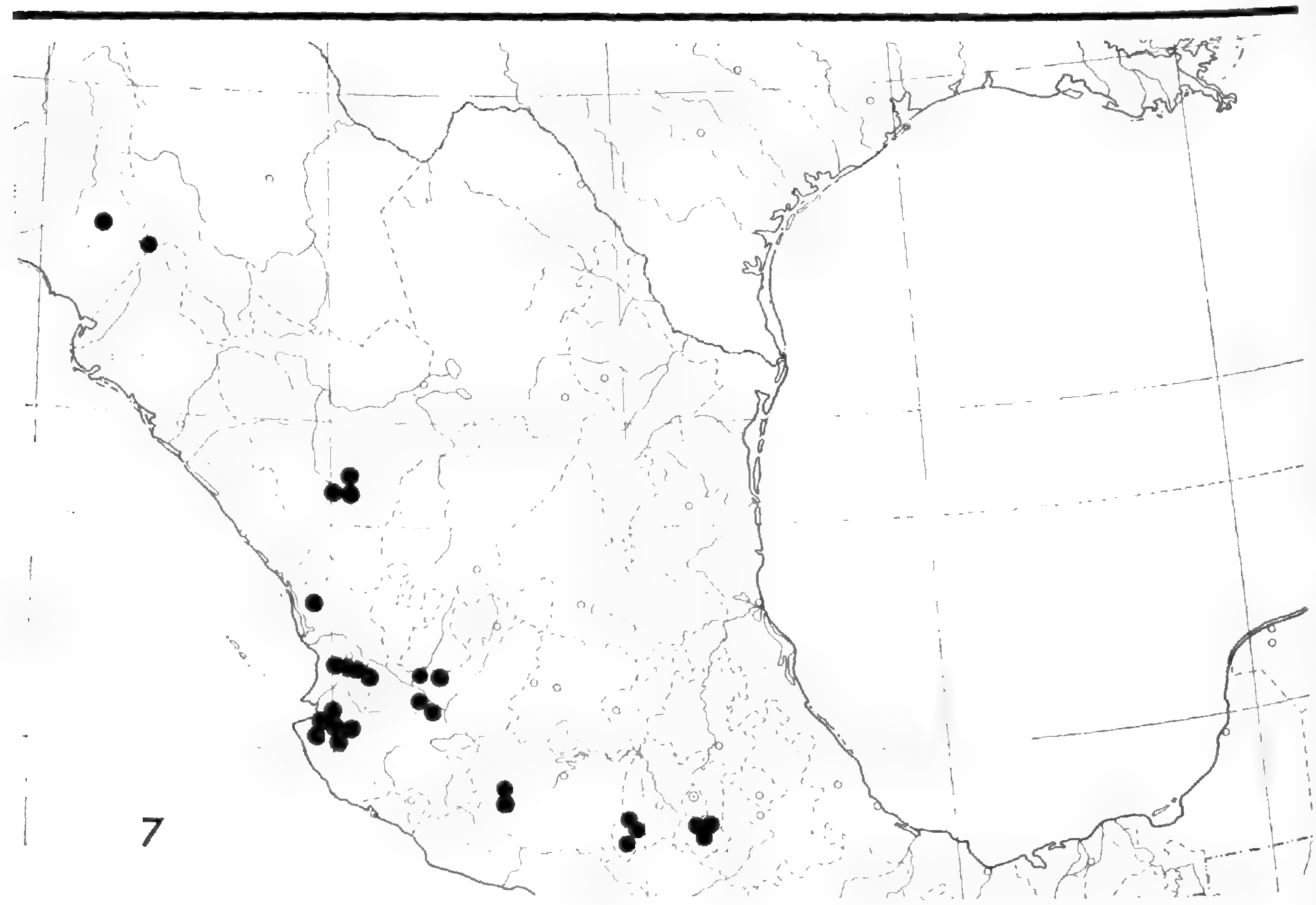

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are rare in forma *salicifolium* as paleae are not present in any other specimen of this forma studied. It is quite unnecessary to describe such abnormalities as formae or subspecies; thus *Ageratum salicifolium* Hemsl. subsp. *annectens* Blake is placed in synonymy.

Ageratum corymbosum f. *salicifolium* most closely resembles *A. corymbosum* f. *lactiflorum* in general leaf shape and in the bright green upper leaf surface sometimes encountered in the former. However, the long, narrow leaves, the subentire margins, and the inconspicuous lower surface venation distinguish forma *salicifolium* from forma *lactiflorum* and all other taxa as well.

This forma is quite common in northwest and west-central Mexico from southern Sonora to Michoacán in association with *Pinus* and *Quercus* and in moist ravines as well as dryer habitats and pastures from *ca.* 300–2000 m elevation (Fig. 7). Flowers are present from August through November; fruits from August through January.

MEXICO. DURANGO: *ca.* 6 miles N of Durango, cytological voucher, *King 3750* (DS, MICH, NY, TEX, UC, US). JALISCO: Sierra de San Estabán, *Barnes & Land 198* (F, K, US); *sine loc.*, *Ferris 5860* (A, DS, F, US); Sierra de la Campana, along road to Mascota, *McVaugh 13686* (K, MICH, US); Guadalajara, *Palmer 290* (BM, GH, MICH, MO, NY, US); 6 miles W of Guadalajara, *Powell & Edmondson 866* (F, MICH, TEX). MEXICO: Vigas, Temascaltepec, *Hinton 1815* (BM, F, GH, MO, NY, US). MICHOACAN: *ca.* 13 miles S of Uruapan, *Cronquist 9749* (MICH, MSC, NY). MORELOS: Cuernevaca, *Pringle 9045* (GH, MICH, US). NAYARIT: 12 miles SE of Acaponeta, *Cronquist 9593* (MICH, MO, NY, TEX, US); Cerro de San Juan, SW of Tepíc, *Pennell 19991* (NY, US). SINALOA: 4 leagues N of La Noria, *Mexia 386* (MO, UC). SONORA: Puerot de los Asseradores, *White 3222* (MICH).

13c. **Ageratum corymbosum** Zuccag. forma **lactiflorum** (Robins.) M. F. Johnson, comb. nov.

Ageratum corymbosum Zuccag. var. *jaliscense* Robins. forma *lactiflorum* Robins., Contr. Gray Herb. 42: 476. 1913. (Holotype: MEXICO. Jalisco: Tequila, *Palmer 351* (GH); isotypes, BM, MO, NY, US; photograph, MIN.)

Ageratum corymbosum Zuccag. var. *jaliscense* Robins., Contr. Gray Herb. 42: 476. 1913. (Holotype: MEXICO. Jalisco: Río Blanco, *Palmer 715* (GH, not seen); isotype, US.)

Shrubs 5–10 dm tall; *stems* rarely rhizomatous; *leaves* elliptic-lanceolate, 4.2–8.5 cm long, 1.5–3.3 cm wide, base cuneate, entire, apex acute, margin revolute, scabrous, coarsely and conspicuously crenate-dentate, teeth at times becoming large and lobe-like, especially toward base, upper surface bright, shiny green to dull green, sparingly scabrous to pilose, venation reticulate, white, generally conspicuous, lower surface dull, pale green, short white pilose and dotted with yellow glanduliferous atoms, reticulate venation white, conspicuous; *involucral bracts* (4.5–)5–7 mm long, outer ones 0.65–0.8 mm wide, white pilose; characters of achene, corolla, stem coloration, and tomentum as in f. *corymbosum*, pappus also nearly identical except for an occasional seta.

The distinguishing feature of forma *lactiflorum* is the leaves as described above. At the narrow extreme, they resemble leaves of f. *salicifolium* and at the wider extreme are similar to f. *euryphyllum*. *Ageratum corymbosum* f. *lactiflorum*

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FIGURES 6–7. The distribution of *Ageratum corymbosum* in Mexico and Central America. — 6. Forma *corymbosum*. — 7. forma *salicifolium*. (Base maps copyright University of Chicago.)

is separated from f. *euryphyllum*, however, by the brighter green, narrow elliptic-lanceolate leaves with conspicuous reticulate venation and short pilose lower surfaces.

Ageratum corymbosum f. *lactiflorum* occurs in west central Mexico in rocky soil and often in association with *Quercus* from *ca.* 500–2500 m elevation (Fig. 8). Flowers and fruits are present from July through November.

MEXICO. AGUASCALIENTES: Near city of Aguascalientes, *Rose & Painter 7749* (GH, NY, US). CHIHUAHUA: Rocky hills near Chihuahua, *Pringle 669* (BM, F, GH, MICH, NY, P, UC, US). DURANGO: Tejamen, *Palmer 486* (F, GH, MO, UC); Río Blanco, *Palmer 715* (US); La Purísima, *Shreve 9188* (GH, MICH, UC). JALISCO: Hacienda San Marcos, E of Volcano Colima, *Goldsmith 81* (F, GH, MO, UC, US); Tequila, *Palmer 351* (BM, GH, MO, NY, US). MICHOACAN: Vicinity of Morelia, W of Zapota, *Arsène 2695* (BM, GH, K, MO, NY). SAN LUIS POTOSI: *Sine loc.*, *Parry & Palmer 317* (F, GH, NY, P, US).

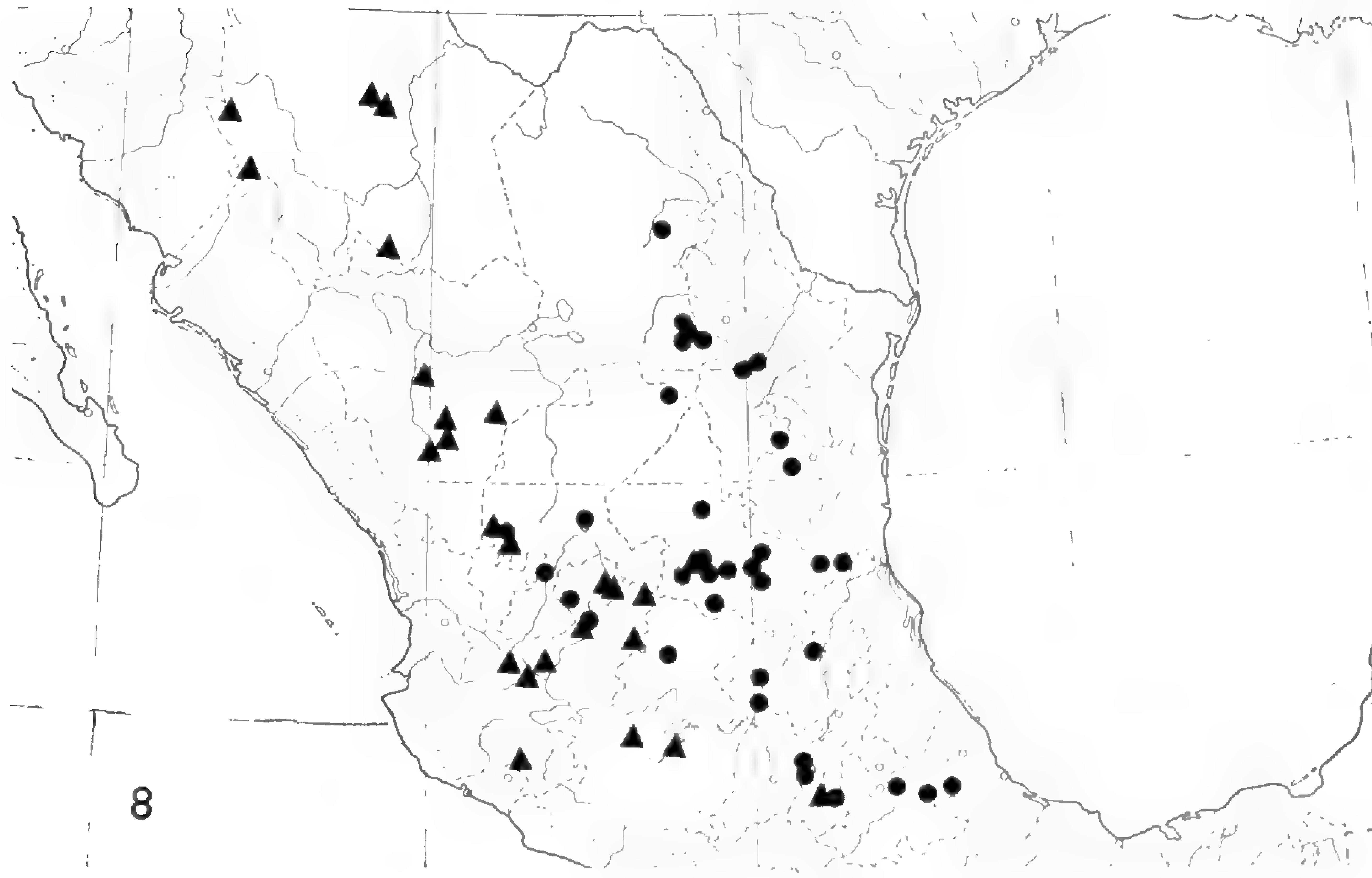
13d. **Ageratum corymbosum** Zuccag. f. **albiflorum** (Robins.) M. F. Johnson, comb. nov.

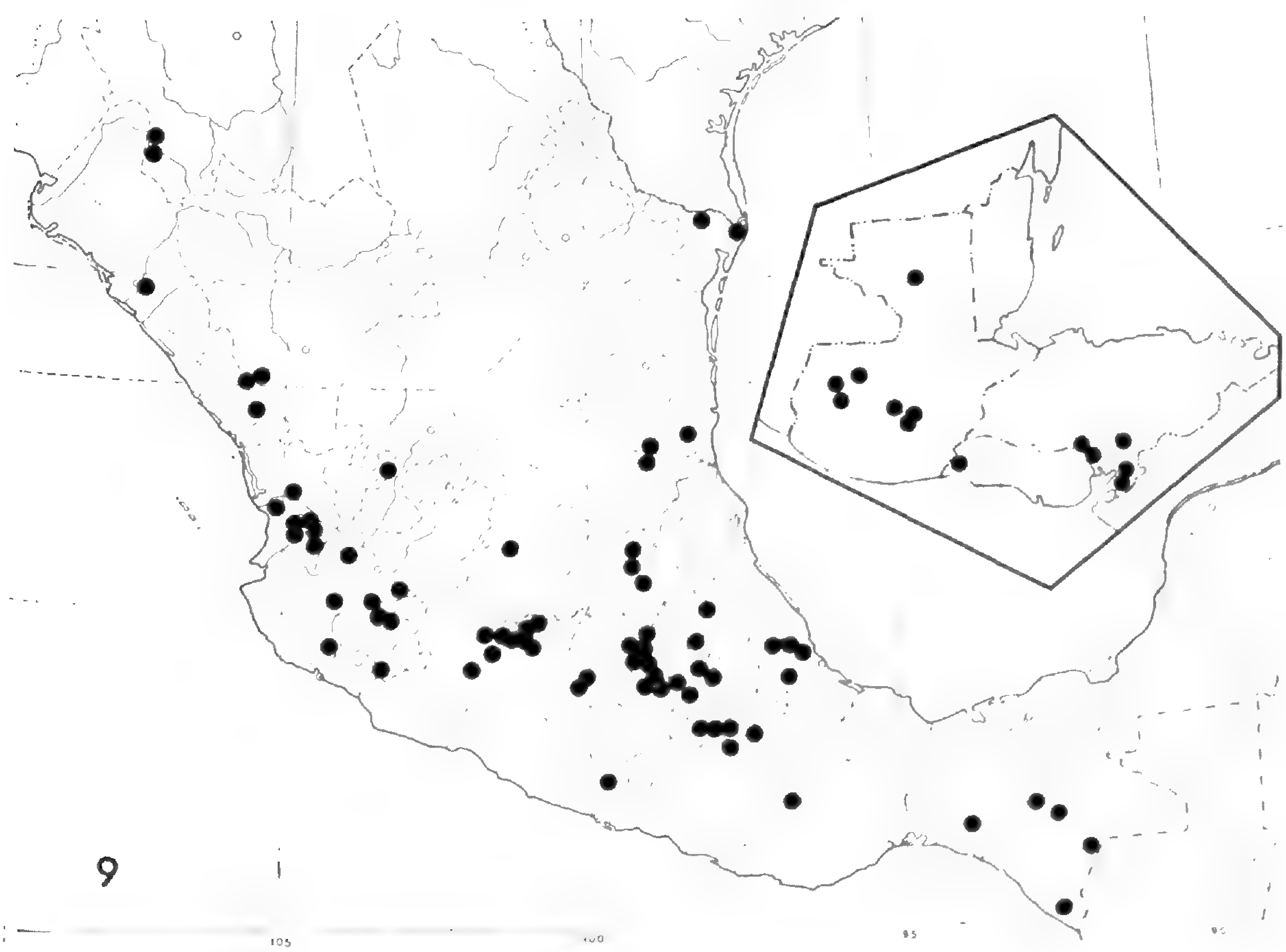
Ageratum corymbosum Zuccag. var. *latifolium* (DC.) Robins. forma *albiflorum* Robins., Contr. Gray Herb. 42: 476. 1913. (Holotype: MEXICO. Morelos: Hills near Yautepec, *Pringle 9842* (GH); isotypes, F, NY, MO, US; photograph, MIN.)
Coelestina ageratoides HBK, Nov. Gen. Sp. Pl. 4: 151. 1820.
Coelestina ageratoides HBK var. *latifolia* DC., Prod. 5: 108. 1836.
Ageratum corymbosum Zuccag. var. *longipetiolatum* Robins., Contr. Gray Herb. 42: 477. 1913. (Holotype: MEXICO. Chihuahua: Southwestern Chihuahua, *Palmer 110* (GH); isotypes, K, MICH, NY, US.)
Ageratum corymbosum Zuccag. var. *latifolium* (DC.) Robins., Contr. Gray Herb. 42: 476. 1913. (Holotype: MEXICO. Without collector and location (DC-C, not seen); photograph, MIN.)

Shrubs 5–15 dm tall; *stems* densely white pilose to subglabrous; *leaves* ovate to triangular-lanceolate, 4.5–8(–11.3) cm long, 2.3–4.5(–5.9) cm wide, somewhat thickened, base truncate to obtuse, apex acute to broadly so, margin crenate to dentate to subentire, slightly scabrous-pilose to pilose, rarely glandular-atomiferous, lower surface dull, pale green, densely white pilose and dotted with yellow to amber glanduliferous atoms, the 3–5 principal veins and secondary venation white, densely pilose and glandular dotted; *petioles* 0.5–2.6 cm long, pilose-scabrous, adaxially channeled; characters of inflorescence, involucres, corollas, achenes, and pappus as in f. *corymbosum*.

Robinson (1913*b*) separated his var. *longipetiolatum* and var. *latifolium* f. *albiflorum* using lanceolate-triangular leaves borne on petioles 3 cm or more long in *longipetiolatum versus* ovate leaves on shorter petioles in *latifolium* forma *albiflorum*. After studying a number of specimens, it became evident that these varieties merged readily as both leaf shape and petiole length are quite variable. The consistent and characteristic feature is the softly pubescent under surface of the leaves which was shared by both varieties as Robinson interpreted them. Distinctions between these varieties break down and the name forma *albiflorum* is applied.

Ageratum corymbosum f. *albiflorum* is distinguished among the formae by the presence of ovate to triangular-lanceolate leaves with dense pubescence on the under side which gives them a soft, downy feeling. There is a tendency toward larger leaves than in other formae, though this is by no means as con-





Figures 8–9. The distribution of *Ageratum corymbosum* in Mexico and Central America. — Triangle, forma *lactiflorum*; solid circle, forma *euryphyllum*. — 9. Forma *albiflorum*. (Base maps copyright University of Chicago.)

sistent as the pubescent lower leaf surfaces. *Ageratum corymbosum* f. *euryphyllum* also possesses leaves which are pubescent beneath but which are widely ovate with coarsely crenate margins.

This forma is, at times, confused with *Ageratum rugosum*, especially in Central America. However, these taxa are readily distinguished by the dark green to brown leaves in *A. rugosum* as opposed to the light green leaves in *A. corymbosum* f. *albiflorum*.

The chromosome number $n = 10$ is reported in the literature (Turner, Powell & King, 1962; Powell & Turner, 1963) and verified in this study.

This forma is widespread in Mexico, Guatemala, Honduras, and El Salvador in association with *Quercus* and *Pinus* as well as along dry roadsides and in moist ditches from *ca.* 100–2500 m elevation (Fig. 9). Flowers are present from June through November; fruits from July through November.

EL SALVADOR. Vicinity of Ahuachapan, *Standley & Padilla 2908* (F).

GUATEMALA. Chinautla, *Holway 482* (GH); SE of Huehuetenango, *Steyermark 48173* (F).

HONDURAS. Region of El Jicarito, *Standley 27458* (BM, F, GH, US).

MEXICO. CHIAPAS: *Ca.* 23 miles SE of Comitan, cytological voucher, *King 3045* (TEX). CHIHUAHUA: 25 miles S of Batopilas, Hacienda San José, *Palmer 31* (BM, GH, K, MICH, MO, NY, US); 1 mile from Batepilas, Hacienda San Miguel, *Palmer 110* (GH, K, NY). DISTRITO FEDERAL: Pedregal, Tlalpam, *Seler 4124* (GH). DURANGO: 1.8 miles W of Revolcaderos, cytological voucher, *Ownbey & Muggli 2927* (MIN). GUANAJUATO: *Sine loc.*, *Duges 427* (GH). GUERRERO: 28 km W of Chilpancingo, *Sharp 441503* (NY). HIDALGO: Ixmiquilpan, *Purpus s.n.* (UC). JALISCO: Huejotitan, *Diguet s.n.* (MICH, P); 45 miles W of Sahuayo, near W end of Lake Chapala, *Powell & Edmondson 841* (F, MICH, TEX). MEXICO: Temascaltepec, *Hinton 2066* (BM, F, MICH, MO, NY, US). MICHOACAN: Vicinity of Morelia, *Arsène 3227* (GH, MO, US); Apatzingan, *Hinton 15171* (K, MICH, NY, P, UC, US). MORELOS: Hills near Yautepec, *Pringle 9842* (F, GH, NY); mountain canyon above Cuernevaca, *Pringle 9843* (F, GH, MO, NY, US). NAYARIT: 4 miles N of Compostela, *McVaugh & Koelz 587* (MICH). OAXACA: Monte Alban, *Pringle 6267* (GH). PUEBLA: Near Río Otlati, *Weaver 954* (GH, TEX, US). SAN LUIS POTOSI: 11.8 miles N of Ciudad Valles, *Johnson & Hofstetter 2010* (MIN). SINALOA: Baromena, *Gentry 6113* (DS, GH, MICH, MO, NY); Lodiego, *Palmer 1587* (F, MICH, NY, UC, US). SONORA: Conejos, *Gentry 1112* (F). TAMAULIPAS: La Vegonia, *Bartlett 10126* (MICH, US). TLAXCALA: Vicinity of San Vernabe Amaxac, *Hernandes 382* (MICH). VERA CRUZ: 5 miles SE of Xalapa, *Barkley et al. 2564* (TEX).

13e. **Ageratum corymbosum** Zuccag. forma **euryphyllum** (Robins.) M. F. Johnson, stat. et comb. nov.

Ageratum corymbosum Zuccag. var. *euryphyllum* Robins., Contr. Gray Herb. 42: 476. 1913. (Holotype: MEXICO. San Luis Potosí: Region of San Luis Potosí, *Parry & Palmer 315* (GH); isotypes, MO, NY, US.)

Ageratum corymbosum Zuccag. var. *subsetiferum* Robins., Contr. Gray Herb. 42: 477. 1913. (Holotype: MEXICO. Zacatecas: Concepción del Oro, *Palmer 382* (GH); isotypes, NY, US; photograph, MIN.)

Shrubs 5–10 dm tall; *leaves* widely ovate, (3–)4.2–7 cm long, (1.5–)3–4.5 cm wide, base obtuse to truncate, apex broadly acute, margin slightly revolute, scabrous, coarsely crenate to less commonly dentate, teeth large, upper surface dull, dark green, rarely bright and shiny green, finely pilose to scabrous, lower surface paler green, rather densely white pilose and dotted with yellow glandular atoms, the 3–5 primary veins and reticulate secondary venation in general not conspicuous; *involucral bracts* narrowly lanceolate, (3.5–)5–7 cm long, 0.55–

0.9(–0.15) mm wide, white pilose and at times glandular-atomiferous; *achenes* 2.25–3.25 mm long, dark black; *pappus* 0.3–0.75 mm long, margin shallowly fimbriate, at times with 1 or more setae, then the pappus 1–3 mm long; *corollas* (2.5–)2.75–3.85 mm long, in general glandular dotted and pilose.

Ageratum corymbosum f. *euryphyllum* approaches f. *lactiflorum* but is separated primarily on the basis of leaf length and width; the leaves of f. *euryphyllum* are about twice as long as wide, while those of f. *lactiflorum* are 2–5 times longer than wide. The less conspicuous leaf venation and duller green upper leaf surfaces of f. *euryphyllum* also aid in distinguishing these formae. Forma *euryphyllum* is distinct from f. *albiflorum* on the basis of wider leaves with coarsely crenate margins in the former.

Robinson (1913*b*) described var. *subsetiferum* employing pappus setae and elongated involucral bracts as distinguishing characters. That these characters are not consistently present in combination is immediately evident upon study of specimens. Both taxa (*euryphyllum* and *subsetiferum*) did possess widely ovate leaves with pilose lower surfaces as well as elongate involucral bracts. Pappus setae do not distinguish var. *subsetiferum*, because setae appear sporadically throughout the species. As distinctions between these varieties break down, it is desirable to consider them as one taxon under the more descriptive name, *A. corymbosum* f. *euryphyllum*.

Turner, Beaman & Rock (1961) reported the chromosome number $n = 20$ for *Rock 456*, a specimen with the characters of forma *euryphyllum*. Plastic peels of the lower leaf epidermis from this plant show stomatal guard cells (27–)32–38 μ long. A random sample of the leaf lower epidermis from specimens determined to be forma *euryphyllum* were measured from plastic peels. Though these plants were very similar to the tetraploid in gross morphology, the guard cells were only 15–20 μ long, suggesting that this sample is diploid throughout. Pollen from the tetraploid is 30–32 μ in diameter while pollen from a random sample is 27–34(–36) μ in diameter. As the diameter of pollen from the tetraploid is within the range of pollen size from assumed diploids, this character cannot be used as a means of determining, with certainty, diploid or polyploid populations. The evidence at hand suggests that the polyploid is rare in the population and that it can only questionably be detected by morphology, *e.g.*, long guard cells in the tetraploid plant. It seems best to consider this forma as basically diploid with a very few widely scattered tetraploid individuals, which may be termed cryptic polyploids as they are morphologically very similar to the diploid population.

This forma occurs in northeast, northwest, and central Mexico in association with *Quercus*, on dry rocky slopes and along roadsides from *ca.* 500–2600 m elevation (Fig. 8). Flowers and fruits are present from June through November.

MEXICO. AGUASCALIENTES: Mountains, *Hartweg 142* (BM). COAHUILA: 13 miles S of Arteago, *Kenoyer & Crum 2755* (A, MICH); Saltillo, *Palmer 307* (BM, F, GH, MO, MSC, NY, UC, US). DISTRITO FEDERAL: Entre Guajimalpa y Río Hondo, *Matuda 26177* (NY). GUANAJUATO: Vicinity of Guanajuato, *Kenoyer 1771* (A). HIDALGO: 7.4 miles E of Jacala, *Johnson & Hofstetter 2007* (MIN). JALISCO: Rancho Viejo, *Rzedowski 17574* (MICH). MORELOS: 20 km NE of Cuautla, *Fischer 44* (MICH). NUEVO LEON: Galeana, *Tayler 122* (DS, F, MO, NY, TEX, UC). PUEBLO: Acatzinco, *Arsène 3604* (US). QUERETARO: Near San Juan del Río, *Rose et al. 9631* (BM, GH, NY). SAN LUIS POTOSI: Alvarez, *Palmer 101*

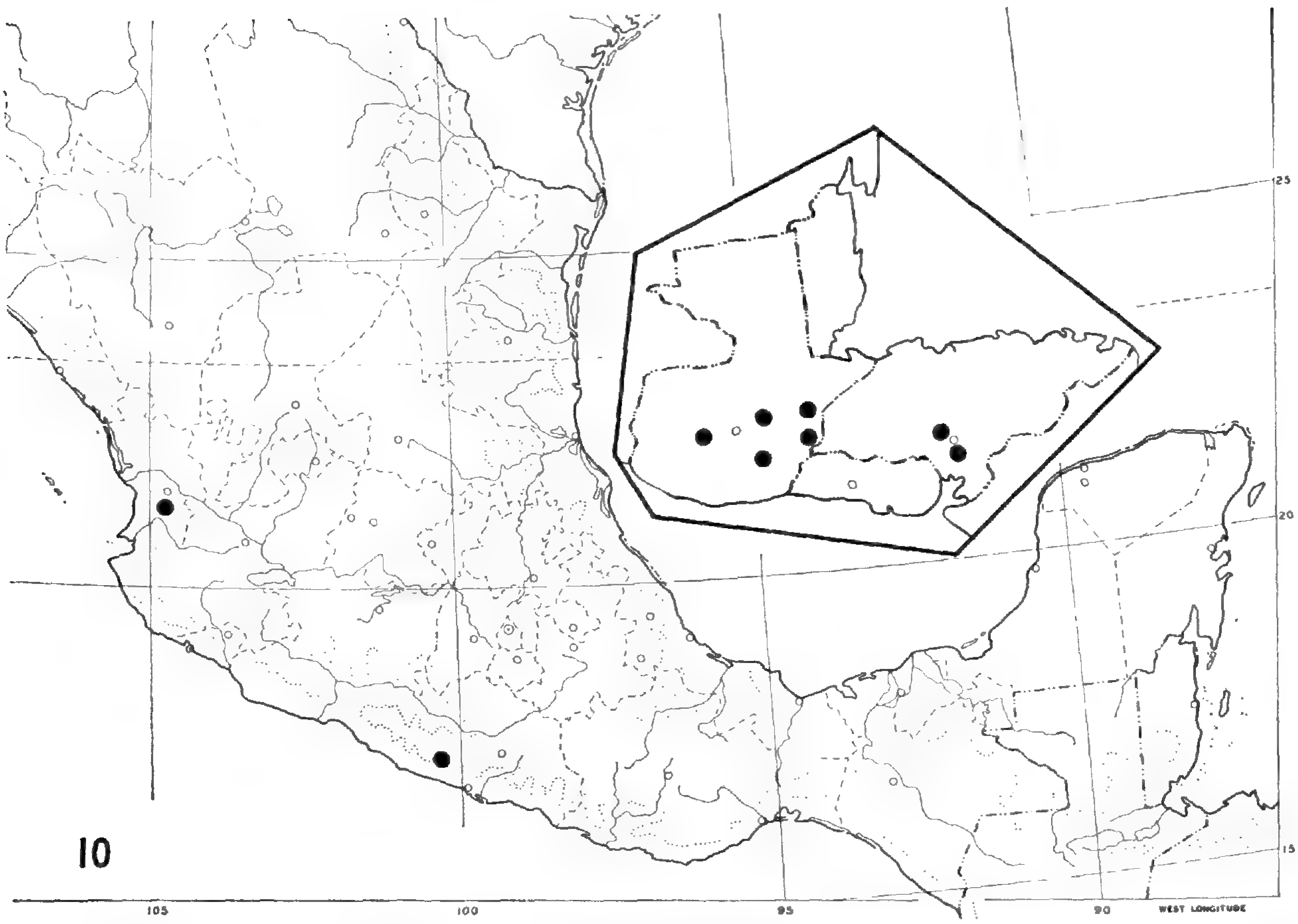


FIGURE 10. The distribution of *Ageratum corymbosum* forma *elachycarpum* in Mexico and Central America. (Base map copyright University of Chicago.)

(BM, F, GH, MSC, MO, NY, UC, US); region of San Luis Potosí, *Parry & Palmer 315* (GH, MO, NY, US), *Parry & Palmer 318* (BM, F, GH, MO, NY, US); La Capilla, cytological voucher, *Rock M-456* (TEX). TAMAULIPAS: 3 km W of Miquihauna, *Stanford et al. 643* (DS, GH, MO, NY). ZACATECAS: S slope of La Bufa, Zacatecas, *Dressler 186* (GH, MO); Concepción del Oro, *Palmer 382* (GH, NY, US).

13f. **Ageratum corymbosum** Zuccag. forma **elachycarpum** (Robins.) M. F. Johnson, stat. et comb. nov.

Ageratum elachycarpum Robins., Contr. Gray Herb. 42: 477. 1913. (Holotype: GUATEMALA. Dept. Santa Rosa: Santa Rosa, *Heyde & Lux 4228* (GH, not seen); isotypes, F, K, US.)

Shrubs to 20 dm tall; *leaves* ovate to lanceolate, *ca.* 5–8(–11) cm long, 2.2–5.5 cm wide, thin to more or less firm, base obtuse to truncate, apex acute margin crenate to dentate, somewhat revolute, scabrous, upper surface dull, dark green, scabrous, lower surface pale green, white pilose, at times densely so, conspicuously dotted with yellow to amber glandular atoms to subglabrous, the 3 primary veins prominent, secondary venation reticulate; *petioles* 0.5–2.5(–5) cm long, pilose-puberulous to scabrous; *involucral bracts* lanceolate, (2.05–)2.4–3.5(–4) mm high, an outer one 0.55–0.65(–0.95) mm wide, pale green, white pilose at times with glandular atoms, prominently 2-ribbed basally, margin entire, herbaceous to scarious, apex acute; *corollas* narrowly funnelform, (1.75–)2–2.35 mm long, tube and throat white, short white pilose and sparingly dotted with yellow glandular atoms, lobes blue to lavender, acute, sparingly pilose to glabrous; *achenes* 1.2–

1.65(–1.75) mm long, black; *pappus* 0.25–0.35 mm long, margin entire to shallowly lobed.

The characters listed in the above key, namely, achenes and involucral bracts shorter than those found in the remainder of the species, prompted Robinson (1913*b*) to describe this taxon as a species separate from *A. corymbosum*. It is my opinion, however, that the overall features of the plant as well as similar habitat, tomentum, and size and shape of pappus and corollas indicate a very close relationship to *A. corymbosum*. The short bracts and achenes are merely one end of a continuum which leads from this extreme to the opposite found in forma *euryphyllum* and forma *lactiflorum* (Fig. 5). As no real discontinuity exists between forma *elachycarpum* and the other formae of this species, it is my opinion that these plants with shorter achenes and bracts should be considered a forma, not a separate species.

In general, this forma grows to the south of the other formae and in the area where the similar *A. rugosum* occurs. Though these taxa may be confused by collectors, the short achenes, involucral bracts, and leaves as well as less dense pubescence on the lower leaf surfaces and involucral bracts set f. *elachycarpum* apart from *A. rugosum*.

Ageratum corymbosum f. *elachycarpum* occurs in Guatemala and Honduras with a disjunction to Guerrero and Nayarit in Mexico, in association with *Quercus* from *ca.* 500–1000 m elevation (Fig. 10). Flowers are present from July through January; fruits from August to January.

GUATEMALA. Santa Rosa, *Heyde & Lux 4228* (F, K, US); near Jalapa, *Kellerman 7969* (NY); Barranca del Incarnación, *Skinner s.n.* (K); between Chimaltenango and San Martin Jilotepeque, *Standley 64432* (F, GH); lower slopes of Sierra de las Minas, *Steyermark 29529* (F, GH); vicinity of Montana Cebollas, *Steyermark 31296* (F).

HONDURAS. Cerrode Hule, 20 km S of Tegucigalpa, *Molina 18462* (F); between Los Laureles and Las Tapías, NW of Tegucigalpa, *Molina 18577* (F).

MEXICO. GUERRERO: Montes de Oca, *Hinton 10596* (GH, NY, US); Vallecito, *Langlasse 310* (GH, K, US). NAYARIT: 9 miles N of Compostela, *McVaugh & Koelz 526* (MICH).

14. **Ageratum rugosum** Coult., Bot. Gaz. 20: 42. 1895.

Holotype: GUATEMALA. Dept. Santa Rosa: Santa Rosa, *Heyde & Lux 4243* (US); photograph, F; tracing and small fragment, GH.

Shrubby *perennial* to 24 dm tall; *roots* fibrous, arising adventitiously from perennial stem base; *stem* erect, branched, reddish when young, to gray, white to tawny puberulous-tomentose throughout, most conspicuously on younger parts, also with scattered amber colored atomiferous glands; *leaves* opposite, rarely alternate above, petioled, ovate, 4–8.5(–12) cm long, 2.4–4.5(–6.5) cm wide, base obtuse to rarely truncate, apex acute, margin crenate to very obscurely so, upper surface conspicuously dark green to brownish, smooth or less commonly rugulose, pilose to scabrous throughout, puberulous over the 3 conspicuous veins, lower surface paler green, abundantly white tomentose at least over the 3 prominent primary veins and secondary reticulate veins, with amber or yellow atomiferous glands or eglandular; *petioles ca.* 0.3–2.5(–3) cm long, abundantly puberulent and tomentose; *inflorescences* terminal, the 3 to *ca.* 20 heads grouped in corymbose clusters; *peduncles* coarse, bracteolate, densely brown to white puberulent and

TABLE 4. A comparison of *Ageratum rugosum* and *A. tomentosum* sens. lat.

Character	*A. rugosum*	*A. tomentosum* s.l.
Habit.	Shrubs to 24 dm tall with fibrous roots.	Shrubs to 5 dm tall with woody taproots.
Leaves.	Ovate, 4–8.5(–12) cm long, 2.4–4.5(–6.5) cm wide, upper surface dark green, tomentum beneath dense, variable.	Deltoid to ovate, (1.6–)2–3.5(–4.1) cm long, 1.1–2.7(–3) cm wide, bright green above, tomentum beneath always dense.
Distribution.	Central America, very southern Mexico, Vera Cruz.	East central and southern Mexico.

tomentose, with glandular atoms; *bracteoles* alternate, puberulent and tomentose, *ca.* 0.5 cm long; *involucres* hemispheric, spreading when older, bracts biseriate, firm lanceolate, 2-ribbed, (3.8–)4–5(–5.5) mm long, outer ones (0.5–)0.6–0.95 mm wide, greenish throughout or apically reddish-purple, densely white pilose or the hairs scattered, also with scattered yellow glandular atoms or eglandular, margin entire, apex acute, inner bracts lanceolate to spatulate, less densely pilose; *corollas* tubular to narrowly funnelform, 2.25–2.6(–3.15) mm long, pilose and glandular atomiferous to nearly glabrous, tube pale green to white, throat pale green to lavender, pale violet or light blue, rarely white; *achenes* 5-angled, dark brown to black, 1.5–2(–2.15) mm long, glabrous, tapering toward small carpopodium; *pappus* coroniform, tawny, 0.25–0.5 mm high, margin entire to irregularly dentate, less commonly with 1–5 firm setae, then pappus 1.25–1.5 mm long.

Coulter (1895) placed *Ageratum rugosum* near *A. conyzoides* because of the presence of awned pappus scales in both. Robinson (1913*b*) followed this concept. After studying a considerable number of specimens, it became evident to me that the awned pappus scales are of a very different nature in *A. rugosum* and *A. conyzoides.* The usual pappus of *A. rugosum* is a coroniform cup-like structure which only rarely has 1–5 subulate awns which are invariably fused into the cup-like basal ring. In *A. conyzoides*, on the other hand, the pappus setae are flat, membranous, marginally erose and basally free. This single character suggests that *A. rugosum* is probably more closely allied to the group of species with a similar pappus.

Ageratum rugosum is often identified as *A. corymbosum* or *A. tomentosum.* Though similar in growth habit and general appearance to *A. corymbosum, A. rugosum* is distinguished by the conspicuous dark green, ovate leaves with the densely white tomentose lower surfaces and the generally more pilose involucral bracts. *Ageratum rugosum* also occurs farther south than does the greater part of *A. corymbosum sens. lat. Ageratum rugosum* is distinguished from *A. tomentosum* as summarized in Table 4.

Ageratum rugosum is similar to *A. nelsonii* in leaf shape and size as well as coloration and pubescence of the leaves but is distinguished by the small heads, receptacle paleae, and the shorter pappus of the latter.

Turner, Ellison & King (1961) published the chromosome number $n = 20$ for

FIGURE 11. The distribution of *Ageratum rugosum* in Mexico and Central America. (Base map copyright University of Chicago.)

Ageratum corymbosum, voucher *King 3291*. I find this specimen to be *A. rugosum*, and the tetraploid number should refer to this taxon.

This species occurs from southern Chiapas to Panama (there is a single collection from central Vera Cruz) on rocky and/or brushy slopes, in open fields, pine and oak forests and often in moist conditions, rarely above 2800 m elevation (Fig. 11). It flowers throughout the year, but most commonly from October through May.

BRITISH HONDURAS. Pine Ridge, Butcher Burn, *Bartlett 11396* (F, GH, MICH, MO, US); All Pines, *Schipp 738* (A, BM, F, GH, K, MICH, MO, NY, UC).

COSTA RICA. La Palma de San Ramón, *Brenes 5804* (F).

EL SALVADOR. Vicinity of San Marcos, *Standley 22777* (GH, NY, US).

GUATEMALA. La Libertad, *Aguilar 15* (A, GH, MICH, MO); Santa Rosa, *Heyde & Lux 4243* (US); 15 miles N of Salama, cytological voucher, *King 3291* (TEX); Santa Maria de Jesus, *Standley 66828* (F); barrancos 6 miles S and W of Tajumulco, *Steyermark 36589* (F).

HONDURAS. Río El Quebracho, above El Jicarito, *Standley 14799* (F); slopes of Cerro Majicoran, *Williams 16935* (F).

MEXICO. CHIAPAS: 45 km E of Ocosingo, *Dressler 1633* (GH, MICH, US); Mt. Ovando, *Matuda 3968* (GH, MICH, MO, NY); Zamapam, *Purpus 10863* (GH, US). VERA CRUZ: Zacuapam, *Purpus 14051* (A, DS, F, GH, NY).

NICARAGUA. Along road to La Cantera and Los Pinos, SW of Jinotega, *Standley 10122* (F).

15. **Ageratum tomentosum** (Benth.) Hemsl., Biol. Cent. Amer. Bot. 2: 82. 1881.

Coelestina tomentosa Benth. *in* Oerst., Vidensk. Meddel. 1852: 71. 1852. (Holotype: COSTA RICA: Candelaria, *Oersted 163* (K).)
Carelia tomentosa (Benth.) Kuntze, Rev. Gen. 1: 325. 1891.

Perennial *shrubs* 2.5–5 dm tall; *root* a woody taproot; *stems* woody, branched, older bark gray, younger reddish, conspicuously tomentose to woolly at nodes and on young shoots, at times glabrous on older parts; *leaves* deltoid to ovate, less commonly elliptic, (1.6–)2–3.5(–4.1) cm long, 1.1–2.7(–3) cm wide, base truncate to obtuse, at times slightly decurrent along petiole, apex broadly acute, margin revolute, crenate, upper surface rugose to smooth, light to dark green, scabrous and tomentose or merely tomentose at least over veins, rarely also farinose over veins, lower surface densely white woolly between veins, less so over the 3 prominent veins; *petioles* 0.6–1(–1.7) cm long, slightly winged toward leaf base, conspicuously woolly; *inflorescences* terminal, the 6–12(–22) heads in dense corymbose clusters; *peduncles* coarse, usually less than 1 cm long, white tomentose with scattered amber glanduliferous atoms, bracteolate; *bracteoles* alternate, firm, subulate, scabrous, tomentose; *involucres* campanulate, bracts biseriate, firm, lanceolate, 3.75–5 mm high, 0.65–0.85 mm wide, green, prominently 2-ribbed, white tomentose and yellow glandular-atomiferous at least toward acute apex, margin entire, inner bracts lanceolate to spatulate, attenuate to acute apex, margin entire, surface less densely tomentose; *receptacle* conical, glabrous or paleaceous; *corollas* infundibuliform to tubular, (2.25–)2.65–3.1(–3.5) mm long, tube pale green, with scattered white hairs and yellow glandular atoms, lobes deltoid, obtuse, tomentose and glandular-atomiferous, bluish-purple, rarely white; *achenes* (1.6–)1.9–2.65(–2.75) mm long, dark brown, glabrous, slightly tapered toward inconspicuous carpopodium; *pappus* coroniform, 0.3–0.55 mm high, margin slightly undulate to shallowly pectinate.

This species can be divided into two formae based upon the presence or absence of receptacle paleae.

1. Receptacle glabrous .... 15a. *A. tomentosum* f. *tomentosum*.
1. Receptacle paleaceous .... 15b. *A. tomentosum* f. *bracteatum*.

15a. **Ageratum tomentosum** (Benth.) Hemsl. forma **tomentosum**.

The type locality is questioned here because the indices to maps do not list Candelaria, Costa Rica. As the remainder of this taxon is found in Central Mexico, one wonders if the type locality may be given incorrectly on the label with the type.

Ageratum tomentosum f. *tomentosum* is often confused with *A. rugosum* but can be readily distinguished (also see discussion under *A. rugosum*). The generally short, shrubby habit, taproot, and deltoid leaves, the lower surfaces of which are densely and conspicuously white woolly, serve to distinguish this attractive taxon from all others.

The chromosome number $n = 10$ is reported (Turner, Beaman & Rock, 1961), voucher *King 3548*. The collection number *3458* was mistakenly given in publication.

This forma occurs in east-central and southern Mexico in dry sandy soil, rocky hillsides and limestone hills from about 1600–2000(–2500) m elevation. It is reported from Guatemala and Costa Rica (Hemsley, 1881; Standley, 1928), though no specimens have been seen from Guatemala and the Costa Rica location is questionable. Buds are present in June; flowers are present from July through August(–December).

COSTA RICA (?): Candelaria, *Oersted 163* (K).

MEXICO: *Sine loc.*, *Schlumberger s.n.* (NY). OAXACA: Tomellin Canyon, *Pringle 5786* (GH). PUEBLA: Road side gravel 5 miles NE of Zapotitlan, *Johnson & Hofstetter 2002* (MIN); *ca.* 7 miles N of Puebla-Oaxaca border, *King 3548* (NY, TEX, UC, US); near Tehuacan, *Rose, Painter & Rose 10161* (GH, US); between Nacozoalco and San Antonio Canada, *Smith, Peterson & Todeda 4084* (F, US); Esperanza, *Pittier 434* (US); limestone hills near Tehuacan, *Pringle 6754* (BM, F, GH, MIN, MO, MSC, NY, P, UC, US); *Pringle 9522* (GH, MICH, MSC, MO); Esperanza, *Purpus 1129* (P); Tehuacan, *Purpus 1179* (F, GH, US); Barranca de las Pilas, *Purpus s.n.* (US). VERA CRUZ: Valle d'Orizaba, *Bourgeau 2924* (F, GH, K, P); Lepinziana, *Mohr s.n.* (US); shrubby mountain top W of Orizaba, *Sharp 44864* (NY); Maltrata, *Seaton 346* (US).

15b. **Ageratum tomentosum** (Benth.) Hemsl. forma **bracteatum** M. F. Johnson, forma nov.

Holotype: MEXICO. Puebla: 12 miles S of Zapotitlan, *Johnson & Hofstetter 2001* (MIN).

Differt ab *A. tomentoso* f. *tomentoso* receptaculo paleaceo. Paleae lanceolatae, 3.85–5.25 mm longae, 0.3–0.4 mm latae, 2-costatae, cacumine acuto, margine integro, superficiebus glabris vel cacumen versus tomentillis.

Very similar to *Ageratum tomentosum* f. *tomentosum*, differing in the presence of receptacle paleae. *Paleae* lanceolate, 3.85–5.25 mm long, 0.3–0.4 mm wide, 2-ribbed, apex acute, margin entire, surface glabrous or apically tomentose.

Robinson noted the presence of receptacle paleae on *Purpus 2547* (F), as he wrote on an annotation label "forma paleis paucis instructo." But he did not recognize the paleaceous form in his revision.

The paleaceous plants are often found in close association with non-paleaceous ones, and both are assigned the same collection number when collected together. *King 3548*, the voucher for the chromosome number $n = 10$ (Turner, Beaman & Rock, 1961), is a collection of paleaceous and non-paleaceous plants. The exact plant from which the chromosome count was made is not known.

Ageratum tomentosum f. *bracteatum* occurs in Chiapas, Oaxaca, Puebla, and Vera Cruz often on limestone or sandstone and among *Pinus* and *Quercus*. Flowering dates are the same as in f. *tomentosum*.

MEXICO. CHIAPAS: Pine and oak forest, near Fenis, *Purpus 10059* (NY). OAXACA: Valley of Oaxaca, *Nelson 1213* (GH, US); Sierra de la Yerba, in the vicinity of San Luis Tultitlanapa, near Oaxaca, *Purpus 2547* (BM, F, GH, MO, UC, US); scattered over steep rocky sandstone slope 12 miles S of Zapotitlan, *Johnson & Hofstetter 2001* (MIN); 7 miles N of the Puebla-Oaxaca border, *King 3548* (DS, MICH); limestone hills near Tehuacan, *Pringle 9522* (US). PUEBLA: Near Tehuacan, *Rose & Hay 5877* (US). VERA CRUZ: Maltrata, near Mt. Orizaba, *Seaton 346* (F, GH).

16. **Ageratum standleyi** Robins. *in* Standley, Jour. Arnold Arbor. 11: 44. 1930.

Holotype: HONDURAS. Dept. de Comayagua: Pine forest in vicinity of Siguatepeque, *Standley 56234* (F); isotypes, A, US.

Perennial *shrubs* 3–6.5(–9) dm tall; *roots* fibrous, coarse, woody; *stem* woody from a basal caudex, branched, older parts gray, glabrous, younger parts dark

TABLE 5. A comparison of *Ageratum standleyi*, *A. chortianum*, and *A. tomentosum* sens. lat.

Character	*A. standleyi*	*A. chortianum*	*A. tomentosum* s.l.
Leaves.	Ovate, glandular-punctate above, 2–3.5 cm long, margin entire.	Lanceolate, eglandular, (3.5–)5–6 cm long, margin entire to crenate.	Deltoid to ovate, eglandular, 2–3.5 cm long, margin crenate.
Petioles.	0.1–0.4 cm long.	0.7–0.8 cm long.	0.6–1.7 cm long.
Corollas.	2–2.2 mm long.	About 2 mm long.	2.25–3.5 mm long.
Involucre.	3.5–4.5 mm long.	4.75–5 mm long.	3.75–5.4 mm long.
Roots.	Fibrous.	Unknown.	Taproot.
Distribution.	Honduras.	Guatemala and Honduras.	Mexico.

red, with white scabrous-puberulent hairs, becoming mixed with amber glandular atoms toward inflorescences; *leaves* opposite, short petioled, xeromorphic, ovate, 2–3.5 cm long, 1–2 cm wide, base obtuse, entire, apex acute, margin entire, somewhat thickened, revolute, upper surface dull green, amber glandular-punctate, at times scabrous, puberulent and/or scabrous over the white veins, lower surface densely white to gray tomentose with scattered amber glandular atoms, veins prominent, 3-veined to pinnately veined; *petioles* 0.1–0.4 cm long, densely white scabrous-puberulent with scattered amber glandular atoms; *inflorescences* terminal, the 4–12 heads in a dense corymbose cluster; *peduncles ca.* 0.4–1 cm long, bracteolate, densely white scabrous-puberulent with mixed amber glandular atoms; *bracteoles* alternate, linear, to 4 mm long, puberulent with glandular atoms; *involucres* campanulate, bracts biseriate, firm, 2-ribbed, lanceolate, 3.5–4.5 mm high, 0.5–0.65 mm wide, green to deep red, puberulous and amber glandular-atomiferous at least basally, margin entire, apex acute; *corollas* funnelform, 2–2.2 mm long, puberulous and glandular atomiferous over the greenish or white tube and throat, the 5 lobes pale lavender to bluish, or white; *achenes* 5-angled, glistening black, 1.5–2.1 mm long, glabrous, slightly tapering toward white carpopodium; *pappus* coroniform, 0.15–0.25(–0.4) mm high, light brown, margin irregularly short dentate.

Ageratum standleyi is a very distinctive species and not easily confused with another, though similarities with *A. tomentosum sens. lat.* and *A. chortianum* are evident in leaf tomentum and shrubby habit. Table 5 summarizes the distinctive characters of these species.

Standley and Steyermark (1944) placed high taxonomic value upon the pinnately nerved leaves of *Ageratum chortianum* as opposed to the 3-veined leaves of *A. standleyi*. This feature, while consistent in the limited material of *A. chortianum* available, is not in *A. standleyi*, as both pinnately nerved and 3-nerved leaves are present on the same specimen. The other characters listed above are more consistent and serve well to separate these species.

This species is apparently endemic to Honduras in rocky *Pinus-Quercus* forests from *ca.* 780–1700 m elevation (Fig. 13). Flowers and fruits are present from July through February; fruits are dispersing in January and February.

HONDURAS. COMAYAGUA: Vicinity of Siguatepeque, *Standley 55853* (US), *Standley 56234* (A, F, US). EL PARAISO: Vicinity of El Zamorano, *Standley 1498* (F); Pinares Norte de Yuscaran, *Standley 28569* (US); cumbre NW of Cuinope, *Standley et al. 2033* (F); along Manzaragua road, near Guinope, *Williams 15829* (BM, GH, US). MORAZAN: Uyuca, *Glassman 2130* (MIN, NY); entre Las Mesas y Guayabillas, *Molina 13163* (F); between Cuesta de las Muertos and Monte Obscuro near La Montanita, *Molina 14686* (F); Chaquito, *Rodriguez 389* (F); Zamorano, *Rodriguez 643* (F); San Antonio de Oriente, *Rodriguez 686* (F); slopes of Cerro de Uyuca, region of El Valle Encantenando, *Standley et al. 960* (F); El Zamorano, *Standley 11761* (F), *Standley 12146* (F); Cerro de La Zopilotera, vicinity of El Zamorano, *Standley 14545* (F), *Standley 22025* (F); mountain slopes along Río Agua Amarilla NW of El Zamorano, *Standley 23272* (F); Piedra Herrada, W slope of Cerro de Uyuca, *Standley 23712* (F); above El Zamorano, *Standley 26608* (F); near Joya Grande, on road from El Zamorano to Suyapa, *Standley & Molina 4485* (F); rocky hillside near Las Mesas, *Williams 17243* (F, GH); along Santa Clara Creek, *Williams & Molina 15874* (F); near Las Mesas, *Williams, Rua & Williams 18936* (F).

17. **Ageratum chortianum** Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 98. 1944.

Holotype: GUATEMALA. Dept. Chiquemala: Near Montana Cebollas, along Río Santa Lucia Saso, SE of Quezaltepeque, *Steyermark 31269* (F).

Perennial *shrub ca.* 1.3 dm tall; *roots* unknown; *stem* woody, branched, bark gray to tan, densely white-scabrous to puberulous-scabrous above, older parts glabrous, eglandular-atomiferous throughout, leafy nearly to inflorescences; *leaves* coriaceous, opposite, petioled, lanceolate, the longest 5–6(–6.5) cm long, 1.5–2.6 cm wide, base obtuse, margin revolute, entire, apex acute to widely so, upper surface dark green, scabrous, puberulous-scabrous over midrib and prominent secondary veins, eglandular-atomiferous, lower surface densely white tomentose, eglandular, rarely with widely scattered glandular atoms, venation pinnate or 3-veined; *petioles* 0.7–0.8 cm long, very densely white to tawny puberulous-pilose; *inflorescences* terminal, the 4–5 or more heads grouped in a corymbose cluster; *peduncles ca.* 3–6 mm long, densely white to tawny pilose-puberulent, bracteolate; *bracteoles* alternate, 3–5 mm long, green, linear, pilose-puberulent; *involucres* campanulate, bracts bi- to triseriate, prominently 2-ribbed basally, dark green, lanceolate, middle and inner-most series (3.25–)4.75–5 mm long, 0.55–0.65 mm wide, outer ones about ½ as long, short white pilose overall, margin ciliate, tapering to an acute apex; *corollas* narrowly funnelform, 2.25–2.45 mm long, externally pilose throughout, tube and narrow throat white (?), lobes lavender to white; *achenes* 5-angled, brown, 1.75–2 mm long, glabrous, slightly tapered toward inconspicuous carpopodium; *pappus* coroniform, *ca.* 0.25 mm long, tawny, margin undulate to minutely dentate.

Ageratum chortianum is known from relatively few collections all of which are incomplete, as only the upper branches are preserved.

Standley and Steyermark (1944) described this species as closely related to *Ageratum standleyi.* Though both species possess similar coriaceous or xeromorphic leaves with dense tomentum on the lower surfaces and a shrubby habit, these shared characters need not indicate relationship but rather may be the result of convergence of these species in a similar environment.

Ageratum chortianum is distinguished from other species by the lanceolate, eglandular, coriaceous leaves. Standley and Steyermark (1944) are of the opinion that the pinnate venation of *A. chortianum versus* three principal veins in *A. standleyi* is an important distinguishing feature. However, this characteristic is not consistent; both venation types are present in *A. standleyi* as well as in *A. chortianum.* Also, see the discussion under *A. standleyi* presented here.

Ageratum chortianum occurs in Honduras and Guatemala on dry hills in pine forests and from *ca.* 600–1000 m elevation (Fig. 13). Flowers and fruits are present from March to November.

GUATEMALA. CHIQUIMULA: Montaña Castilla, vicinity of Montaña Cebollas, along Río Lucia Saso, 3 miles SE of Quezaltepeque, *Steyermark 31269* (F). GUATEMALA: Without locality, *Aguilar 134* (F). JALAPA: 10 miles S of Jalapa, *Steyermark 32218* (F).

HONDURAS. CORTES: Montaña La Cumbra, caserio Las Pinitas, *Molina 10523* (F), *Molina 10585* (F). SANTA BARBARA: Los Dragos, on Río Chamelecon, SW of Quimistan, *Standley & Lindelie 7486* (F), *Standley & Lindelie 7498* (F, UC).

18. **Ageratum guatemalense** sp. nov.

Holotype: GUATEMALA: Totonipacan *ca.* 22 miles S of main turnoff to Huehuetenango, *Ownbey & Muggli 3972* (MIN).

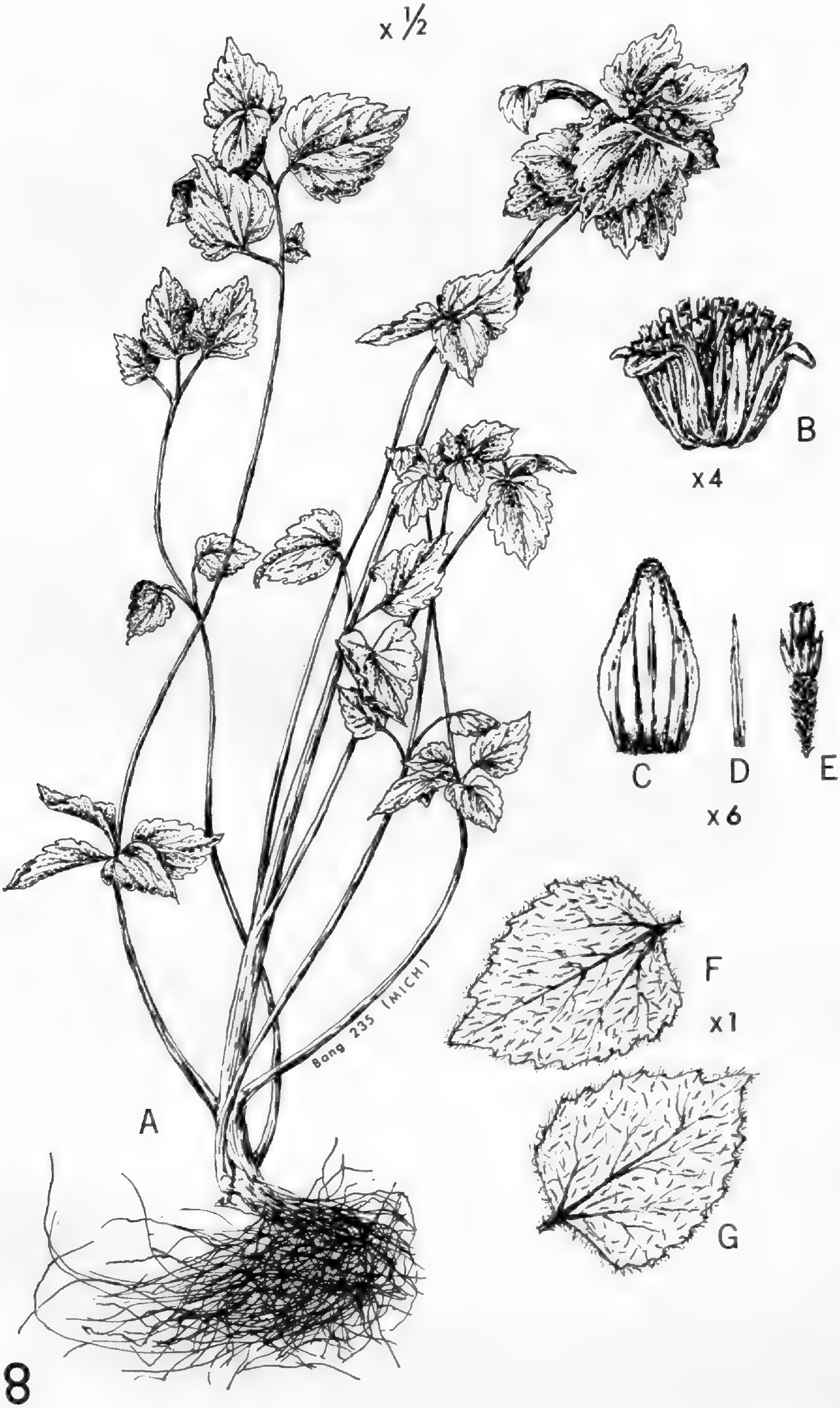
Caulis erectus, simplex, plerumque ramosus ad corymbos, cortice fusco-cinereo obscure rubescente ad cacumen, incano-puberulo vel scabro-puberulo interdum valde dense sed subglabrescente ramulos supernos versus. Folia opposita, remota a corymbis, breviter petiolata, aliquantum crassa et carnosa, veltata, lanceolata vel lanceolate-elliptica, (2.7–)3.1–4.4 cm longa, 1.1–1.4 cm lata, base cuneato-attenuata, integra, margine revoluto, crenato, apicem versus gradatim integro, scabro-puberulo, nonnumquam purpuro, apice attenuato, acuto, in pagina superiore flavovirentia vel virentia, manifeste incano-pilosa, gradatim scabra ad marginem, venis non manifestis; in pagina inferiore folia flavorirentia, manifeste incano-pilosa, cum glandulo-granulosa vel flaventia vel sucinea punctulis, rarius glabra, 3 venis albis manifestis. Involucra campanulata, squamis anguste lanceolatis vel linearibus (3–)3.5–4.75(–5) mm alta, 0.4–0.65 mm lata. Receptaculum conicum, nudum.

Perennials 3.5–5.5 dm tall; *roots* coarse, fibrous; *stems* woody, erect, usually clumped from a woody caudex, simple to branched near inflorescences, bark brown-gray to deep red apically, white pilose-puberulent to pilose-scabrous, at times quite densely so, to becoming subglabrous near upper branches; *leaves* opposite, remote from inflorescences, petioled, somewhat thick and fleshy, velvety, lanceolate to lanceolate-elliptic, (2.7–)3.1–4.4 cm long, 1.1–1.4 cm wide, base cuneate-attenuate, entire, margin revolute, crenate, becoming entire toward apex, scabrous-puberulous, often deep purplish, apex acute, upper surface yellow-green to dark green, often tinged with purple, conspicuously white pilose, becoming scabrous marginally, venation inconspicuous, lower surface yellow-green,

→

FIGURE 12. *Ageratum guatemalense.* — A. Habit. — B. Inflorescence. — C. Single flower showing the achene and coroniform pappus. — D. Involucral bracts. — E. Detail of upper leaf surface. — F. Detail of lower leaf surface. [After *Ownbey & Muggli 3972.*]

12



18

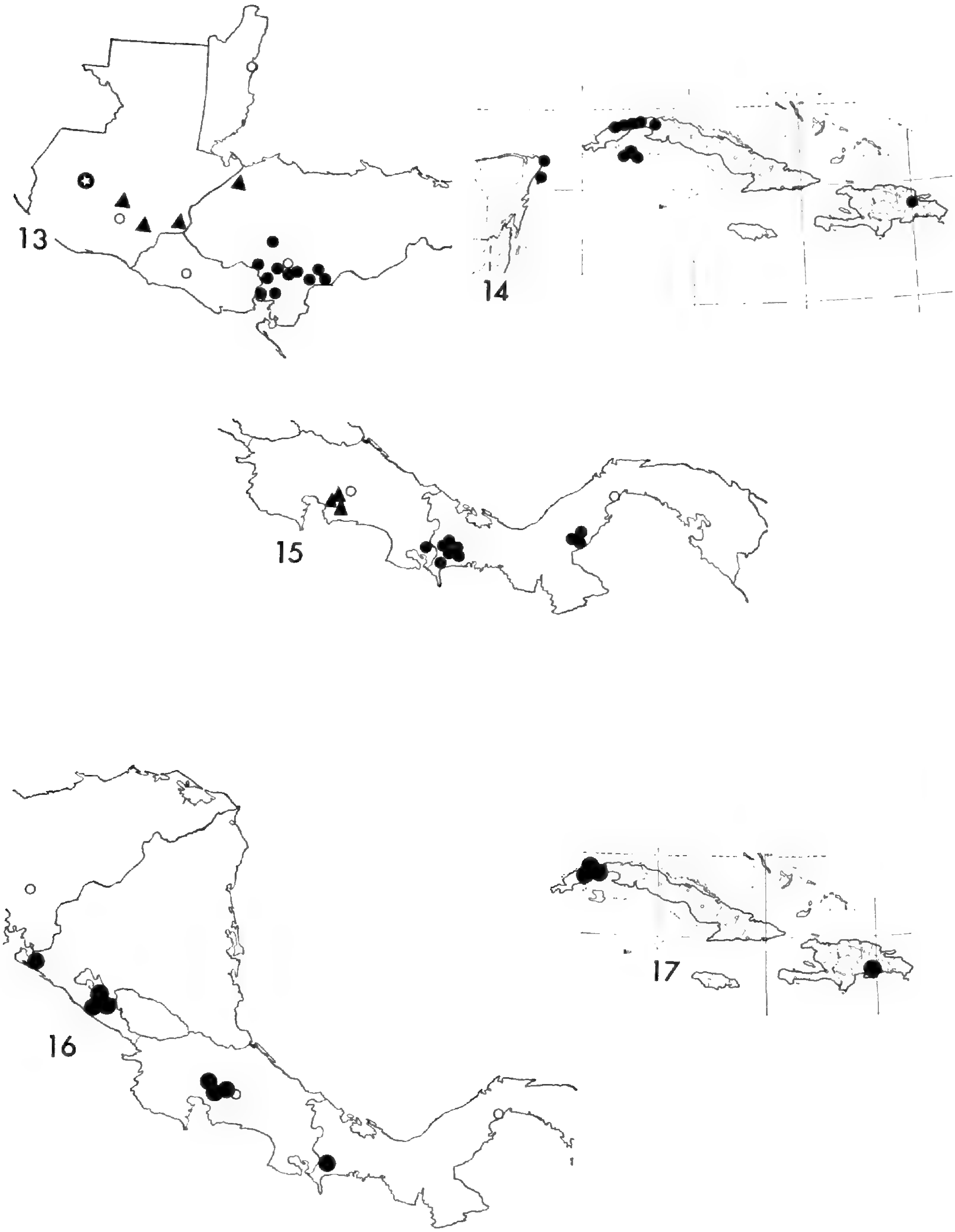
leaves more or less fleshy, petioled, deltoid-ovate to oblong, (0.7–)1.3–2.7 cm long, (0.5–)1.7–1.9(–2.1) cm wide, base obtuse to truncate, margin crenate, apex acute to rounded, both surfaces glabrous, lower surface obscurely 3-nerved, midvein at times with scattered white hairs; *petioles* 0.3–1.5(–2.1) cm long, channeled in cross section, bearing white hairs along margin; *inflorescences* terminal, the 2–5 heads grouped in a corymbiform cluster; *peduncles* 0.5–4.2 cm long, finely puberulous-pilose; *involucres* hemispheric, bracts biseriate, rarely triseriate, prominently 2-ribbed, lanceolate, 3.2–4.2 mm high, 0.5–0.9(–1) mm wide, glabrous to sparingly white pilose basally, margin green or scarious, at times minutely ciliate, apex acuminate to attenuate; *corollas* tubular or very slightly expanded, (1.45–)1.75–2.05 mm long, tube pale green or white, glabrous or puberulous, lobes bluish, rarely white, puberulous; *achenes* dark brown, (1.3–)1.45–1.7(–1.8) mm long, glabrous, slightly curved toward white carpopodium; *pappus* coroniform, 0.2–0.5(–0.7) mm long, margin deeply laciniate and at times pectinate, appearing as if made up of separate scales, or merely undulate, rarely with 1 or 2 setae.

Kunth described this species as having thick leaves as in *Beta maritima*. I have compared dried specimens of *Ageratum maritimum* with *Beta maritima* and find that the *Ageratum* leaves are considerably less thick and appear nearly membranous. Kunth may have based his description on living plants, in which case the leaves may be comparable. Kunth described the corollas of this species as glabrous; however, observation under 15× magnification revealed the corolla lobes to be externally puberulent.

Ageratum maritimum HBK var. *intermedium* (Hemsl.) Robins. was assigned varietal rank because of the pappus setae and slightly longer peduncles on the type specimen. It is my feeling that this disposition is quite arbitrary and artificial. There is considerable variation within a single head on this type so that a pappus with setae sometimes is adjacent to the more conspicuous deeply laciniate coroniform type. No positive diagnostic value can be ascribed to the longer peduncles. As this variety is based on inconclusive evidence, it is placed in synonymy.

Ageratum maritimum HBK f. *calvum* Robins. is also placed in synonymy because of the variability of the pappus in this species. The description, drawn from *Shafer 1099*, calls attention to the calvus, *i.e.*, epappose, achenes. I have seen the isotype in which the pappus varies in a single head from the common laciniate type to a mere crown. The pappus is never completely lacking on the fruit. Other collections also show the variable pappus, *i.e.*, a deeply laciniate coroniform pappus in the same head with a coroniform, non-laciniate one. To separate those plants with the entire pappus from the laciniate pappus becomes very arbitrary and artificial. It is best to consider the pappus here as showing a gradient from the very short ones *ca.* 0.1–0.2 mm long on one extreme and ranging to the opposite extreme where the pappus is to 0.7 mm long, deeply laciniate and, at times, setiferous.

Ageratum maritimum is distinguished by the combination of its creeping decumbent habit, deltoid-ovate to oblong, somewhat fleshy leaves, pilose nodes and coastal sand habitat. As *Ageratum maritimum* and *A. littorale* occupy similar habitats, though they are not known to occur sympatrically, they may be con-



FIGURES 13–17. — 13. The distribution of *Ageratum guatemalense* in Guatemala, *Ageratum chortianum* in Guatemala and Honduras, and *Ageratum standleyi* in Honduras. Circle with star, *A. guatemalense*; solid circle, *A. standleyi*; triangle, *A. chortianum*. — 14. The distribution of *Ageratum maritimum* in Quintana Roo, Cuba, and Hispaniola. (Base map copyright University of Chicago.) — 15. The distribution of *Ageratum oerstedii* in Costa Rica and *Ageratum riparium* in Panama and Costa Rica. Triangle, *A. oerstedii*; solid circle, *A. riparium*. — 16. The distribution of *Ageratum petiolatum* in Panama, Costa Rica and Nicaragua. — 17. The distribution of *Ageratum domingense* in Cuba and Hispaniola. (Base map copyright University of Chicago.)

fused in the herbarium. *Ageratum maritimum* usually has a longer, laciniate pappus that appears to be made up of scales compared to the coroniform type in *A. littorale*, and it is generally more pilose and more fleshy than *A. littorale*. There is a tendency for the heads to be single on an elongated peduncle in *A. maritimum* so that it may resemble *A. gaumeri*. However, the distinctions listed above will separate these species readily.

This species occurs on beaches and limestone near beaches in Cuba, Hispaniola, and islands off Quintana Roo (Fig. 14). Flowers and fruits are present the year around.

CUBA. Bay of Mariel, *Britton & Gager 7551* (F, NY, US); Isle of Pines, *Britton et al. 14930* (F, GH, NY, US); sand banks near the sea near Havana, *Curtiss 650* (BM, F, GH, K, MIN, MO, NY, US); back of spray zone on low coralline limestone terrace, Punta Barlovento, N of Mariel, *Sauer 1789* (WIS); Old Fort to Punta Barlovento, *Shafer 1099* (BM, F, GH, NY, US); Mariano, *van Hermann 447* (BM, F, NY, US); without locality, *Wright 1631* (BM, F, GH, K, MO).

DOMINICAN REPUBLIC. VEGA: Cotuy, *Abbot 749* (US).

MEXICO. QUINTANA ROO: Cozumel Island, *Gaumer 93* (GH, K); Isla Mugeres, *Sauer & Gade 3238* (WIS); Cozumel Island, *Steere 2984* (MICH).

20. **Ageratum littorale** Gray, Proc. Amer. Acad. Arts 16: 78. 1880.

Lectotype: UNITED STATES. Florida: Key West, *Bennett s.n.* (GH); isotype, NY.

Perennial *herb* (1.5–)2–5(–7) dm tall; *roots* coarse, fibrous, at times adventitious at lower nodes; *stems* somewhat succulent, decumbent to erect, abundantly branched from base, branches opposite, erect, surface deep red to pale green, glabrous to sparsely tomentose at least at nodes, leafy at base, leafless toward inflorescences; *leaves* opposite, long petioled, thin though somewhat succulent, ovate to deltoid, (1.5–)2–4.1(–4.7) cm long, (0.7–)1–3.7 cm wide, base obtuse, entire, apex acute to broadly so, margin crenate, teeth slightly thickened at apex, upper surface green, glabrous to sparingly tomentose especially when young, lower surface very similar, the 3 main veins more conspicuous from beneath; *petioles* 1–4 cm long, thin, sparingly tomentose near node; *inflorescences* terminal, the 3–10 heads grouped in tight corymbose clusters; *peduncles* usually 1 cm or less long, glabrous to tomentose directly beneath involucres, bracteolate; *bracteoles* alternate, subulate, glabrous to sparingly tomentose; *involucres* campanulate, bracts bi- to triseriate, outer series firm, 2-ribbed, oblong to lanceolate, (2.75–)3–4(–4.15) mm long, 0.5–0.9(–1.55) mm wide, pale green to brownish, margin green or scarious, basally entire, at times variously erose and scabrous toward the acute apex, surface glabrous to sparingly tomentose usually only basally, at times scabrous apically; *corollas* narrowly funnelform, 1.15–2.5 mm long, tube and throat tomentose to glabrous, pale green, lobes puberulent to glabrous, blue-purple to bright blue, rarely white; *achenes* shining black, (1.25–)1.5–1.8 mm long, glabrous, tapering toward white carpopodium; *pappus* coroniform, 0.05–0.15 mm long, margin entire to variously undulate, plants from islands in Bay of Honduras often with setiferous pappus scales, then pappus 0.25–1.3(–2.25) mm long.

The species can be divided into formae based upon characters of the pappus and to some extent, geography.

1. Pappus coroniform, margin entire to undulate, not setiferous; south Florida, Grand Cayman Island, rarely in the islands of the Bay of Honduras .... 20a. *Ageratum littorale* f. *littorale*
1. Pappus setiferous, setae to 2.25 mm long; mainly in the islands of the Bay of Honduras .... 20b. *Ageratum littorale* f. *setigerum*

20a. **Ageratum littorale** Gray forma **littorale**.

Coelestina maritima Torrey & Gray, Flora 2: 63. 1841, fide Robinson (1913*b*).
Carelia littorale (Gray) Kuntze, Rev. Gen. 1: 325. 1891, fide Robinson (1913*b*).
Ageratum littorale Gray var. *hondurense* Robins., Contr. Gray Herb. 42: 468. 1913. (Holotype: Bay of Honduras, Ruatan Island, *Gaumer 1* (B, not seen); photographs, NY, US; isotypes, GH, US; photograph, MIN.)
Ageratum littorale Gray f. *album* Moldenke, Amer. Midl. Naturalist 32: 562. 1944. (Holotype: UNITED STATES. Florida: Monroe County, Big Pine Key, *Moldenke 817a* (NY).)

Torrey and Gray (1841) described this species under the genus *Coelestina* Cass. and applied the appropriate epithet *maritima*. Later, Gray (1880) transferred the species to *Ageratum*, but due to the specific name being preoccupied under *Ageratum* by *A. maritimum* HBK, he adopted *A. littorale*.

Robinson's variety, *hondurense* was proposed to include plants possessing leaves longer and wider than average. It appears that Robinson did not see many specimens and that his decisions were based on minimal data. Personal study of about 40 different collections shows that leaves of Robinson's variety are well within the range of variation in leaf size throughout the species. There are no grounds for retaining taxonomic recognition of *A. littorale* Gray var. *hondurense* Robins.

Moldenke (1944) described a plant with white florets as forma *album*. As floret color is quite variable in this species and in the genus as a whole, it does not seem taxonomically sound to recognize taxa based only on corolla color.

Ageratum littorale is the only species native in the United States. Its semi-succulent, glabrous nature, and the minute pappus in combination with a coastal habitat set it apart from other taxa.

Ageratum littorale f. *littorale* occurs in beach sand and in thickets along the sea in the Florida Keys, the West Indies, and in islands in the Bay of Honduras. Flowers and fruits are present throughout the year as local conditions permit.

BRITISH HONDURAS. Half Moon Cay, *Stoddart 43* (BM).

CUBA. Sand dunes, Corrientes Bay, Pinar del Río, *Britton & Cowell 9954* (NY).

GRAND CAYMAN ISLAND. Sand along road side, Georgetown, *Kings GC176* (BM); 25 m from sea in low thicket on roughly pitted ironstone shore, between Jacson Point and Southwest Point, *Sauer 3285* (WIS).

UNITED STATES. FLORIDA: Indian Key, *Bates s.n.* (MICH, MSC); Key West, *Bennett s.n.* (NY), *Blodgett s.n.* (GH, NY), *Chapman s.n.* (MO, NY, US), *Pollard et al. 12* (BM, F, MIN, NY, US); sand dunes, east end of Key West, *Small & Small 4984* (MO, NY); coral soil, Boca Chica Key, *Curtiss 1163* (BM, F, GH, MIN, MO, NY, US); dry sandy soil, Lower Marecumbe Key, *Moldenke 662* (K, MO, NY).

20b. **Ageratum littorale** Gray forma **setigerum** Robins., Contr. Gray Herb. 42: 468. 1913.

Holotype: Bay of Honduras, Mugeres Island, *Gaumer s.n.* (B, not seen); isotype, US; photograph, MIN.
Ageratum littorale Gray var. *hondurense* Robins. forma *setigerum* Robins. Contr. Gray Herb. 42: 468. 1913.

Forma *setigerum* is very similar to forma *littorale*, differing primarily in the presence of a setiferous pappus in the former. *Ageratum littorale* f. *setigerum* occurs mainly in British Honduras but does reach Florida where forma *littorale* is common. Due to the overlap in geographic range and the single character of the pappus which distinguishes these taxa, the status of forma is maintained.

This forma occurs on the offshore islands and cays of British Honduras; it is apparently more rare on the Keys of Florida. Flowering and fruiting occurs year around as local conditions permit.

BRITISH HONDURAS. Stann Creek, Water Cay, *Robertson 251* (BM); Turneffe Islands, Deadman II Cay, *Stoddart 130* (US).

UNITED STATES. FLORIDA: Shore of Jewfish Key, *Curtiss 5446* (MO, NY, P).

21. **Ageratum platypodum** Robins., Contr. Gray Herb. 42: 464. 1913.

Holotype: MEXICO. Jalisco: Guadalajara, *Palmer 437* (GH); isotypes, BM, NY, US.

Annuals or short-lived perennials 6–9.5 dm tall; *roots* coarse, fibrous, at times adventitious at lower nodes; *stems* simple to branched above, deep red, minutely puberulent; *leaves* opposite at base of stem to alternate above, petioled, ovate, 5–9.5 cm long, 3–6 cm wide, base obtuse, slightly decurrent along petiole, apex obtuse to acute, margin crenate or dentate, scabrous to glabrous, upper surface yellow-green, glabrous or scabrous, lower surface pale green, abundantly yellow glandular-punctate to sparingly so, sparingly white pubescent over the conspicuous reticulate, sometimes red, veins; *petioles* 1–2.2 cm long, slightly winged and flattened, *ca.* 2.5 mm wide, 3-veined, sparingly pilose on the margin; *inflorescences* terminal, the 4–10 heads grouped in an irregular corymbose cluster; *peduncles* coarse, bracteolate, from *ca.* 0.75–2 cm long, pilose-puberulent; *bracteoles* linear, 3–6 mm long, marginally sparingly pilose; *involucres* campanulate, bracts bi- to triseriate, firm, green to reddish, 2-ribbed, ribs prominent basally, lanceolate, (5.25–)5.5–6.5 mm long, (0.85–)1–1.35 mm wide, pubescent with irregularly scattered white, pilose hairs, margin entire, ciliate at least apically, apex acute; *corollas* narrowly funnelform, (2.7–)3–3.3 mm long, tube greenish, puberulent, throat greenish, becoming glabrous toward the 5 pale lavender, glabrous lobes; *achenes* 5-angled, 1.5–1.85 mm long, shiny black, minutely and sparingly scabrous on angles, very slightly tapered toward white carpopodium; *pappus* coroniform, (0.3–)0.5–0.7 mm long, tawny, margin finely and irregularly pectinate to dentate.

Robinson (1913*b*) placed *Ageratum platypodum* in his section *Euageratum* in which he included those species with free pappus scales. None of the specimens available to me for study indicate this relationship—the pappus is coroniform in all cases. Projecting teeth, if present, are basally united into a cup-like pappus. This feature suggests a closer relationship to those species with a similar pappus structure.

The holotype and isotype of *Ageratum platypodum* were distributed as whole plants but mounted with inflorescences of *A. houstonianum* in the upper right-hand corner of the sheet. Characteristics of the pappus, *i.e.*, the 5 elongate basally free setae, as well as the pubescent corolla lobes and shorter, pilose stipitate-glandular, acuminate bracts of *A. houstonianum* set the species apart in this mixed collection.

Ageratum platypodum shows outward similarities to *A. petiolatum*. Ovate leaves borne on elongate petioles are present in both species. However, the distinguishing characters of *A. platypodum*, the large, ovate leaves with reddish veins, borne on wide petioles, and the prominent ribs toward the base of the involucral bracts, set these species apart.

Ageratum platypodum is a tetraploid species. The chromosome number $n = 20$ was determined from buds (voucher *Ownbey & Muggli 3941*, MIN) and recorded here for the first time.

This species is known only from Jalisco in wet meadows and along road sides in the pine forest zone from *ca.* 1700–2100 m elevation. Flowers and fruits are present in August and September.

MEXICO. JALISCO: Sierra del Tigre, 2 miles NE of Maxamitla, *McVaugh 13133* (MICH, US); mountain plateau 4 miles E of Tapalpa, *McVaugh 20700* (MICH); low, wet roadside 6.5 miles E of Tapalpa, cytological voucher, *Ownbey & Muggli 3941* (MIN); Guadalajara, *Palmer 437* (BM, GH, NY, US).

22. **Ageratum riparium** Robins., Contr. Gray Herb. 42: 473. 1913.

Holotype: COSTA RICA. In arenosis secundum flumen Ceibo, *Pittier 4914* (GH).
Ageratum rivale Robins., Contr. Gray Herb. 61: 3. 1920, *non Ageratum riuale* Ses. & Moc., La Naturaleza, ser. 2, app. 1: 136. 1887. (Holotype: PANAMA. Chiriqui Prov.: Vicinity of El Boquete, *Maxon 5240* (US); isotype, GH.)
Ageratum panamense Robins., Contr. Gray Herb. 104: 4. 1934.

Annuals or short-lived perennials; *roots* fibrous, commonly adventitious at stem base; *stems* repent to erect, (1.5–)3–4.6(–8.4) dm tall, branched, branches often vertical or ascending, surface dark red above to brown, glabrous below, becoming puberulous to pilose-puberulous toward apex; *leaves* opposite below to alternate above, petioled, ovate to lanceolate, (1.1–)2.5–6.5(–8) cm long, 0.7–2.4(–2.9) cm wide, base obtuse to oblique, entire, apex acute, margin dentate to more or less wavy, upper surface bright green, scabrous to glabrous, puberulous over veins, lower surface pale green, orange glandular-punctate, scabrous at least over the 3 larger veins, to nearly glabrous; *petioles* 0.1–0.5(–1) cm long, pilose; *inflorescences* terminal, the 3–7 heads in an irregular corymbose cluster, rarely borne singly; *peduncles* usually less than 1.5 cm long when in a cluster, to 6 cm long if head solitary, densely pilose-puberulent, bracteolate; *bracteoles* alternate, leaf-like, green to reddish, linear, to 0.5 cm long, pilose to scabrous; *involucres* campanulate, spreading with age, bracts biseriate, 2-ribbed, firm, green to deep red, lanceolate, 4.2–6(–6.85) mm long, (0.7–)1–1.3 mm wide, sparingly pilose at least over the rather prominent ribs to glabrous, margin entire, green to scarious, ciliate at least apically, apex acute, white tipped, at times becoming spine-like; *corollas* funnelform, (2–)2.4–3(–3.75) mm long, tube and throat white to greenish, glabrous, lobes purple to lavender, sparingly pilose; *achenes* dark brown to black (1.5–)2–2.35(–2.8) mm long, glabrous, curved and tapering toward white carpopodium; *pappus* coroniform, (0.1–)0.2–0.8 mm high, tawny, margin variously dentate to laciniate, at times a tooth elongating into a scabrous, subulate awn, then pappus 2–2.3(–2.65) mm long.

Robinson (1913*b*) described *Ageratum riparium* on the basis of Pittier's collection of a portion of a single robust branch. Later Robinson (1920) described

TABLE 6. A comparison of *Ageratum riparium* and *A. petiolatum*.

Character	*A. riparium*	*A. petiolatum*
Leaves.	Ovate to lanceolate, firm, green beneath, sharply dentate.	Ovate to triangular, thin, pale green to gray beneath.
Petioles.	To 1 cm long.	To 3 cm long.
Involucral bracts.	Glabrous to nearly so, pale green, (0.7–)1–1.3 mm wide.	Short pilose, pale green to reddish, 0.5–0.8 mm wide.
Flowering.	January to March, again July to August.	May to July.
Altitudinal range.	(600–)1200–1400 m.	300–900 m, rarely to 1400 m.

A. rivale with a more complete plant as the holotype. As the epithet *rivale* was previously occupied under *Ageratum* (*A. riuale*, Ses. & Moc.), Robinson (1934) chose the name *panamense* to replace *A. rivale* Robins.

Robinson (1913*b*) employed the oblique leaf bases as noted on the type of *Ageratum riparium* as an important key character. This feature is evident on the type of *A. rivale* as well, though it is very inconsistent on both specimens. The wide, nearly glabrous, light green involucral bracts are shared by both type specimens. Stem color and pubescence are identical on both types as is the dentate to laciniate coroniform pappus. Measurements of structures on both specimens and on the collections as a whole show obvious similarities. Finally, the location of Pittier's collection in Costa Rica and the remainder of the taxon in adjacent Panama suggests that they are the same entity. Since *A. riparium* Robins., *A. rivale* Robins. and *A. panamense* Robins. are conspecific, the oldest validly published name for the taxon, *A. riparium* Robins. must be adopted.

Ageratum riparium and *A. petiolatum* are the only species of *Ageratum* present in Panama besides the weedy and pantropic *A. conyzoides* subsp. *conyzoides*. Though sharing the same type of habitat in part, *i.e.*, moist banks and slopes, these species are readily separated as summarized in Table 6.

Ageratum riparium is distinguished by the combination of wide, glabrous or nearly glabrous involucral bracts with ciliate margins, the sharply dentate ovate leaves, and its moist habitat.

This species is endemic to Panama and adjacent Costa Rica in pastures, wet meadows, and along bogs and river banks from *ca.* 700–1400 m elevation (Fig. 15). It is in flower from January to March; fruits are present in March. Flowering occurs again in July with fruits present in July and August.

COSTA RICA. Gravien du Rio Ceibo, près du Bornea, *Pittier 4914* (GH).

PANAMA. Marsh in valley, El Valle de Antón, *Alston 8804* (BM); Boquete, *Davidson 590* (F, US); marshy ground and marshes along R. Antón, El Valle de Antón, *Hunter & Allen 377* (BM, K); along Río Caldera S of El Boquete, *Killip 3612* (US); meadow, El Valle de Antón, *Maurice 773* (US); pasture below Alto Lino, *Maurice 874* (US); along wet bank of brook, vicinity of El Boquete, *Maxon 5240* (US); Boquete, *Pittier 2905* (US); llano del volcán, *Seibert 342* (GH, US); El Valle de Antón and vicinity, *Seibert 472* (GH, MIN, NY, US); near El Volcán, *White 222* (GH, US); vicinity of Boquete, *Woodson & Schery 734* (GH); Finca Lerida to Boquete, *Woodson et al. 1102* (GH, NY), *Woodson et al. 1147* (GH, US); between Las Margaritas and El Valle, *Woodson et al. 1767* (GH, NY, US).

23. **Ageratum oerstedii** Robins., Contr. Gray Herb. 42: 472. 1913.

Coelestina latifolia Benth. *in* Oersted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn. 1852: 71. 1852. (Holotype: COSTA RICA. Monte Aguacate, *Oersted 251* (K); isotype, C; photograph, GH, fide Robinson (1913*b*).)
Ageratum latifolium (Benth.) Hemsl., Biol. Centr. Amer. Bot. 2: 82. 1881, *non* Cav. (1797), fide Robinson (1913*b*).
Carelia latifolia (Benth.) Kuntze, Rev. Gen. 1: 325. 1891, fide Robinson (1913*b*).

Annual 3–5(–6.6) dm tall (*cf.* Robinson, 1913*b*; Standley 1938); *roots* fibrous, at times adventitious at basal nodes; *stems* erect, branched, puberulous and long white pilose, bark mottled deep red and green; *leaves* opposite, long petioled, semi-membranous, widely ovate (5.4–)7–9(–13) cm long, (3.6–)6.5–9 cm wide, base cordate to truncate, entire, slightly decurrent along petiole, margin ciliate, crenate, apex acute, upper surface bright green with widely scattered white pilose hairs, lower surface pale green, abundantly dotted with yellow glandular atoms and white pilose over the conspicuous palmate venation; *petioles* (1–)2.5–4(–6) cm long, white pilose, slightly winged distally; *inflorescences* terminal on stems and branches, numerous heads in loose corymbose clusters; *peduncles ca.* 3–7 mm long, white puberulent, bracteolate; *bracteoles* 1.5–3.5 mm long, subulate, pale green, glabrous, merging with the involucral bracts; *involucres* campanulate, bracts biseriate, 2-ribbed, pale brown at base, becoming pale green above, lanceolate, (3–)4–4.25 mm high, (0.7–)0.8–0.9 mm wide, glabrous, margin entire, scarious, glabrous to ciliate toward acute apex; *corollas* funnelform, (2–)2.25–2.5 mm long, glabrous throughout, tube and throat pale green to white, lobes lavender; *achenes* dark brown to black, 1–1.35(–1.5) mm long, glabrous, slightly tapered toward white carpopodium; *pappus* coroniform, 0.15–0.2 mm high, margin entire to minutely dentate.

This species was described by Bentham and Oersted (1852) under the genus *Coelestina* Cass., and the epithet *latifolia* was applied. Hemsley (1881) transferred *C. latifolia* to *Ageratum* and retained Bentham's epithet, apparently unaware of Caviniile's use of the same epithet in 1797. Robinson (1913*b*), noting that the epithet *latifolium* was preoccupied under *Ageratum*, published *A. oerstedii*, honoring the collector of the type.

Ageratum oerstedii is poorly represented in herbaria and thus not well known. Nevertheless, the data suggest that *A. oerstedii* is distinct. The combination of large, ovate, membranous leaves with yellow glandular atoms beneath and the pale green, lanceolate, glabrous involucral bracts is common only to this taxon.

Ageratum oerstedii is endemic to Costa Rica (Standley, 1938) in mountains at *ca.* 600 m elevation (Fig. 15). Plants collected in November and December are in flower and fruit.

COSTA RICA. Del Cacao de Alajuela, *Brenes s.n.* (NY), *Brenes s.n.* (NY); 25 miles E of Punta Arenas, *Cronquist 8840* (MICH, NY); *Orotina, Holway 324* (GH, MIN); Aguacate, *Oersted 251* (C, K); without locality, *Oersted 253* (K). Reported from San Ramon (Robinson, 1913*b*; Standley, 1938).

24. **Ageratum petiolatum** (Hook. & Arn.) Hemsl., Biol. Centr. Amer. Bot. 2: 83. 1881.

Caelestina petiolata Hook. & Arn., Bot. Beechey Voy. 433. 1841, fide Robinson (1913*b*). (Holotype: NICARAGUA. Realejo, *Sinclair s.n.* (K); photograph, GH.)

Coelestina scabriuscula Benth. *ex* Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn. 1852: 72. 1852. (Holotype: COSTA RICA. El Veijo, *Oersted 250* (C).)
Carelia petiolata (Hook. & Arn.) Kuntze, Rev. Gen. 1: 325. 1891, fide Robinson, 1913*b*.
Carelia scabriuscula (Benth.) Kuntze, Rev. Gen. 1: 325. 1891.
Ageratum scabriusculum (Benth.) Hemsl., Biol. Centr. Amer. Bot. 2: 83. 1881.

Annual or longer lived, 2.5–5.6(–7) dm tall; *roots* fibrous, rarely adventitious at lower nodes; *stems* simple or sparingly branched, erect, surface reddish to green when young, becoming brownish, white puberulous on upper parts and lower nodes, glabrous or nearly so toward basal internodes; *leaves* opposite, petioled, rather thin, ovate to triangular, 3–6.6(–9) cm long, 1.4–3.8(–4.15) cm wide, base obtuse to very slightly cordate, entire, apex acute, margin crenate, sometimes revolute, upper surface shiny, green, pilose to puberulent and pilose at least over veins, at times yellow glandular-punctate, at times scabrous near margin, lower surface dull, pale green to gray, yellow glandular-punctate, sparingly pilose over the conspicuous reticulate veins; *petioles* (0.7–)1.2–3 cm long, pilose-puberulous marginally; *inflorescences* terminal, the 3–7 or rarely more heads in corymbose clusters; *peduncles ca.* 0.5–3 cm long, densely white puberulent-pilose, bracteolate; *bracteoles* alternate, linear, puberulent-pilose, to *ca.* 5 mm long, merging with involucre; *involucres* campanulate, bracts biseriate, 2-ribbed, firm, pale green to reddish, lanceolate, (3.5–)4–4.85 mm long, 0.5–0.8 mm wide, sparingly pilose at least basally, becoming glabrous apically, margin entire, glabrous to ciliate, apex acute; *corollas* funnelform, 2.25–3 mm long, glabrous throughout, tube and narrowly expanded throat greenish, lobes and style branches lavender; *achenes* glistening black, 1.45–2 mm long, glabrous, slightly tapering toward white carpopodium; *pappus* coroniform, white, 0.15–0.5 mm long, margin variously dentate, at times with a single subulate, scabrous awn to 2.5 mm long.

The type locality of *Ageratum petiolatum* is given as Realejo, Guatemala, by Hooker and Arnott (1841) who also list the location at 12° 45′ N. Modern maps show this latitude to be within Nicaragua. Robinson (1913*b*) was aware of the correct locality, and listed the type from Nicaragua.

Comparing the type specimens of *Ageratum scabriusculum* and *A. petiolatum* readily shows them to be conspecific. Robinson, apparently, was of the same opinion. He placed the penciled note "the type material of *A. scabriusculum* (Benth.) Hemsl. is just this sort of smoothish thing, clearly identical. B. L. R. 1925" on *Wright s.n.* (GH). Both possess the characteristics of *A. petiolatum*, namely nearly glabrous, thin, long petioled, ovate leaves which are pale green to gray beneath. The binomial *A. petiolatum* (Hook. & Arn.) Hemsl., published eleven years before *A. scabriusculum* (Benth.) Hemsl., must be adopted for this species.

The chromosome number $n = 10$ was determined from meiotic material of *King 5289* but published (Turner & King, 1964) as *A. corymbosum*. Study of the voucher leaves no question but that it should be referred to this taxon.

This species occurs from Nicaragua (Guatemala?) to Panama in moist habitats on slopes and along road sides from *ca.* 300–900 m elevation, uncommon to 1400 m (Fig. 16). Flowers are present from May through July; fruits are present from July through September(–January).

COSTA RICA. De la route a Alta Río Jesús en San Ramón, *Brenes 3542* (F, NY); vicinity of San Ramón, *Brenes 4350* (F, NY); "La Calera" de San Ramón, *Brenes 6435* (F); Cerro de San Isidro, *Brenes 14494* (GH); San Miguel de San Ramón, *Brenes 14930* (F); San Juanello, *Smith 9818* (F).

NICARAGUA. Managua, *Artemio 70* (US); Masaya, *Baker 2220* (GH); Sierra de Managua, *Garnier 199* (US); slope of Santiago Volcano near Masaya, *Maxon 7661* (GH, US); Las Nubes and vicinity S of Managua, *Maxon et al. 7464* (US); El Vieja, *Oersted 250* (C); Realejo, *Sinclair s.n.* (K); vicinity of Casa Colorado near El Curcero, summit of Sierra de Managua, *Standley 8188* (F, GH); without locality, *Chaves 335* (F, US), *Wright s.n.* (GH, US).

PANAMA. 25 miles N of Concepción, cytological voucher, *King 5289* (TEX, UC); without locality, *Oersted s.n.* (BM).

25. **Ageratum lucidum** Robins., Proc. Amer. Acad. Arts 36: 475. 1901.

Holotype: MEXICO. Morelos: On mossy sides of conglomerate knobs of Sierra de Tepoxtlan, 7500 ft., *Pringle 8362* (GH); isotypes, BM, C, F, K, MICH, MIN, MO, MSC, NY, P, UC, US.

Perennial *shrubs* 3–5(–8.5) dm tall; *roots* fibrous; *stems* erect, finely striate, branched, branches opposite, usually curved, ascending, younger parts reddish, older bark gray, densely white puberulous with scattered orange glandular atoms at least on younger parts to glabrous or nearly so on older, leafy nearly to inflorescences; *leaves* opposite, petioled, firm, ovate, 3–5(–7) cm long, 1.6–2.2(–4) cm wide, base obtuse, apex acute, margin slightly revolute, scabrous, serrate, teeth white tipped, to entire, upper surface bright, shining green, orange-glandular punctate, sparingly white puberulous at least over the prominent reticulate veins, lower surface shiny, pale green, densely orange glandular-punctate, sparingly puberulous over the conspicuous venation; *petioles* 0.4–1 cm long, very narrowly winged, adaxially channeled, puberulous with scattered orange glandular atoms; *inflorescences* terminal, heads 0.6–0.9(–1) cm in diameter, solitary or 3–7 grouped in an irregular, corymbose cluster; *peduncles* 0.5–3.6 cm long, often subtended by opposite, linear-lanceolate, green, reduced leaves, bracteolate, densely puberulous with scattered, glandular atoms; *bracteoles* alternate, narrowly linear, puberulous, glandular-atomiferous, about 5 mm long, merging with involucre; *involucres* campanulate, bracts biseriate, firm, 2-ribbed, prominently so basally, outer bracts lanceolate to lance-oblong, rarely linear, (4.75–)5–6(–6.25) mm long, 0.75–1.1(–1.8) mm wide, green throughout to variously tinged with reddish-purple, white puberulous with orange glandular atoms basally, less puberulous toward apex, margin entire, green or scarious, at times ciliate, apex acute, inner bracts similar though less puberulous; *corollas* funnelform, (2.25–)2.5–3 mm long, orange-glandular atomiferous, sparingly puberulous or glabrous, white (?); *achenes* 5-angled, shiny, black, (1.35–)1.5–2.2(–2.5) mm long, glabrous, slightly tapered toward white carpopodium; *pappus* coroniform, white, (0.2–)0.3–0.5 mm long, margin shallowly dentate, rarely producing a single subulate awn, then pappus 2–3.1 mm long.

Ageratum lucidum, an attractive shrubby species, is apparently rare and local in its distribution. All specimens, except one, available for study were collected from the same location by Pringle, most recently in 1906. The most distinctive characteristics are the very bright and shiny green leaves, the short shrubby habit, and the heads which are somewhat larger than in other species.

Ageratum lucidum is seemingly restricted to Sierra de Tepoxtlan, Morelos, and eastern Jalisco. Buds, flowers and fruits were noted on specimens collected from August to November.

MEXICO. JALISCO: Near farm land, 42 miles E of Guadalajara, *Waterfall 15638* (MICH). MORELOS: Sierra de Tepoxtlan, *Pringle 8362* (BM, C, F, K, GH, MICH, MIN, MO, MSC, NY, P, UC, US), *Pringle 13022* (F, GH, K, MICH, MO, MSC, UC, US), *Pringle 13805* (F, MICH, MO, MSC, UC, US).

26. **Ageratum scorpioideum** Baker *in* Mart., Fl. Bras. 6(2): 197. 1876.

Holotype: BRITISH GUIANA. *Rob. Schomburgk 353* (K).

Perennial (?) *herbs*; *roots* coarse, fibrous, adventitious at nodes and internodes; *stems* erect or repent, branched, branches erect, 3–4 dm tall, deep reddish, glabrous throughout, leafy nearly to apex; *leaves* opposite, very short-petioled to sessile, lanceolate, 5–8 cm long, 1.3–1.7 cm wide, base entire, gradually acuminate, apex acute, margin crenate on distal ¾, upper surface glabrous, inconspicuously pinnately veined, lower surface glabrous, conspicuously pinnately veined; *petioles*, if present, glabrous, less than 4 mm long; *inflorescences* terminal, the solitary heads grouped in an irregular panicle; *peduncles* glabrous, 0.2–1 cm long, bracteolate only at nodes; *bracteoles* semi-membranaceous, keeled, *ca.* 2 mm long; *involucres* campanulate, bracts biseriate, inconspicuously 2-ribbed, outer series lanceolate, 2.6–3 mm long, 0.9–1.15 mm wide, glabrous to very sparingly short pilose, apex acute, margin entire, glabrous to sparingly ciliate, inner series spatulate; *corollas* funnelform, 1.1–1.3 mm long, glabrous throughout, tube *ca.* 0.25 mm long, abruptly expanded into the throat; *achenes* dark brown, glabrous, 1.2–1.5 mm long, contracted apically, slightly tapered toward inconspicuous carpopodium; *pappus* coroniform, 0.3–0.5 mm high, margin 5-dentate.

Some confusion exists as to the correct designation of a type specimen for this species. Three different collections are referred to as the type on herbarium labels, namely *Schomburgk 353, 355,* and *1188*. The only specimen cited in the original description of *Ageratum scorpioideum* is *Schomburgk 353.* I have seen this specimen at Kew, and since it is the only one cited by Baker it should automatically become the holotype. *Schomburgk 355,* also at Kew, bears a label reading "Type Specimen." And although it was presumably seen by Baker, it can hardly be accepted as type. *Schomburgk 1188* is designated on the label as the type for *Coelestina repens* Sch. Bip., a *nomen nudum* listed in Schomburgk (1848). Though Schultze's name is older, its publication is not valid, and it cannot be applied.

Ageratum scorpioideum is a poorly known species, and apparently it has not been collected since Schomburgk obtained it in 1842. Nevertheless, the limited material available shows a distinctive species separated from all others by the combination of glabrousness, the very small, paniculate heads, and the sessile, lanceolate leaves.

This species is known only from moist savannahs in British Guiana. No dates of flowering or fruiting are known.

BRITISH GUIANA. Moist savanne, Canuku Mountains, *Richard Schomburgk 488* (GH, P); Savanne, *Richard Schomburgk 1188*; photograph (F, TEX), specimen at (B) undoubtedly destroyed during World War II; Pirara, *Robert Schomburgk 355* (BM, K, MO); without locality, *Robert Schomburgk 353* (K).

Section III. **Pectinellum** DC., Prod. 5: 109. 1836.

Annuals; *roots* fibrous and adventitious at nodes; *stems* repent; *leaves* opposite, on long vertical petioles, cordate-orbiculate, margin lobed ⅓–½ way to midline of leaf; *inflorescences* borne singly; *involucral bracts* biseriate, oblong to spatulate, pilose, unribbed; *corollas* pale lavender to white, abruptly expanded into the campanulate throat; *achenes* glabrous, carpopodium very small or lacking; *pappus* of free oblong tan scales apically fimbriate to short setiferous.

The single species of this section is confined to moist habitats in Cuba and Hispaniola. Data concerning flowering and fruiting is incomplete and inconclusive.

Type species: *Ageratum domingense* Spreng.

27. **Ageratum domingense** Spreng., Syst. 3: 446. 1826.

Holotype: SANTO DOMINGO. Without specific location, *Bertero s.n.* (DC-G, not seen); isotype, P; photograph, US; tracing, GH.
Phania domingensis (Spreng.) Griseb., Cat. Pl. Cub. 145. 1866, fide Robinson (1913*b*).
Carelia domingensis (Spreng.) Kuntze, Rev. Gen. 1: 325. 1891, fide Robinson (1913*b*).
Eupatorium planellasianum Maza & Molt., Anales Hist. Nat. 29: 271. 1890. *Nomen nudum*, fide Robinson (1913*b*).

Annual, to 1.5 dm long; *roots* fibrous, adventitious at nodes; *stems* green, sparsely branched, repent, white pilose; *leaves* numerous, opposite, petioled, cordate-orbiculate, 0.5–1.1 cm long, 0.5–1.2 cm wide, margin lobed ⅓–½ way to midline of leaf, lateral lobes oblong, pointing toward apex, apical lobe slightly larger, all lobes entire, apically obtuse, upper lamina surface dark green, lower surface paler, both surfaces white-pilose and glandular-punctate, punctae yellow to amber, the 3 veins inconspicuous from beneath; *petioles* (0.2–)0.4–1.5(–2.5) cm long, white pilose, vertical along repent stem; *inflorescences* of a single head borne on pilose-puberulent, bracteolate peduncle, 2.5–4.5 cm long; *bracteoles* alternate, pilose, *ca.* 1 mm or less long; *involucres* turbinate, bracts biseriate, oblong to spatulate, (2–)2.4–3(–3.5) mm high, an outer one 0.6–1(–1.9) mm wide, green to brownish, apex acute or obtuse, surface unribbed, pilose, margin entire; *corollas* pale lavender to white, (1.25–)1.75–2.2 mm long, glabrous to sparsely dotted with yellow-amber glandular atoms, tube abruptly expanded into the campanulate throat and 5 spreading acute lobes; *achenes* 1.4–1.5 mm long, glabrous, brown to black, tapering toward sharply acute base; *carpopodium* very small or absent; *pappus* of 5 free, oblong, tan scales, 0.4–1 mm long, apically variously fimbriate to short setiferous.

Ageratum domingense is placed in a separate section and is unique in the genus in the following features. It alone possesses trailing, repent stems, ribless involucral bracts, cordate-orbiculate leaves with lobed margins disposed on vertical petioles, and pollen grain exines about 5 μ thick, which is 2–3 μ thicker than observed in other species. That *A. domingense* does belong with *Ageratum* is obvious from the five oblong, flattened pappus scales and anther appendages.

Both *Ageratum domingense* and *A. gaumeri* have the elongated peduncle bearing a single terminal inflorescence, though I do not believe this common character necessarily indicates a close relationship. *Ageratum domingense* has too many unique features to suggest a close relationship with any species of *Ageratum.*

Ageratum domingense is restricted to river banks and rocky hill sides in Cuba and Hispaniola (Fig. 17). Dates of flowering and fruiting are incomplete, but on the specimens studied, flowers and fruits are present in March, July, and December.

CUBA. PINAR DEL RIO: Vinales, *Alain 4427* (NY); Bahía Honda, *Ekman 10398* (F), *Wilson 9405* (GH, NY); Sierra de les Orgonos, valley of Río Santa Cruz, *Ekman 16401* (NY); banks of Eaco Eaco River, *León 12517* (NY); without locality, *Wright 2798* (K, NY).

HISPANIOLA. Without locality, *Bertero s.n.* (P).

Section IV. **Stachyofolium** M. F. Johnson, sect. nov.

Perennis. Radix fibrata. Folia alterna, elliptica. Capitula formata in corymbum terminalem. Involucra squamis lineari-spatulatis, 4-costate, margine integro. Receptaculum nudum. Corollae infundibuliformes, albae, pilosae et glandulosae. Achenia glabra, basin versus decresentia, carpopodio carentia. Pappus coroniformis, margine integro vel dentibus exiguis.

Perennials; *roots* fibrous; *leaves* alternate, elliptic; *inflorescences* grouped in a loose corymbose cluster; *involucral bracts* biseriate, linear to spatulate, 4-ribbed, margin entire; *receptacle* naked; *corollas* funnelform, white, pilose and glandular; *achenes* glabrous, tapering to base, carpopodium lacking; *pappus* coroniform, margin entire to obscurely dentate.

Data concerning distribution and flowering are incomplete.

Type species: *Ageratum stachyofolium* Robins.

28. **Ageratum stachyofolium** Robins., Proc. Amer. Acad. Arts 36: 476. 1901.

Holotype: MEXICO. Oaxaca: Vicinity of La Parada, *Nelson 991* (GH); isotypes, F, K, US; photograph, MIN.

Perennial, 5.5–6 dm tall; *roots* coarse, white, fibrous; *stems* erect, simple, reddish, white pilose throughout, becoming densely so toward inflorescences; *leaves* alternate throughout or very rarely opposite below and alternate above, sessile or short-petioled, elliptic, 3–3.5 cm long, 1.1–1.4 cm wide, base obtuse, apex widely acute, margin revolute, crenate, teeth slightly thickened, upper surface dark green, white pilose, lower surface pale green, white pilose and mixed with yellow glandular atoms, veins reticulate, prominent; *petioles* 1–5 mm long, white pilose or absent; *inflorescences* terminal, the 7–10 heads disposed in a loose corymbose cluster; *peduncles ca.* 1.5–3 cm long, densely canescent-pilose, bracteolate; *bracteoles ca.* 1 cm long, filiform to spatulate, white pilose; *involucres* campanulate, bracts biseriate, firm, 4-ribbed, pale green, linear to spatulate, (5–)6–6.5 mm high, 0.55–0.7 mm wide, margin entire, apex acute, surface white pilose, becoming densely so at apex, at times with scattered yellow glandular atoms; *corollas* white, funnelform, 3.25–3.55 mm long, the narrow tube and slightly expanded throat white-pilose with scattered glands, lobes glabrous, style branches long exerted *ca.* 4× corolla in length; *achenes* brown to black, 2.25–2.7

mm long, glabrous, tapering to pointed base, carpopodium lacking; *pappus* coroniform, tan, firm, 0.35–0.55 mm long, margin entire to obscurely dentate.

Ageratum stachyofolium is poorly represented in herbaria and is not well known. However, characteristics of the pappus in particular and of the inflorescences in general place the species in *Ageratum*.

The combination of the oblong, 4-ribbed involucral bracts, the sharply pointed achene lacking a carpopodium, and the alternate leaves is unique in the genus and suggests that *A. stachyofolium* is only distantly related to the other species of *Ageratum*. Thus it is disposed in a separate section. The affinities of *A. stachyofolium* may become more clear when a greater abundance of specimens is available for study.

This species is known only from the type locality, La Parada, Oaxaca, at *ca.* 2500–2800 m elevation. I have been unable to find this site on the maps I consulted. Plants studied were collected in August and were in flower and fruit.

Section V. **Perplexans** M. F. Johnson, sect. nov.

Herba annua. Radix fibrata. Folia opposita, deltata vel rhombea. Capitulis in cymas formatis. Involucra squamis sub-membranaceae, 5-nervatis, ovatae, margine integro. Receptaculum paleaceum. Paleae sub-membranaceae, lanceolatae. Corollae anguste infundibuliformes, scabrisque. Achenia paginae scabris pilis luteis; carpopodio non manifesto. Pappus 5–6 squamis lanceolatis, membranaceis.

Annual *herbs*; *roots* fibrous; *leaves* opposite, deltoid or rhomboid; *heads* grouped into cymose clusters; *involucral scales* sub-membranaceous, 5-nerved, ovate, margin entire; *receptacle* paleaceous, paleae sub-membranaceous, lanceolate; *corollas* narrowly infundibuliform, scabrous externally; *achenes* coated with scabrous yellow upward pointing hairs, the carpopodium inconspicuous; *pappus* of 5–6 lanceolate, membranaceous scales.

The single species in this section is known only from Yungas, Bolivia. Dates of flowering and fruiting are not known.

Type species: *Ageratum perplexans* M. F. Johnson.

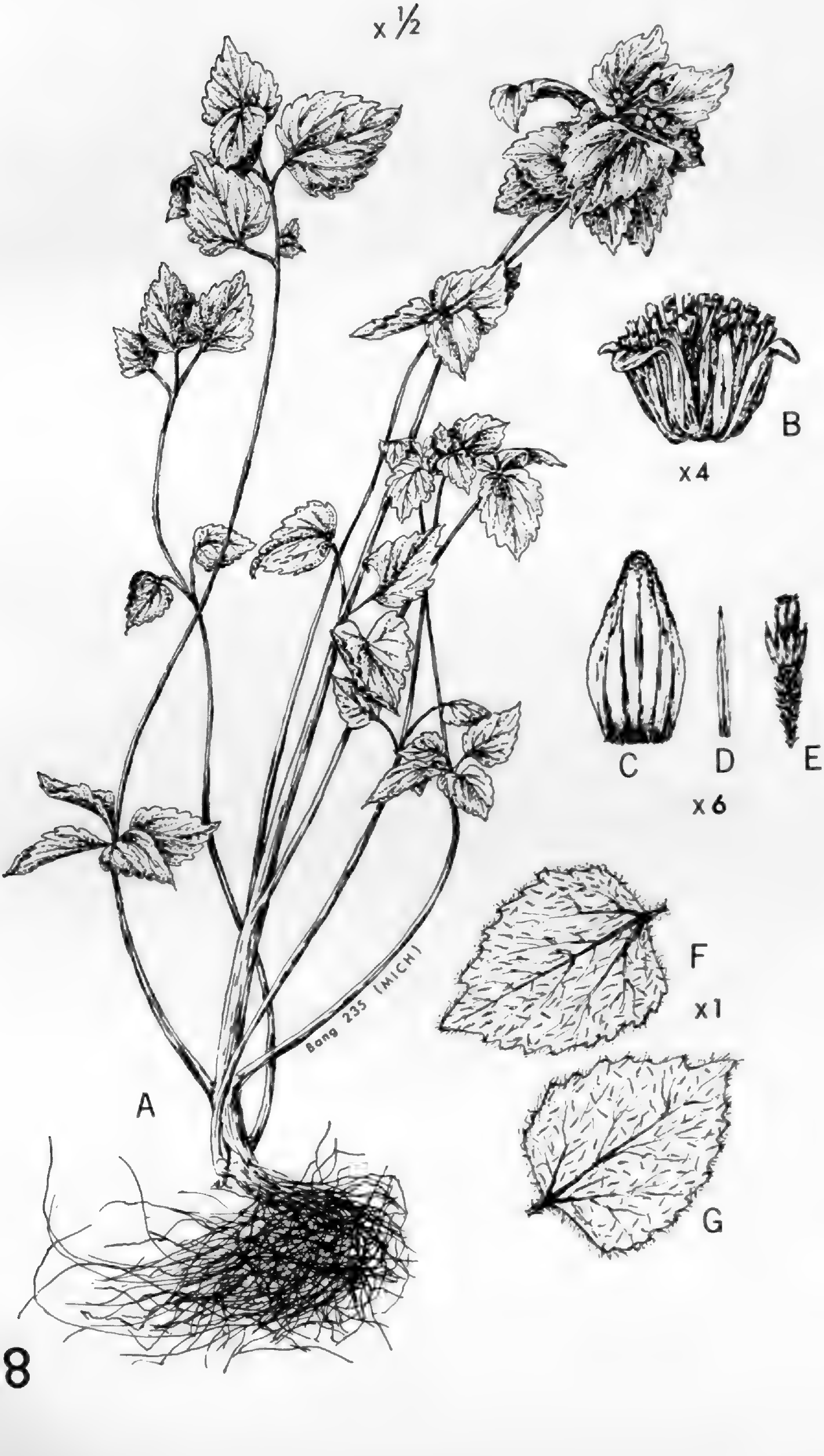
29. **Ageratum perplexans** M. F. Johnson, sp. nov.

Holotype: BOLIVIA. Yungas, 1890, *A. Miguel Bang 235* (MICH); isotype, NY. Distributed as *Ageratum conyzoides* L.

Involucra hemisphaerica. Squamae 3-seribus submembranaceae, 5–6 nervis non manifestis, ovatae, 3.25–3.5 mm altae, 2–2.25 mm latae, pallide viridulae, purpureae apicem versus et insuper vervis, paginis glabris, rarius sparsissime breviter pilosae, marginem versus herbae naturam habentes, margine integro, apice ciliato, late rotundae. Receptaculum conicum, paleaceum. Paleae submembranaceae, 1 vel 2 nervis, lanceolatae, ca. 2.75 mm longae, ca. 0.5 mm latae,

→

FIGURE 18. *Ageratum perplexans*. — A. Habit. — B. Inflorescence. — C. Involucral bract. — D. Receptacle palea. — E. Flower with scabrous achene and pappus scales. — F. Detail of lower leaf surface. — G. Detail of upper leaf surface. [After *Bang 235*.]


x 1/2
B
x4
C
D
E
x6
F
x1
G
A
Bong 235 (MICH)
18

paginis glabris, margine aliquantulum eroso, apice acuto. Achenia nigra, paginae acheniorum scabris pilis luteis. Pappus 5–6 squamis, fulvis.

Annual, ca. 3.5–4 dm tall; *roots* fibrous; *stems* erect, branched from base, glabrous or sparingly puberulent basally, becoming densely white pilose toward inflorescences; *leaves* opposite, deltoid to rhomboid, *ca.* 3.6 cm wide, 4.5 cm long, apex acuminate, base truncate or obtuse, entire, margin pilose, coarsely crenate to very shallowly lobed, teeth cuspidate, upper surface dark green, sparingly pilose over the inconspicuous palmate venation; *petioles ca.* 2–2.2 cm long, sparingly pilose to more densely so when young; *inflorescences* terminal on stem and branches, the few heads grouped in a cymose cluster; *peduncles* 3–5 mm long, puberulous-pilose, ebracteolate; *involucres* hemispherical, bracts 3-seriate, sub-membranaceous, obscurely 5-nerved, ovate, 3.25–3.5 mm high, 2–2.35 mm wide, pale green, purple over nerves and apically, surface glabrous to rarely very sparingly short pilose, margin entire, herbaceous, apex ciliate, broadly rounded; *receptacle* conical, paleaceous, paleae sub-membranaceous, 1 or 2 nerved, lanceolate, 2.75 mm long, 0.5 mm wide, surface glabrous, margin somewhat erose, apex acute; *corollas* tubular to narrowly funnelform, *ca.* 1.75 mm long, white (?), tube and throat and short obtuse lobes externally scabrous; *achenes* 5-angled, black, *ca.* 1.75 mm long, tapering to inconspicuous carpopodium, surface covered with upward pointing yellow scabrous hairs; *pappus* of 5–6 lanceolate, tawny membranaceous scales *ca.* 1 mm long, margin finely fimbriate, apex fimbriate, acute (Fig. 18).

Ageratum perplexans, so named because of the perplexing nature of the characters combined in a single plant, has been collected but once, in 1890, and was determined as *Ageratum conyzoides* L. It was immediately apparent to me, however, that this plant could not be referred to that species.

Though possessing a pappus of scales which resembles that of section *Ageratum*, the scales lack the setae so common in that section. Another similarity to section *Ageratum* is seen in the scabrous achenes. However, the achenes in section *Ageratum* are scabrous only along the angles, while in *A. perplexans* the entire achene is conspicuously covered with yellow scabrous hairs.

An affinity to some species in section *Coelestina* is noted in the presence of receptacle paleae in both. However, receptacle paleae are not found in combination with a pappus of scales elsewhere in this genus. A third perplexing feature of *A. perplexans* is the extremely wide (to 2.35 mm wide) and relatively smooth involucral bracts which resemble the unribbed ones of *A. domingense.*

Ageratum perplexans shows outward similarities to species which are very probably only remotely related to it. Also, the combination of achenes with yellow scabrous hairs, the wide, ovate, merely nerved involucral bracts, and the receptacle paleae is found nowhere else in the genus. Because of this unique mixture of characters, which suggests a quite remote relationship to other species in the genus, a new section is erected to encompass it. Hopefully more collections of *A. perplexans* will become known so that a more complete study of this strange and extremely interesting *Ageratum* can be made.

Ageratum perplexans is known only from the type locality, Yungas, Bolivia. Dates of flowering and fruiting are not known.

Excluded Names

Though I have not personally seen specimens for all the excluded names, I have studied their descriptions and concur with B. L. Robinson's disposition where indicated. Dr. Rogers McVaugh has studied type specimens of several species; I am following his determinations where indicated.

Ageratum adscendens Sch. Bip. *ex* Benth. & Hook., Gen. Pl. 2: 242. 1873, is *Oxylobus adscendens* (Sch. Bip.) Robins. & Greenm. (Robinson, 1913*b*).

Ageratum agrianthus O. Hoffm. *in* Engler & Prantl, Nat. Pfl. 4(5): 134. 1890, is *Trichogoniam* sp. (Robinson, 1913*b*).

Ageratum alternifolium (Gardn.) Baker *in* Martius, Fl. Bras. 6(2): 195 is a species dubium (Robinson, 1913*b*).

Ageratum altissimum L., Sp. Pl. 2: 839. 1753, is *Eupatorium urticaefolium* Reichard (Robinson, 1906*a*; 1906*b*).

Ageratum angustifolium Spreng., Syst. 3: 446. 1826, is *Calea angustifolia* (Spreng.) Sch. Bip. *ex* Baker *in* Martius, Fl. Bras. 6(3): 256. 1884.

Ageratum aquaticum Roxb., Hort. Bengal. 61. 1814, is *Adenostemma lavenia* (L.) Kuntze, Rev. Gen. Pl. 1: 304. 1891.

Ageratum arbutifolium HBK is *Oxylobus arbutifolius* (HBK) Gray (Robinson, 1913*b*).

Ageratum callosum Wats. is *Alomia callosa* (Wats.) Robins. (Robinson, 1913*b*).

Ageratum campuloclinioides Baker *in* Martius, Fl. Bras. 6(2): 196. 1876, is *Trichogoniam* sp. (Robinson, 1913*b*).

Ageratum ciliare L., Sp. Pl. 2: 839. 1753, is of uncertain application. See discussion under "History of Taxonomic Literature."

Ageratum coeruleum Desf., Tab. École Bot. 98. 1804, is a nomen nudum.

Ageratum coeruleum Sieber *ex* Baker *in* Martius, Fl. Bras. 6(2): 345. 1876, is *Eupatorium macrophyllum* L. (Robinson, 1913*b*).

Ageratum confertum (Gardn.) Benth. *ex* Baker *in* Martius, Fl. Bras. 6(2): 195. 1876, is excluded because of the clavallate pappus scales but needs further study (Robinson, 1913*b*).

Ageratum conspicuum Hort. *ex* C. Koch & Fint, Wochenshr. Gärtnerei Pflanzenk. 1858: 33. 1858, is *Eupatorium glechonophyllum* Less. (Robinson, 1913*b*).

Ageratum conyzoides Sieber *ex* Steudel, Nom. Bot. Ed. 2. 2: 37. 1841, is *Eupatorium repandum* Willd. (Robinson, 1913*b*).

Ageratum corymbosum (DC.) Benth., Bot. Voy. Sulphur 111. 1844, is *Trichogoniam* sp. (Robinson, 1913*b*).

Ageratum corymbosum Zuccag. var. *st-antonii* Sch. Bip. *ex* Klatt, Leopoldiana 20: 75. 1884, is a nomen nudum.

Ageratum febrifugum Ses. *ex* DC, Prodr. 5: 104. 1936, is *Piqueria trinervia* Cav. (Robinson, 1913*b*).

Ageratum glanduliferum Sch. Bip. *ex* Hemsl. *in* Godman & Salvin, Biol. Centr. Amer. Bot. 2: 82. 1881, is *Oxylobus glanduliferus* (Sch. Bip.) Gray (Robinson, 1913*b*).

Ageratum glanduliferum Sch. Bip. var. *albiflorum* Sch. Bip. *ex* Gray, Proc. Amer. Acad. Arts 15: 26. 1879, is *Oxylobus glanduliferus* (Sch. Bip.) Gray (Robinson, 1913*b*).

Ageratum glaucum Hort. *ex* Vilmorin, Blumengärtnerei, Ed. 3. 1: 448. 1894—The description suggests a *Eupatorium*.

Ageratum guianense Aublet, Hist. Pl. Gui. Fr. 2: 800. 1775, is *Eupatorium macrophyllum* L. (Robinson, 1913*b*).

Ageratum heterolepis Baker *in* Martius, Fl. Bras. 6(2): 198. 1876, is *Alomia heterolepis* (Baker) Robins. (Robinson, 1913*b*).

Ageratum isocarphoides (DC.) Hemsl. *in* Godman & Salvin, Biol. Centr. Amer. Bot. 2: 82. 1881, is *Alomia isocarphoides* (DC.) Robins. (Robinson, 1913*b*).

Ageratum laciniatum Ses. & Moc., La Naturaleza, ser. 2. 1: 136. 1887, is *Stevia trifida* Lag. (personal communication, R. McVaugh).

Ageratum lasseauxii Carr., Rev. Hort. 42: 90. 1870, is *Eupatorium lasseauxii* Carr. (Robinson, 1913*b*).

Ageratum latifolium Cav. var. *galapageium* Robins., Contr. Gray Herb. 42: 466. 1913, is *Alomia* sp.

Ageratum lineare Cav., Ic. Descr. Pl. 3: 3. *t. 205*. 1795, is *Palafoxia linearis* (Cav.) Lag. (Robinson, 1913*b*).

Ageratum longifolium (Gardn.) Benth. *ex* Baker *in* Martius, Fl. Bras. 6(2): 197. 1876, is *Alomia longifolia* (Gardn.) Robins. (Robinson, 1913*b*).

Ageratum matricarioides (Spreng.) Less., Syn. Gen. Composit. 155. 1832, is *Phania matricarioides* (Spreng.) Griseb. (Robinson, 1913*b*).

Ageratum melissaefolium DC, Prodr. 5: 109. 1836, is *Trichogoniam* sp. (Robinson, 1913*b*).

Ageratum microcarpum (Benth.) Hemsl. *in* Godman & Salvin, Biol. Centr. Amer. Bot. 2: 82. 1881, is *Alomia microcarpa* (Benth.) Robins. (Robinson, 1913*b*).

Ageratum microcephalum Hemsl. *in* Godman & Salvin, Biol. Centr. Amer. 2: 82. 1882, is *Alomia microcephala* (Hemsl.) Robins. (Robinson, 1913*b*).

Ageratum microphyllum Sch. Bip. *in* Seemann, Bot. Voy. Herald 298. 1856, is *Ageratella microphylla* (Sch. Bip.) Gray, Proc. Amer. Acad. Arts 22: 419. 1887.

Ageratum obtusifolium Lam., Encycl. Méth. 1: 54. 1783, is not well enough described for proper disposition.

Ageratum paniculatum Hort. *ex* Steudel, Nomen. Bot., Ed. 2. 1: 609. 1840, is *Brickellia paniculata* (Mill.) Robins. (Robinson, 1906*b*).

Ageratum pedatum Ort., Hort. Reg. Bot. Matrit. 38. 1797, is *Florestina pedata* (Cav.) Cass. (Robinson, 1913*b*).

Ageratum pohlianum Baker *in* Martius, Fl. Bras. 6(2): 197. 1876, is not described well enough for proper disposition.

Ageratum polyphyllum Baker *in* Kew Bull. 139: 148. 1898, is *Ageratinastrum polyphyllum* (Baker) Mattf.

Ageratum punctatum Jacq., Hort. Schoenb. 3: 28. *t. 300.* 1798, is *Stevia serrata* Cav. (Robinson, 1913*b*).

Ageratum purpureum Aubl., Hist. Pl. Gui. Fr. 2: 800. 1775, is *Eupatorium* sp. (Robinson, 1913*b*).

Ageratum purpureum Ses. *ex* DC, Prodr. 5: 122. 1836, is *Stevia viscida* HBK or *Stevia pilosa* Lag. (personal communication, R. McVaugh).

Ageratum quadriflorum Blanco, Fl. Filip. 1: 624. 1837, is *Elephantopus spicatus* B. Juss. *fide* Villarii *in* Blanco, Fl. Filip., Ed. 3. Append. 114. 1880. (Robinson, 1913*b*).

Ageratum riuale Ses. & Moc., La Naturaleza, ser. 2. 1: 136. 1889, is *Pectis uniaristata* DC. (personal communication, R. McVaugh).

Ageratum rubens Viviani, Elenchus Pl. Hort. Bot. 9. 1802, is insufficiently described for proper disposition.

Ageratum salicifolium Coult. *in* J. D. Smith, Enum. Pl. Guatemal. 4: 72. 1895, is *Alomia guatemalensis* Robins. (Robinson, 1913*b*).

Ageratum sandwichense Levl., Repert. Spec. Nov. Regni Veg. 11: 63. 1913, is excluded because of its capillary pappus, but its proper disposition needs study. A type, *Fauri 940*, was seen (P) in 1966.

Ageratum serratum Glaziou, Bull. Soc. Bot. France 55(3): 382. 1909, is a *nomen nudum.*

Ageratum sessilifolium Schauer, Linnaea 19: 715. 1847, is *Trichocoronis sessilifolia* (Schauer) Robins. (Robinson, 1906*b*).

Ageratum sordidum Blake, Contr. U. S. Natl. Herb. 20(13): 534. 1924, is *Oxylobus glanduliferus* (Sch. Bip.) Gray (Robinson, 1913*b*).

Ageratum striatum Ses. & Moc., La Naturaleza, ser. 2. 1: 136. 1889, is probably *Stevia serrata* Cav. (personal communication, R. McVaugh).

Ageratum strictum Sims, Bot. Mag. *t. 2410.* 1823, is *Adenostemma lavenia* (L.) Kuntze (Robinson, 1913*b*).

Ageratum viscosum Ort., Hort. Reg. Bot. Matrit. 37. 1797, is *Stevia salicifolia* Cav. (Robinson, 1913*b*).

Ageratum viscosum Ses. & Moc., La Naturaleza, ser. 2. 1: 135. 1889, is *Stevia* sp. (personal communication, R. McVaugh).

Ageratum wrightii Torrey & Gray *ex* Gray, Proc. Amer. Acad. Arts 1: 46. 1848, is *Trichocoronis wrightii* (T. & G.) Gray.

Phalacraea latifolia DC. and *P. coelestina* Regel are given in lists of synonymy under *Ageratum conyzoides* L. by Hooker & Jackson (1893) and Vilmorin (1896) respectively. These names, I feel, should not be included in lists of synonyms under any *Ageratum* species because *Phalacraea* has the following characteristics, none of which occur in *Ageratum*: laterally compressed achenes, 3-ribbed involucral bracts, corolla tubes pilose-hispid at the base, lack of a pappus, and apical anther appendages (*cf.* Delessert, 1839; and Regel, 1854).

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NOTES

A NEW MOSS FROM WESTERN PANAMA—*SQUAMIDIUM CHIRIQUENSE*

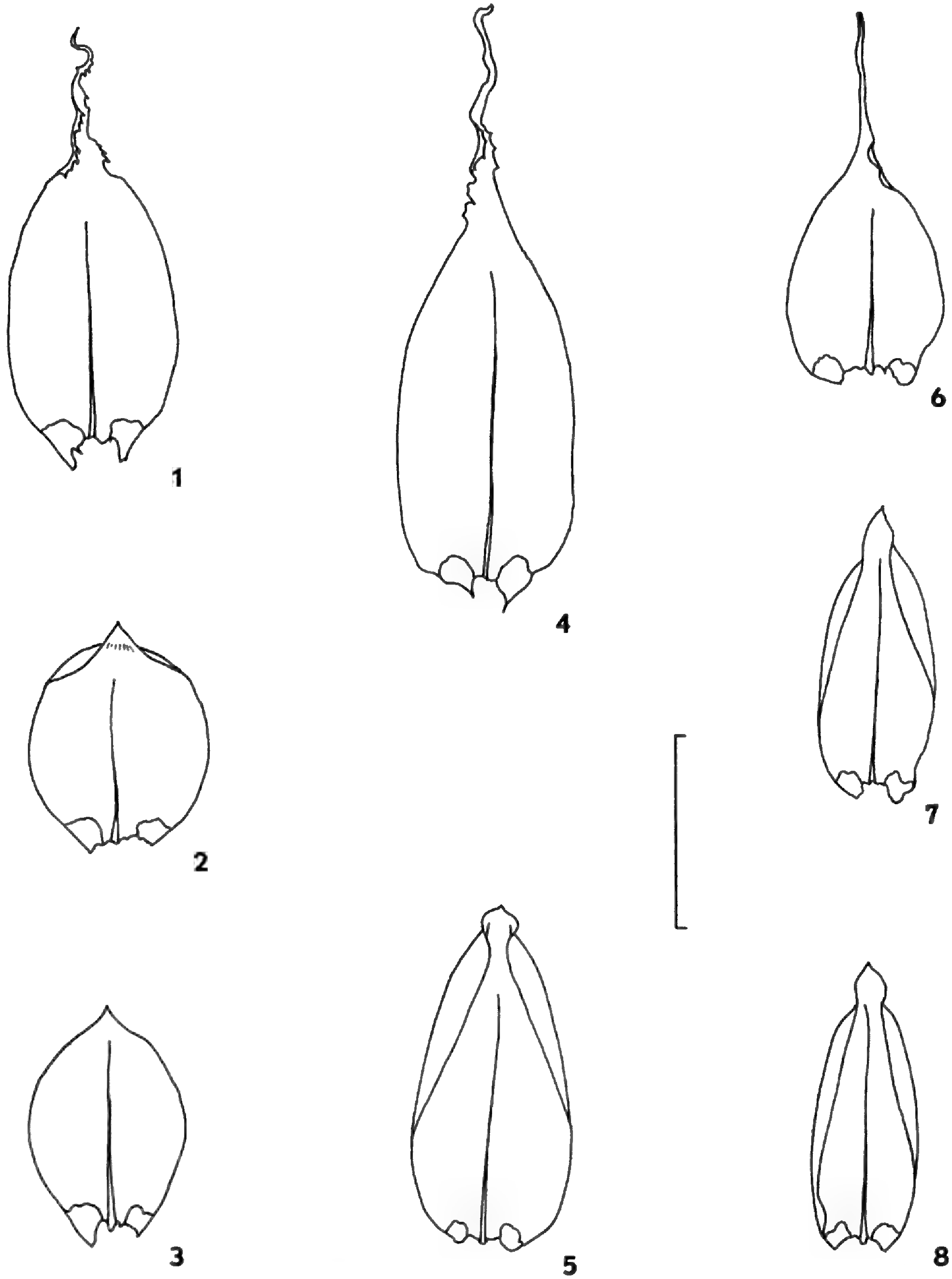
In the course of a preliminary review of the essentially neo-tropical moss *Squamidium* (C. Müll.) Broth., it has become apparent that a recent collection from Chiriquí, Panama, represents a new species. *Squamidium* is the meteoriaceous genus with smooth laminal cells, strongly differentiated alar cells, and one costa. The only other genus in the family with this combination of characters is *Floribundaria.* Some species of *Floribundaria* have papillose laminal cells; and all are laxly, somewhat complanate-foliate. *Squamidium* is densely, terete-foliate.

Species of *Squamidium* are typically epiphytic with both horizontal and pendent stems, each of which produce short branches. The leaves of the stems are in most cases strikingly different in apperance from those of the branches. Hopefully, these differences will provide the basic characters for a taxonomic revision of the entire genus—*Squamidium* fruits very rarely. The new Panamanian species exhibits this dimorphism in the leaves as do two other species from nearby areas.

Squamidium chiriquense M. R. Crosby, sp. nov.

Squamidio crispipilo simile sed foliis ramularum acutis non galatis.

Primary *stems* horizontal; secondary stems pendent, produced by indeterminate growth of branches; leaves appressed when moist with lower, broader portion clasping stem; little changed when dry; *branches* 12–15 mm long, produced at 3–5 mm intervals; leaves concave, erect-spreading, not conspicuously helically seriate when moist, somewhat flattened, appressed, slightly wrinkled when dry. *Stem leaves* ovate with gradually acuminate apex, (1.25–)1.5–2.25 × 0.7–0.8 mm; margins plane below, irregularly inflexed at base of acumen and along acumen; entire below, with scattered teeth just below acumen, acumen serrate with large often recurved teeth; laminal cells linear throughout, shortest, 23–35 × 4–6 μ, and thin-walled to slightly incrassate and porose just below acumen, longest, 45–80 × 4–7, and usually thinnest-walled at mid-leaf, shorter and broader, 57–70 × 8–9 μ, and incrassate and porose above base; cells of acumen linear; 55–70 × 4–6 μ, marginal row broader and lax, 20–45 × 10–14 μ, portions of outer walls produced into teeth; alar cells similar to those of branch leaves; costa extending to near base of acumen. *Branch leaves* broadly ovate with acute to rounded acute apex, 1.12 × 0.75–0.9 mm; margins plane throughout to slightly inflexed just below apex; entire below, serrulate at apex, laminal cells linear throughout, 45–60 × 2 μ, thin-walled above, becoming thicker-walled and porose toward base, often thinnest-walled and shorter, 20–40 μ long, just below apex; cells of acumen elliptic to narrowly elliptic, 18–23 × 7–10 μ; alar cells rather incrassate, in subquadrate cluster, 100–150 μ on a side, 10–15 cells along margin and 10–12 cells wide, marginal row transversely rectangular, 9–11 × 15–16 μ, to occasionally triangular, inner cells rounded-quadrate to broadly



FIGURES 1–8. — 1–3. *Squamidium chiriquense.* — 1. Stem leaf. — 2–3. Branch leaves (1–3, *Crosby 3975*). — 4–5. *Squamidium crispipilum.* — 4. Stem leaf. — 5. Branch leaf (4–5, *Stork 1388*). — 6–8. *Squamidium macrocarpum.* — 6. Stem leaf. — 7–8. Branch leaves (6–8, *Spruce 1191-1194*). — The scale represents 1 mm.

transversely rectangular, 13–18 × 11–18 μ; costa usually extending to base of apicus. *Sporophyte* unknown.

Type. PANAMA. CHIRIQUI: About 2 miles S of Boquete. *Crosby 3975* (holotype, MO; isotypes, DUKE, U).

Squamidium chiriquense is distinguished by the coarsely serrate acumen of the stem leaves (Fig. 1) and the concave, acute branch leaves (Fig. 2–3). The stem leaves of *S. crispipilum* Bartr. (holotype, Costa Rica, *Stork 1338*, FH) are similar (Fig. 4). The marginal cells of the acumen in *S. crispipilum* are not conspicuously lax as they are in *S. chiriquense.* And if leaf-length is a stable character here, the leaves of *S. crispipilum* are longer, 2.7–3.4 mm *versus* 1.5–2.25 mm. The branch leaves of *S. crispipilum* (Fig. 5) are very different from those of *S. chiriquense.* They are longer, 1.8–2 mm, and ovate in *S. crispipilum* and shorter, 1–1.2 mm, and broadly ovate in *S. chiriquense.* The margins in *S. crispipilum* are broadly inflexed in the upper half to just below the apex; they then abruptly become plane to produce the galeate shape described by Bartram (Jour. Washington Acad. Sci. 24: 476. 1934). In *S. chiriquense* the margins are plane to slightly inflexed just below the apex.

Squamidium macrocarpum (Mitt.) Broth. (type, Peru, *Spruce 1191-1194*, NY) also has somewhat galeate leaves (Fig. 7–8), but the margins are not as deeply inflexed and do not become plane again as abruptly as in *S. crispipilum.* Furthermore, the very apex of the leaf in *S. macrocarpum* is rather gradually acuminate, while in *S. crispipilum* it is rounded acute to obtuse and often minutely apiculate. The stem leaves of *S. macrocarpum* do not resemble those of the other two species. The apex is gradually acuminate and entire (Fig. 6), and they are a bit shorter, 1.8–2.0 mm long, than even in *S. chiriquense.*

I thank the curators of FH and NY for the loan of specimens.—*Marshall R. Crosby, Missouri Botanical Garden.*

SELECTIVE INSECT DAMAGE IN A TROPICAL HERBARIUM COLLECTION

At Summit Gardens in the Panama Canal Zone in September 1969, I found a collection of about 500 specimens of angiosperms made by Paul C. Standley in 1923–24. The majority were from the rain forest of the Canal Zone and neighboring Province of Panamá. The specimens were in an old metal storage case with doors fitting poorly. Specimens were in genus folders filed alphabetically by family and represented a broad sample of 87 families.

The collection was sent there from the Smithsonian Institution (US) about 1930 and presumably had been in this case for most of the subsequent time. I sent the material to St. Louis for fumigating with the hope of salvaging some specimens, but it was in an appalling state with major insect (and mouse ?) damage throughout specimens, paper, and genus folders. The damage was so great that only 16 specimens were saved (although labels for all collections were kept).

The interesting aspect of this story is that 14 of these specimens belong to four families, all related phylogenetically, with the majority in the Bignoniaceae. In values from 1 (light damage) to 3 (moderate damage), I found:

Bignoniaceae—

Amphilophium paniculatum (L.) H.B.K. (2)
Arrabidaea pachycalyx Sprague (2)
A. rotundata (DC.) Bur. (1)
Cydista aequinoclialis (L.) Miers (2)
Kigelia africana (Lam.) Bentham (1)
Parmentiera cereifera Seem. (2)
Phryganocydia corymbosa (Vent.) Bur. (1)
Tabebuia pentaphylla (L.) Hemsley (3)
[*Tecoma stans* (L.) Juss. and *Spathodea campanulata* Beauv. heavily damaged and discarded]

Pedaliaceae—

Sesamum indicum L. (2)

Gesneriaceae—

Achimines panamensis (Seem.) Hemsley (3)
Columnea purpurata Hanst. (3)
[*Kohleria tubiflora* (Cav.) Hanst. discarded]

Acanthaceae—

Mendoncia macrocarpa Leonard (1)
Ruellia geminiflora H.B.K. (2)
Trichanthera gigantea (H.B.K.) Humb. & Bonpl. (3)
[10 genera and *Ruellia albicaulis* Bert. discarded]

Of the remaining two sheets, both with moderate damage (3), one was a legume (*Cassia patellaria* DC.) and the other a composite (*Elvira biflora* (L.) Cass.). My immediate thought was that similar or related chemical residues might have deterred insects and other pests from severely damaging these family representatives. For example, the widespread occurrence of lapachol in the Bignoniaceae (Record, Trop. Woods 1: 7–9, 1925), which might possess insecticide properties, should be studied in relation to other substances common to that family and particularly to the Pedaliaceae and the Gesneriaceae.—*Walter H. Lewis, Missouri Botanical Garden, St. Louis.*

STUDIES IN BIGNONIACEAE III. TWO NEW PANAMANIAN SPECIES OF BIGNONIACEAE

1. **Tynnanthus croatianus** A. Gentry, sp. nov.

Liana scandens. Folia bifoliolata vel trifoliolata, saepe trifida cirrhosa, foliola ovata. Inflorescentia floribus in breves paniculas axillares vel terminales dispositis. Calyx truncatus, pubescens eadem ac corolla et rami inflorescentiae. Corolla valde bilabiata, parva, 1.3–2.0 cm longa. Antherae glabrae, reflexae, connective ultra locules producto. Ovarium conicum, dense pubescens. Capsula linearis, complanata, margine laterali prominenti.

Liana lacking noticeable pseudostipules and interpetiolar glands. *Twigs* tetragonal, becoming subterete, finely striate, becoming noticeably lenticellate with age; young twigs more or less puberulent. *Leaves* 2-foliolate, often cirrhose, or 3-foliolate; leaflets membranaceous, papillose on both surfaces with scattered lepidote scales especially above; minutely puberulous, below mostly on and near nerves, above more or less glabrescently so over whole surface; when dried light green to yellowish in color below with distinct network of yellow to reddish-brown veinlets, darker green to brownish above; tendril, when present, strongly trifid, 11–12 cm long to bifurcation, the 3 arms 1.6–2.0 cm long; terminal leaflet when present broadly ovate, obtusely acuminate, truncate to very broadly cuneate, 8–12 cm long, 6–8 cm wide, lateral leaflets broadly ovate, obtusely acuminate, more or less asymmetrically truncate or subcordate on one side, 6–10 cm long, 4–6 cm wide; terminal petiolule 2.8–3.3 cm long, laterals 1.2–2.5 cm long; petiole 2.2–7 cm long, dark reddish in color. *Flowers* sweetly aromatic, disposed in small mostly axillary panicles, inflorescence branches strongly puberulent; panicles 3–8 cm long, 2–6 cm wide. *Calyx* pubescent, eglandular, truncate to minutely sub-denticulate, 3 mm long, 3–4 mm wide. *Corolla* white with two yellow lines in throat, 1.2–2 cm long, bilabiate, split about half its length, the 2 upper lobes almost fused, the 3 lower ones 4–5 mm long; the outside pubescent throughout, the inside pubescent on lower 3 lobes, margins of upper 2, at base of lower side of tube, and very sparsely elsewhere. Fertile *stamens* four, didynamous, anther thecae glabrous, 1.5 mm long, divergent, twisted at base and reflexed forward, connective extended 0.3 mm beyond point of anther attachment, longer filaments 1.0–1.2 cm long, shorter 0.9–1.0 cm long; staminode 0.5 cm long. *Pistil* 16 mm long, stigma bilamellate, 1 mm long, style pubescent, ovary conical, 1.5–2 mm long, 1 mm wide at base, densely pubescent; disk reduced, shortly cupuliform, densely pubescent on margin. *Capsule* linear, long acuminate, flattened, to 35 cm long, ca. 1 cm wide and 0.5 cm thick, the lateral margins prominently raised, sparsely to densely pubescent (at least when young); seeds 6–7 mm long, to 17 mm wide.

Holotype: PANAMA. CANAL ZONE: Shoreline of broad-mouthed cove NE of Drayton House on Barro Colorado Island, vine, flowers white with yellow nectar guides, strong sweet aroma, abundant locally, *T. B. Croat 11927* (MO).

Occurs in lowland tropical rain forest from the Canal Zone almost to the


PANAMA
COLON PROVINCE
Collected by Al Gentry
Herbarium, University of Wisconsin

2


PLANTS PANAMA
BIGNONIACEAE

1

Colombian border. Flowers in the rainy season mostly in July and August (*Killip 3403* with buds only was collected on 20 April).

PANAMA. CANAL ZONE: Barro Colorado Island, *Starry 149* (MO); Gigante Bay, *Shattuck 1108* (US). DARIEN: Río Balsa, between Manene and Tusijuanda, vine, flowers white, *Duke 13544, 13579* (both MO). PANAMA: Alhajuela, vine, flowers white, yellow at base of throat, *Dwyer 1144* (MO); at edge of woods along road between Empire and Chorrera, altitude 30–100 m, *Killip 3403* (US).

I have seen several misidentified specimens of this distinctive new species. One specimen at MO was labelled *Lundia corymbifera* (Vahl) Sandw. and two *Arrabidaea panamensis* Sprague; at US one specimen was determined as *A. panamensis* and another doubtfully as *Mansoa difficilis* (Cham.) Bureau. Nevertheless, the generic affinities are clearly with *Tynnanthus*. The small, strongly bilabiate corolla, lack of interpetiolar glands, glabrous reflexed anthers with twisted thecae and apiculate connective, and densely pubescent conical ovary all point to this genus. The corolla is larger than in most species of the genus, but *T. macranthus* L. Wms. has significantly longer corollas. Within *Tynnanthus* the relationship of *T. croatianus* would appear to be with *T. cognatus* Miers and *T. elegans* Miers of Brazil on the bases of calyx and inflorescence pubescence and calyx shape and with *T. fasciculatus* (Vell.) Miers also of Brazil on the basis of corolla size.

The genus *Tynnanthus* is noteworthy as including the smallest flowers in the Bignoniaceae. It consists of about a dozen species, mostly from Brazil. Supposedly disjunct species include *T. caryophylleus* (Bello) Alain (= *T. myrianthus* Bur. & Schum. *fide* Sandwith, Kew Bull. 15: 465. 1962) of the West Indies, *T. guatemalensis* Donnell-Smith of Guatemala and the Yucatan Peninsula, and *T. macranthus* L. Wms. recently described from Costa Rica. This is the first record of the genus in Panama; the collections along the Río Balsas in Darién Province indicate that *T. croatianus* almost surely occurs across the border in Colombia as well, thus eliminating the disjunction from the range of this genus.

2. **Anemopaegma santa-ritensis** A. Gentry, sp. nov.

Liana scandens. Folia bifoliolata saepe trifidis cirrhis (interdum simplicibus cirrhis) ornata, foliola ovata, coriacea vel subcoriacea, margine revoluto. Phylla stipulas simulantia deficientia. Inflorescentia floribus in breves racemes dispositis. Calyx truncatus, glaber. Corolla lutea, longi-campanulata, 5–8 cm longa, extra lepidota. Ovarium stipitatum, complanatum ovatum. Capsula ignota.

Liana without pseudostipules or interpetiolar glands. *Twigs* more or less subtetragonal with wrinkled surface forming longitudinal ridges, epidermis finely and regularly papillate with scattered lepidote scales and sometimes a very minute puberulence near the nodes. *Leaves* 2-foliolate, often cirrhose, tendril when present sometimes simple, usually trifid, base 3–12 cm long, the 3 arms 0.4–1.0 cm long; leaflets coriaceous to subcoriaceous, margins revolute, epidermis regularly and densely papillose with regularly scattered lepidote punctations,

←

FIGURES 1–2. New Panamanian Bignoniaceae. — 1. Holotype of *Tynnanthus croatianus* A. Gentry (*Croat 11927*). — 2. Holotype of *Anemopaegma santa-ritensis* A. Gentry (*Gentry 454*).

smaller veinlets very obscure, glabrous above and below to rarely minutely puberulent at base of midvein below, green to olive above, light green to yellowish below, ovate, obtusely acuminate, truncate, 5.9–11 cm long, 2.8–5.3 cm wide; petiolule 0.6–1.3 cm long; petiole 1.2–2.5 cm long. *Inflorescence* an axillary (1–) few-flowered raceme with opposite flowers. *Calyx* glabrous, truncate, eglandular, 5–8 cm long, 7–9 cm wide. *Corolla* yellow, campanulate above the narrowed base; outside lepidote, inside with glandular-hairs below stamen insertions and sparsely on lobes; 5–7.5 cm long, 1.7–1.9 cm wide at mouth of tube, tube 3.8–5.3 cm long, lobes 0.8–1.1 cm long. Fertile *stamens* four, filaments 1.8–2.0 cm long, anthers 0.6–0.8 cm long; staminode 0.8 cm long. *Pistil* 4.1 cm long, ovary stipitate, flattened ovate, 2 mm long, 1.2 mm wide, and 0.6 mm thick; disk conspicuous, pulvinar, 1.5 mm long, 2.5 mm wide. *Capsules* unknown.

Holotype: PANAMA. COLON: Santa Rita Ridge, vine trailing along roadside, flowers pale yellow, *Gentry 454* (MO, isotype WIS).

Seemingly endemic to the Santa Rita Ridge area of Colón Province, Panama, for which it is named. This area is mostly advanced secondary tropical evergreen forest (now being rapidly cleared). The four flowering collections are from February, April, September, and October.

PANAMA. COLON: Santa Rita Ridge, *Lewis et al. 5288*; *Dressler & Lewis 3721*; Santa Rita, *Gomez-Pompa et al. 2990, 3305*; Summit of Cerro Santa Rita, altitude 1200–1500 feet, *Allen 5105* (all MO).

Anemopaegma santa-ritensis is basically a climbing liana but sometimes trails along the ground in cleared areas. It is characterized by the combination of lepidote corolla exterior, truncate calyx, coriaceous to subcoriaceous bifoliolate leaves with revolute margins and obscure ultimate venation, usually trifid tendrils, and no pseudostipules. Although other species of the genus have all of these features separately, no one species shares more than a few of them. The leaves are especially diagnostic, being very similar only to those of conspicuously pseudostipulate *A. laeve* DC. of the Brazilian catingas. *Anemopaegma carrerense* Armitage of Venezuela, Trinidad, Taboga, and British Guiana has trifid tendrils and lepidote corolla but conspicuous pseudostipules.

Differences between geographically related congeners and *Anemopaegma santa-ritensis* include: *A. orbiculata* (Jacq.) DC. (Costa Rica to Colombia) has 4–5-foliolate leaves; *A. chrysoleucum* (H.B.K.) Sandw. (widespread in Central America and northern South America—includes *A. belizeanum* Blake, *A. punctulatum* Pittier & Standl., and *A. macrocarpum* Standl.) has the corolla glabrous outside, conspicuous leafy pseudostipules, and simple tendrils; *A. lehmannii* Sandw. (Colombia) has strongly pubescent leaves; *A. chrysanthum* Dugand (Colombia) has a glabrous corolla. None of these species has the distinctive leaves of *A. santa-ritensis*. Detached leaflets of 4–5-foliolate *A. orbiculata* might be confused with those of *A. santa-ritensis*, but they have more lateral veins, 5–7 as opposed to 4(–5), and less suppression of the smaller veinlets.

This study was made possible through the support of an NSF Graduate Fellowship. The author also wishes to thank the U.S. National Herbarium under whose auspices this work was begun and Dr. John Dwyer for reading the manuscript.—*A. H. Gentry, Missouri Botanical Garden.*

FURTHER NOTES ON THE SKUNK CABBAGE IN MISSOURI

In a recent article by Erna R. Eisendrath (Ann. Missouri Bot. Gard. 56: 287. 1969), the matter is discussed as to whether or not *Symplocarpus foetidus* (L.) Nutt. is native to Missouri. As the present author is cognizant of the circumstances related to the appearance of this plant presently growing on the estate of Mr. Jay G. Rice in Jefferson County, the following information is presented.

The present author was an intimate friend of the late Charles Rice and was invited to visit the above-mentioned estate, approximately 8 miles south of Antonia, in 1935, during the time that the "Annotated Catalogue of the Flowering Plants of Missouri" (Ann. Missouri Bot. Gard. 22: 375–758. 1935) was being readied for publication. At that time Mr. Rice showed me a number of species of wild flowers he was attempting to introduce and cultivate on his property with the idea of establishing a wild flower sanctuary there.

The Skunk Cabbage was planted (several plants) in a wet habitat where a portion of the stream had been dammed. These plants had been obtained by Mr. Rice from a nursery outside the state. When discussion arose as to whether such plants should not be included in the flora of Missouri, I indicated that we could not include the large multitude of species grown in private and public gardens or those deliberately introduced through purchases or by other means. Only species could be included which were a part of the native flora or had become naturalized or introduced spontaneously as escapes from cultivation and persisting on their own. One could add literally hundreds of species to the flora of a given state, if all were included which were grown in private gardens and estates from plants purchased from out-of-state nurseries or obtained on travels away from Missouri. Therefore, it was concluded that the Skunk Cabbage could not be included in the flora of Missouri.

So far as the specimens collected in 1903 and 1907 by Mr. Kellogg are concerned, this matter was checked with Mr. Kellogg at the time of the preparation of the "Annotated Catalogue" published by Mr. Palmer and myself. And Mr. Kellogg stated that the herbarium specimens came from plants grown at the Missouri Botanical Garden.

To answer the questions submitted by Mrs. Eisendrath, it may be stated then that the Skunk Cabbage plants originally introduced by Mr. Charles Rice are still growing (as a single remaining plant) from the time the present author first saw them there planted, beginning in the year 1935.

As to why the plant has not spread, one can only conjecture that the Skunk Cabbage is not growing under optimum conditions and that it is merely surviving, rather than increasing at present. As is well known, some species of wild flowers, when grown outside their natural range, are easily propagated and thrive, reproducing themselves easily, whereas others are more difficult to grow or do not respond to either ordinary or especial treatment.—*Julian A. Steyermark, Instituto Botanico, Ministerio de Agricultura, Caracas, Venezuela.*

Editor's Note

The banner on this issue of the Annals features a portion of an illustration of *Tribulus terrestris* L. from A. de Jussieu's "Mémoire sur le groupe des Rutacées" (Mém. Mus. Hist. Nat. 12: 384–542. 1825). The intrastaminal glands, which stand out conspicuously in figure D of the plate, are an important character in the taxonomy of *Tribulus*. See the article "Notes on the floral glands in *Tribulus* (Zygophyllaceae)" on pages 1–5 of this volume of the Annals.—*Editor.*

The 1971 Greenman Award

The fourth annual Jesse M. Greenman Award was presented to Arne Strid, Lund, for his imaginative and thorough study of *Nigella arvensis* in Greece and western Turkey (Studies in the Aegean flora. XVI. Biosystematics of the *Nigella arvensis* complex with special reference to the problem of non-adaptive radiation. Opera Bot. 28. 1970).

The Alumni Association of the Missouri Botanical Garden presents the Greenman Award in recognition of the best paper in plant systematics based on a doctoral dissertation published during the previous year. Papers published in *1971* are now being considered and may be submitted until 1 May 1972. Reprints of such papers should be sent to Peter H. Raven, Director, Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.—*Editor.*

The previous issue of the Annals of the Missouri Botanical Garden, Vol. 57, No. 3, pp. 265–388, was published on 14 June 1971.

PREPARATION OF MANUSCRIPT

The ANNALS publishes original manuscripts in systematic botany and related fields. There is a charge of $25 per printed page to help defray costs of publication. Authors are asked to follow the suggestions below in order to expedite editing and publication. If an author feels that his manuscript presents special problems, he should write the editor concerning the best way to handle these before submitting the manuscript.

Manuscripts must be typewritten on one side of substantial weight paper, 8½ × 11 in. The manuscript should have wide margins and be double spaced throughout, including the abstract, footnotes, legends, tables, lists of specimens, and the bibliography. Tables should be typed separately and placed at the end of the text. Authors should indicate in the margins the approximate places for illustrations and tables. Submission of the original and one carbon or xerographic copy of the manuscript is desirable, and the author should also retain a copy of the final, typed draft.

Acknowledgements to granting agencies, herbaria, illustrators, and technical assistants may be conveniently placed as a footnote on page one. The author's full mailing address should appear as a second footnote.

An abstract must accompany each paper other than "Notes." The abstract should succinctly summarize the findings and conclusions of the paper and should be completely comprehensible itself.

A brief Latin diagnosis for each new taxon is preferred to a complete Latin description. A complete description should be given in English.

The citation of specimens should be concise. Geographic names are put in order of decreasing political magnitude. Only the barest essential data concerning each specific locality should be given. Collectors are cited by family name and collection number. If there is no collection number, the year of collection should be given. Herbaria are designated according to the current edition of *Index Herbariorum.*

Abbreviations should be checked for consistency and to make sure they are unambiguous. Periods are used after all abbreviations except metric measures, compass directions, and herbarium designations.

All illustrative material should be mounted on stiff cardboard. If the originals are too large to be conveniently mailed, photographic reductions should be submitted. The maximum size of a printed illustration is 5 × 7¾ in., and therefore, the height of an illustration must not exceed about 1.5 its width. Figures are numbered consecutively, since they are not printed as "plates." Numbering must be done with a mechanical device or with dry-transfer lettering and never by hand. The amount of reduction should be noted on the back of each illustration, together with the figure numbers, author's name and title of the paper. Photographs should be sharp, glossy prints. Numbering should be applied directly to the surface of the photograph. Several photographs may be assembled to form a composite block, and each photograph should be numbered separately. The individual photographs should be mounted with the interior edges flush. Line drawings are prepared with India ink and must never be placed in the same block with photographs. Authors wishing to have original illustrations returned must notify the editor when proofs are returned.

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Author will receive page proof. Since changes in proof are expensive, authors should not make revisions at this stage. Authors will be charged for alterations other than corrections of printer's errors.

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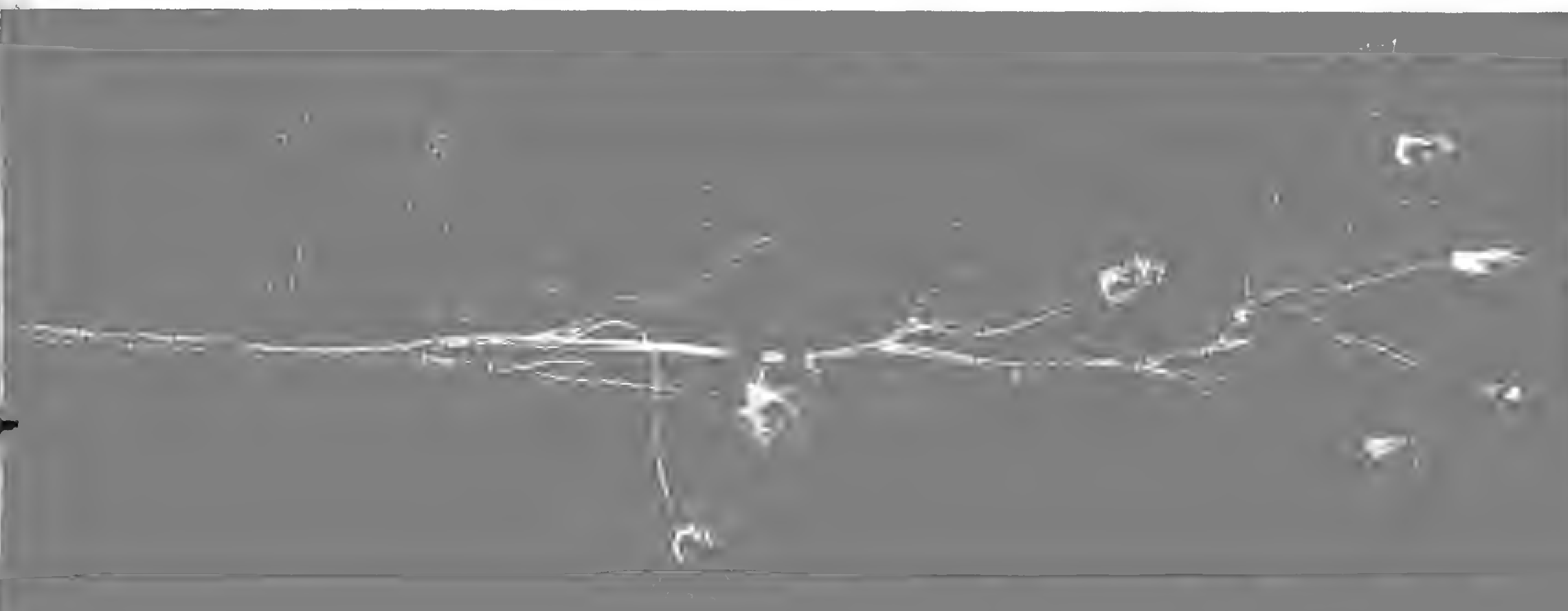

CONTENTS

VOLUME 58
1971
NUMBER 2

ANNALS OF THE
Missouri Botanical Garden

The ANNALS contains papers, primarily in systematic botany, contributed from the Missouri Botanical Garden and the Department of Biology of Washington University. Papers originating outside the Garden or University will also be accepted. For information on preparation of manuscripts, see the inside back cover.

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THE WOODY PLANTS OF ALABAMA[1]

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Abstract

Woody plants of 437 taxa in 177 genera and 74 families are presently verifiable as native, naturalized, or escaped in Alabama. The occurrence of six major physiographic provinces and a broad climatological range are contributing factors to the persistence of high floristic and vegetational diversity. Keys to the taxa and maps of the distributions of the plants are included.

Introduction

State-wide treatments of Alabama plants by Mohr (1901) and Harper (1928), while of consistent quality, display shortcomings which the present study hopefully may begin to remedy. Both Mohr and Harper were limited by transportation,

[1] One of the surest effects of completing a floristics project of this scope must be an awareness of unrepayable debt to one's colleagues. Indeed, the taxonomic judgements of the present writer's predecessors and contemporaries are the principal means through which his own concepts of groups have evolved. In a very real sense, one's judgements are not his own, but represent a modified amalgam of those of others. In this regard, appreciation is due the following: W. W. Ashe, H. R. Totten and C. H. Muller (*Quercus*), H. E. Ahles (Rosaceae), W. P. Adams (*Hypericum*), J. R. Baird (Myricaceae), and P. C. Baker (*Vaccinium stamineum* complex).

Other persons have aided the writer in a more tangible way, by examination of certain groups: J. W. Hardin (*Fraxinus, Aesculus, Spiraea*), S. McDaniel (*Vaccinium*), R. L. Wilbur (*Wisteria, Amorpha, Robinia, Gleditsia*), W. H. Duncan (*Vitis, Smilax*), E. W. Chester (*Halesia*), P. J. Crutchfield (*Quercus*). Their determinations and verifications have been valuable to this project. In addition, the following treatments have been important to the formulation of concepts concerning certain groups: Adams (1957, 1962), Camp (1942), Eyde (1963), Hardin (1957), Logue (1967), and Wood (1961).

Portions of this work were completed while the writer held a Coker Fellowship in the Department of Botany, University of North Carolina, Chapel Hill.

In large measure, the successful completion of this project has been due to the continual hostelry and hospitality extended by the T. A. Heard family, formerly of Weaver, Alabama. Collection of the northern Coastal Plain was greatly facilitated by a stay at the residence of the C. T. Stovalls, formerly of Marion, Alabama.

Special appreciation is expressed to A. E. Radford for his direction and support of and enthusiasm for this work.

Finally, I wish to thank my wife Nancy for the tremendous sacrifices she underwent and the large amount of careful assistance she rendered.

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Mohr's work being accomplished largely from horseback, and Harper's through transport by others. While, in the opinion of this writer, the taxonomic penetration of Mohr was superior, that of Harper was occasionally uneven (though quite excellent for an ecologist!).

The present study provides material which has been previously unavailable relating to the occurrence and distribution of Alabama woody plants. Ideally, through its vouchers, this study will furnish useful data regarding patterns of variability of Alabama woody plants. Hopefully, the present study will function as a stimulus for more active collecting in the area studied. Some of the material presented here should be useful—in a larger context—to further investigations of the distribution and evolution of the Southeastern flora.

Part of the value of this work should lie in the re-exposed problems of a taxonomic nature posed by a significant percentage of the taxa treated. One hopes that among these possibilities of usefulness, this study might also enable amateurs and laymen to become more aware and appreciative of a fast-disappearing, irreplaceable aspect of their environment.

It is widely recognized that no uncontestable definitions exist of what a Temperate Zone woody plant is. Plants considered woody in this study are those which do not die back approximately to ground level during the winter in Alabama. Most of these also display significant secondary growth, although some (*e.g.*, *Chimaphila maculata* L., *Clematis virginiana* L.) do not. Plants excluded as herbaceous by the dieback criterion in Alabama include species of *Clematis*, *Cynanchum scoparium* Nuttall, *Cardiospermum halicacabum* L., *Menispermum canadense* L., *Dioclea multiflora* (T. & G.) Mohr, and *Calycocarpum lyoni* (Pursh) Gray.

Sixty-three of Alabama's sixty-seven counties were objects of intensive field work. Tuscaloosa, Lee, Hale, and St. Clair counties were considered in advance to have probably been well-collected by others previous to the start of this study, and they were not collected by the writer, except in sporadic fashion.

In order to augment distributional data for Alabama woody plants the following institutional herbaria were examined: University of North Carolina at Chapel Hill, University of Georgia, Vanderbilt University, University of Alabama, Auburn University, Jacksonville (Alabama) State University, Florence State University, Mississippi State University, and St. Bernard College. In addition, the Herbarium of the Geological Survey of Alabama (Mohr collection) in Tuscaloosa was examined. Data from these sources are included as distribution maps for each taxon treated.

Explorers and Botanical Collectors in Alabama

Rostlund (1957) has compiled a list of the early travelers known to have journeyed through Alabama and has commented extensively upon their journals relative to the plants and vegetation they noted. Rostlund's treatment includes the commentaries of four writers with the DeSoto expedition of 1540, Dalgado's comments from southeastern Alabama in 1686, Romans' travels in western Alabama from 1771 to 1772, Swain's 1790 observations, Hawkins' 1798–1799 remarks, as well as the statements of others. Most of these accounts appear to be of minimal value botanically, since the persons noted were not particularly interested in the plants or vegetation through which they travelled; nor were they familiar with the plants they encountered.

The first notable botanist to visit Alabama was apparently William Bartram, who travelled through southern Alabama in 1775 and 1776. Bartram described several taxa as new from Alabama and was a careful observer of the territory through which he passed. Bartram (1791) contains excellent annotations of his observations by Francis Harper.

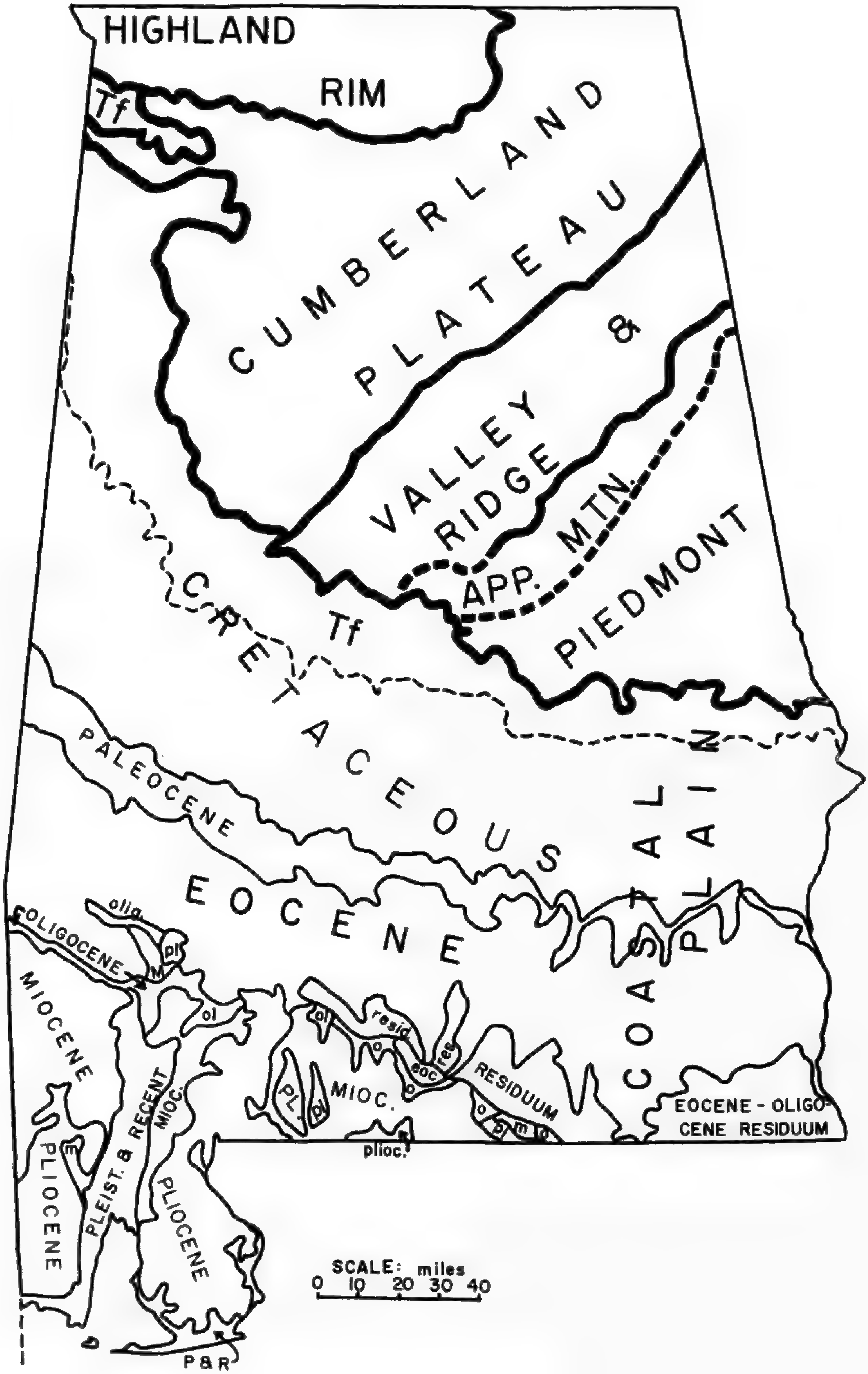
Mohr (1901) lists other botanists, including Buckley, Gates, Peters, and Nevius. S. B. Buckley was a resident of Wilcox County for more than 25 years, during which he described *Quercus shumardii* and *Quercus durandii* from the same county. Evidently (according to Mohr, 1901), he was also the first to discover *Cotinus obovatus* Raf. east of the Mississippi River. H. Gates' collections, which were utilized by Torrey and Gray, are cited by Mohr as the first collections from coastal Alabama. T. M. Peters, a noted Alabama legislator, was also an enthusiastic amateur botanist with broad interests. He was the discoverer of *Trichomanes petersii* Gray, as well as a collector of *Carex* and advisor to Mohr. R. D. Nevius discovered *Neviusia* near Tuscaloosa in the 1850's. F. S. Earle, C. F. Baker, and L. M. Underwood are also mentioned by Mohr. They collected extensively near Auburn in the late 1890's.

Charles Mohr should undoubtedly be considered the pre-eminent Alabama botanist to date, and his *Plant Life of Alabama*—published in 1901 near the time of his death—remains the definitive work on Alabama plants. It is safe to state that until the time of the present study the majority of specimens of Alabama plants were Mohr's.

Roland M. Harper succeeded Mohr as Botanist of the Geological Survey of Alabama and became known as the most active botanist in the state over a period of many years. Harper published quite extensively, mostly concerning himself with rarities and interesting aspects of the vegetation of Alabama. His collections of Alabama plants were, unfortunately, rather meagre, though his knowledge of Alabama plants was certainly extensive. He remained active until his death in 1966 at age eighty-seven.

Other significant contributions were made in the early portions of the twentieth century by several men. T. G. Harbison (1902*a*, 1902*b*) and W. W. Ashe collected many specimens of woody Alabama plants; W. Wolf collected extensively near Cullman; R. S. Cocks (1925) published a lengthy paper from Dallas County; and E. J. Palmer (1932) made a collecting trip to the state, apparently in search of *Quercus georgiana* Curtis.

Later collectors of Alabama plants include the following: D. Demaree, C. E. Wood, Jr., W. H. Duncan, J. W. Hardin, J. C. Avery, L. H. Shinners, S. McDaniel, P. E. Bostick, J. T. Thomas and his students, M. Lelong, and J. D. Freeman, as well as the writer. At the present time, the most active resident amateur field botanist is probably Mrs. Blanche E. Dean of Birmingham, a well-known naturalist and authoress of several books.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Field work toward a comprehensive flora of the state has been in progress since 1967 by R. Kral and associates of Vanderbilt University.

Geology

Alabama is geologically quite diverse. Besides a complete representation of the Appalachian system (Cumberland Plateau, Valley and Ridge, Appalachian Mountain, Piedmont Provinces), Alabama displays the most highly diversified exposure of the Gulf Coastal Plain outside of that portion complicated by Mississippi Embayment strata. Figure 1 illustrates the relationships of the major Provinces, which are discussed below.

THE HIGHLAND RIM

The Highland Rim area of extreme northern Alabama is a southernmost portion of the Interior Low Plateaux Province. Throughout most of its extent in Alabama it is characterized by extensive exposure of Tuscumbia limestone and Fort Payne chert (of upper Mississippian age). Exceptions to this characterization occur when major streams (the Elk River, for instance) expose strata of greater age. Maximal elevations on the Highland Rim are in the vicinity of 900 feet above sea level near the Tennessee border, and decline to 500–600 feet above sea level near the Tennessee River. Most of the province approximates 700 feet above sea level, while the surfaces of Hartselle sandstone "mountains" south of the Tennessee River occasionally are 50 feet higher.

Current erosion to the base level of the province is perhaps illustrated by such areas as Newsome Sinks in Alabama and Sinking Cove in Tennessee, where large areas of the Cumberland Plateau have slumped due to subterranean solution of limestones. These areas seem to tend toward a new base level approximating that of the Highland Rim. Extensive exposures of Tuscumbia limestone also occur into Jackson County along the Tennessee and Paint Rock Rivers (Stose, 1926). In extreme northwestern Alabama, the Tuscumbia limestone is often overlain by mixed, unconsolidated deposits of the Tuscaloosa formation.

Topography on the Highland Rim is generally flat to rolling, with rather frequent evidence of subsurface solution, such as dolines. The entire Alabama portion of the province is within the Tennessee River watershed and most is cultivated. The Tennessee emerges into the southeasternmost portion of the Alabama Highland Rim, as a result of a westward turn from the Sequatchie Valley, and flows westward across northern Alabama.

Together with the Cumberland Plateau and the southern Appalachian Mountains, the Interior Low Plateau forms the oldest unglaciated and exposed area in the eastern United States.

Areas where extensive exposed outcrops of Tuscumbia limestone occur are characterized by the development of cedar barrens (Quarterman, 1950), a unique vegetation type.

←

FIGURE 1. Alabama showing geologic provinces and ages of Coastal Plain sediments. Base map and data modified from treatments of Fenneman (1938), Stose (1926) and MacNeil (1946, 1947). Tf = Tuscaloosa formation.

THE CUMBERLAND PLATEAU

The Cumberland Plateau is the southern extension of the Appalachian Plateaux Province (or Allegheny Plateau). This plateau (and its outliers) occupies all of north-central Alabama, where major portions of it are locally known as Sand, Lookout, and Brindley Mountains. Northwestwardly, it is bounded by the Highland Rim, and eastwardly by the Valley and Ridge Province. Westward and southward, Plateau strata are gradually buried by the Tuscaloosa formation of the Coastal Plain. The Plateau surface is composed of Pennsylvanian strata of the Pottsville formation, which include significant shale members and coal-bearing strata (the "Coal Measures").

The surface of the Cumberland Plateau declines in elevation southward. Elevations of Plateau uplands near the Tennessee border reach 1900 feet, declining to only 500 or so feet above sea level in the vicinity of Tuscaloosa.

The eroded Sequatchie anticline (Sequatchie Valley) is a striking contrast to the Plateau surface in northeastern Alabama and is evidently related orogenically to Wills Valley. Both valleys once probably were represented by a range of mountains whose rocks—being less resistant than those of the Plateau proper—were more rapidly eroded. Both of these anticlines apparently were formed by the same forces responsible for folding the Valley and Ridge Province (Fenneman, 1938). For most of its length, the Sequatchie Valley of Alabama constitutes a pathway for the Tennessee River. The River leaves the Valley near Guntersville to complete its two-stage traverse through the Plateau, the first stage of which began at Chattanooga. Why the Tennessee cuts through the Cumberland Plateau instead of remaining in the Valley and Ridge Province has been the subject of much discussion (G. I. Adams, 1928; Fenneman, 1938).

In northeastern Alabama, the Cumberland Plateau is within the drainage of the Tennessee River. The southeastern part of the Plateau (Lookout Mountain and Wills Valley) is ultimately drained by the Coosa River. The remainder of the Plateau is drained by major streams arising on its own surface and flowing south- and westward, the Black Warrior and its several major tributaries being the principal agents. Hence, the western portion of the Plateau in Alabama is within the Tombigbee River drainage. The Black Warrior system, particularly, displays many entrenched meanders, suggesting possible uplift of an older stream system. Exactly when this may have taken place is not known, but it is thought to have occurred also in related areas, particularly the Tennessee Highland Rim (Fenneman, 1938).

Topography on the Cumberland Plateau is rolling in interstream areas. Its surface is submaturely dissected by young valleys which become more entrenched toward the edges of the province. Southward, the old peneplain surface (Schooley) becomes increasingly eroded, resulting in rougher terrain and the virtual disappearance of flat uplands (Fenneman, 1938).

Though the relatively shallow and much-eroded soils of the Plateau are not especially favorable for agriculture, large areas are cultivated or grazed, particularly in the area from Fort Payne to Cullman. The relative sterility of the soil is partially compensated for (for some crops) by its texture and the relatively cool summer nights and high rainfall on the Plateau surface.

The Appalachian plateaux (south of the glacial moraines) have evidently been continually exposed since at least early Tertiary and thus have been available to terrestrial plants for an extremely long period of time.

THE VALLEY AND RIDGE

The Valley and Ridge Province occurs between the Appalachian Plateaux and Appalachian Mountains Provinces and is orogenically related to both of them. In Alabama this relationship is accentuated because of the narrow width of the province relative to the extensiveness of the outlier ridges. In fact, as Fenneman (1938) points out, the Lookout Mountain portion of the Cumberland Plateau could easily be considered as being in the Valley and Ridge, except that its inclusion is awkward because of its extensiveness. The broad ridges forming the so-called Cahaba "coal field" and Coosa "coal field" are massive Cumberland Plateau outliers usually considered to be part of the Valley and Ridge in spite of their expanse. Examples of prominent outliers from the Alabama Appalachian Mountain Province are Coldwater and Choccolocco Mountains in Calhoun County.

Elevations of the Cumberland Plateau outliers approximate 1500 feet above sea level, while that of peaks in the Choccolocco Mountains may approach 500 feet higher. Base level elevations near the Coosa River are generally 500–600 feet above sea level.

The valley floors of the Valley and Ridge in Alabama are underlain at the surface by Paleozoic sediments (mostly Cambrian and Ordovician) which, as Fenneman (1938) has pointed out, represent the base level of the current peneplanation cycle (Coosa or Harrisburg). The structure of the ridge outliers, of course, reflects their relationships to either the Cumberland Plateau to the west or the Appalachian ridges east of the Valley and Ridge.

This province is often known as the Coosa Valley in Georgia and Alabama, after the major river which lies within it and drains it. Numerous large limestone springs occur within the Coosa Valley, an indication of extensive phreatic cavern development in the valley sides and floor. Topography in the Alabama Valley and Ridge has been conditioned by erosion, faulting, and extensive exposure of less resistant rocks. Soils are moderately deep, generally circumneutral, and quite fertile, and they are thus extensively farmed.

As they approach the Fall Line, the Appalachian Mountain and Valley and Ridge Provinces become more indistinct and apparently very difficult to separate. The former province seems to degenerate into lower and less discrete complexes of ranges. The Coosa River appears to cut its way through these toward the Piedmont. As it nears the Fall Line at Wetumpka, most of the rocks in the river bed seem to be schistose and slate-like, not at all resembling those typical of lower elevations in the Coosa Valley proper. On the other hand, extensive areas of limestone in the southern valley floor have been partially metamorphosed, so that marble is quarried near Talladega and Sylacauga. Metamorphosed limestone is exposed as far south as the Fall Line in Bibb County. For these reasons, it is evident that province boundaries are obscured in this general area. Possibly, the Rebecca Mountains and associated lower ridge systems represent the roots of a once much higher and more well-defined system subject to greater erosional stress because of proximity to the ancient sea-land interface. It is thought (G. I. Adams, 1928) that the Tuscaloosa formation once extended much farther inland in some places than it does presently. If these facts are indeed valid, it would seem rather likely that (probable) frequent or prolonged marine transgression of the lower portions of the Appalachian system could easily have rendered them indistinct and confusing to observers in the present. It is also generally thought by geologists that the identical spatial arrangement of the valley, mountain and plateau provinces in Arkansas possibly indicates their homology with the Appalachian system, although proof of this possibility has been elusive.

THE APPALACHIAN MOUNTAINS

The Alabama Valley and Ridge Province is bounded eastward by a series of high ridges, the Talladega and Horseblock ranges. These ranges are quite similar in several ways to the ranges bordering the Great Valley farther north, *i.e.* the Unakas, and average over 1500 feet above sea level in Alabama. It is readily discernible from examination of topographic maps that the topography of these ranges resembles much more closely that of the Unakas and Blue Ridge than that of the Piedmont Province. Furthermore, geological examination indicates a closer relationship to the Unakas or Blue Ridge than to the Piedmont. At least one structural component, the Brevard schist, is common to the Blue Ridge and Talladega ranges, and in addition the Talladega Mountains appear to lie along the same axis as the Great Smokies. Even though he does not formally recognize a "Blue Ridge" province in Alabama, Fenneman (1938: 165) states that: "These low ridges represent what would have been a continuation of the mountain range had the uplift been greater and the expansion of the newer peneplain less easy." Since the Appalachian and Cumberland uplifts are thought to have been less pronounced toward the south, it is logical that the Talladega and Rebecca Mountains would be of lower relief than their northern counterparts. Even so, the highest point in Alabama occurs within this range (Mt. Cheaha, 2407 feet). The primary problem in recognizing the equivalence of the Alabama ranges and those to its northeast is the discontinuity which exists in western Georgia. In that area, the Valley and Ridge Province appears to border directly on the Piedmont (Dugdown Mountain area). But following the lines of reasoning reiterated here, the present writer believes that there is ample evidence for the formal recognition of the Appalachian mountains as a physiographic entity in Alabama. Due to the discontinuity in Georgia, the term Appalachian Mountain Province would seem to be more appropriate than a more specific name for the region, such as the "Blue Ridge."

The western slopes and southern extremity of the province are drained by tributaries of the Coosa River, while most of the eastern slopes are in the Tallapoosa River watershed. Due to the extremely steep slopes and shallow soils, only a modicum of marginal cultivation exists, and most areas are presently repeatedly cut over for pulpwood.

The structural units of this province are quite complex, consisting of metamorphics: schists, gneisses, slates, quartzites, marbles, *etc.* Certain of these rocks are as old as Precambrian.

THE PIEDMONT

The Piedmont is the presently nonmountainous portion of the "Old Appalachian" land area. It is underlain throughout in Alabama by quite resistant rocks and is bounded northward by the closely related Appalachian Mountain Province.

The Piedmont is often spoken of as the Piedmont Plateau and, indeed, throughout most of its extent it displays topographic features one would expect on an older peneplain now undergoing dissection. This dissection is more pronounced in the vicinity of the Fall Line than it is farther into the province. As a whole, the predominant slope of the Piedmont as a province or a plateau is toward the south (in Alabama).

Elevations in the Alabama Piedmont range from about 1000 feet above sea level in the upper portion of the province, to 500–700 feet above sea level near the Fall Line zone. Monadnocks in the upper Piedmont (Turkey Heaven and Oak Mountains, for examples) are several hundred feet higher than their surroundings.

The Fall Line constitutes the southern boundary of the Piedmont, which probably occurred somewhat farther inland prior to erosion of the Coastal Plain sediments from the more inland provinces (Fenneman, 1938; G. I. Adams, 1928). The Fall Line has been interpreted as a portion of a re-exposed ancient peneplain, joining the Piedmont peneplain along the top of the present Fall Line (Fenneman, 1938).

Topography in the Piedmont is generally rolling, with few prominent structural exceptions. Drainage of the Alabama Piedmont takes place through tributaries of the Chattahoochee and Tallapoosa Rivers. Triassic lowlands are missing in the Alabama Piedmont.

Ubiquitous slopes and the primitive agricultural practices of the early white settlers combined long ago to strip the Piedmont of its topsoil. As a result, the subsoil has been farmed successfully only by repeated heavy applications of inorganic fertilizers (Fenneman, 1938).

THE COASTAL PLAIN

The Coastal Plain of Alabama constitutes well over half the surface area of the state. Geologically, it seems quite without rival in its complexity, throughout the non-peninsular Southeast. It is composed principally of unconsolidated sediments of Cretaceous age and younger, although significant consolidated sediments do occur. Comments by the present writer have largely been conditioned by Stose (1928), Fenneman (1938), and MacNeil (1946).

As may be seen from Figure 1, the boundary delimiting the Coastal Plain from the more northern provinces in Alabama is generally quite irregular. This is particularly so at the Coastal Plain-Cumberland Plateau interface, where the Tuscaloosa formation of the Coastal Plain is higher in altitude than the plateau surface. This is fairly impressive, since the Cumberland Plateau is the highest extensive surface in the state, averaging some 500 feet or more higher than the Highland Rim or Valley and Ridge Provinces. Coastal Plain sediments attain maximal elevations of about 1000 feet above sea level in the vicinity of Phil

Campbell. In this area the strange experience can be had of descending from Coastal Plain onto the Cumberland Plateau or climbing up onto the Coastal Plain from the Cumberland Plateau.

As intimated above, the oldest Coastal Plain deposit is the Tuscaloosa formation, which is upper Cretaceous. It probably extended somewhat farther inland at one time but has been easily eroded, due to its unconsolidated character. Other extensive Cretaceous formations are exposed seaward from the Tuscaloosa formation—the Eutaw formation, Selma Chalk, and the Ripley formation. The exposed portions of the Tuscaloosa formation in Alabama contain a larger proportion of clays and gravels than the formation generally displays in eastern Georgia and the Carolinas (at least on its exposed surfaces). Parts of the Alabama Tuscaloosa formation, however, are known to overlie extensive sands, and a few areas of deep sand deposits are exposed in Russell County (extreme eastern Alabama). The Cretaceous formations were once probably covered by more recent sediments known as the Lafayette formation, which is now mostly eroded away.

Overlying the Tuscaloosa formation are two other Cretaceous formations, the Eutaw formation and the Selma Chalk. The Eutaw resembles the Tuscaloosa to rather high degree, being also somewhat sandy and poorly consolidated but of generally lower relief. Areas underlain by Selma Chalk form the widely known Black Belt, containing some of the most desirable agricultural land in the state. Soils developing over Selma Chalk are generally deep and quite dark, resembling the soils of the Prairie Peninsula and tall grass prairies of the Midwest. Black Belt topography is gently rolling. The original vegetation over Selma Chalk is not known for certain, although there seems to be good probability that portions of it were prairie-like. Aspects of this problem are mentioned further under "Alabama Vegetation, an Annotated Catalogue" (below).

There is evidently no concensus regarding the presence of Paleocene deposits outcropping in Alabama, as MacNeil (1946) indicates them and Fenneman (1938) does not.

The base of the Eocene deposits of Alabama form a cuesta, the Ripley, and south of the Ripley the Eocene strata (Clayton and Wilcox members) form a recognizable subprovince called the Red Hills.

It appears that the farther south one goes in the Alabama Coastal Plain, the less the geology is understood or agreed upon. The Hatchetigbee anticline in Choctaw and Clarke counties has been of perennial interest to geologists because of its magnitude as a Coastal Plain structure. This is apparently associated with another cuesta, the Buhrstone, on its inner side. MacNeil's (1946) treatment of the limestone-underlain areas in southeastern Alabama (which are closely related to Florida's lime sink region or the Dougherty Plain of Georgia) is at striking variance with Fenneman's (1938). The areas mapped as Ocala limestone by Stose and associates (1926) appear to have been remapped by MacNeil (1946) as Oligocene limestones in western Alabama and as "residuum" in southeastern Alabama (see Figure 1, which follows MacNeil's treatment). The residual character is attributed by MacNeil to the slumping and mixing of Miocene sandstones and sands, subsequent to the solution of underlying Chickasawhay (Oligocene) and Ocala (Eocene) limestones.

Most of the area south of the Red Hills was mapped by MacNeil as being of Miocene and Pliocene age. The Pliocene formations (Citronelle) have become of great interest in petroleum prospecting, and several oil fields have been established during the past few years.

The Mobile delta and extreme coastal Alabama are considered to be Quaternary in age. For further geological insight into this area, the reader is referred to Carlston (1950).

Much of the Alabama Coastal Plain is drained by the three major rivers with headwaters outside the province—the Alabama, Tombigbee and Chattahoochee. However, two sizeable rivers, the Choctawhatchee and the Conecuh, arise on the Eocene of southeastern Alabama and drain that region. The Ripley cuesta, incidentally, is rather clearly indicated by the headwaters of many south-flowing streams, particularly in eastern Alabama.

Alabama Soils

Due to great geological diversity, there is also notable variety in substrata and, consequently, in soils of Alabama. The following remarks regarding the principal soils (Soil Associations) of Alabama are based on the treatments in *Soils and Men* (United States Department of Agriculture, 1938).

Soils of the Dickson-Baxter Association characterize the inner Highland Rim of extreme northern Alabama. These (red-yellow podzolic) soils are derived from deposits of massive dolomites and limestones, with frequent cherty elements. Compaction or weak hardpan formation is not uncommon in Dickson-Baxter soils, which are also relatively deep, fertile and circumneutral in reaction. Land usage on these soils varies from timber production to diversified agriculture.

The Cumberland Plateau area of northern Alabama is overlain by Hartsells-Muskingum soils, which may be represented as gray-brown podzolic lithosols, underlain by sandstones and shales. These soils are usually shallow, extremely well-drained, inherently low in fertility and often extremely rocky, but are quite productive when supplemented with fertilizers.

Soils of the Decatur-Dewey-Clarksville Association (red-yellow podzols) are characteristic of the outer Highland Rim and the Coosa Valley (Valley and Ridge Province) of the state. Karst conditions are usually a prominent factor in subsurface drainage in these soils, which have generally developed over limestones, dolomites, cherts and shales. These soils are correspondingly diverse, and vary in fertility, the most productive being those derived from calcareous substrata. Diversified agriculture, including much cotton production, is presently accomplished on these soils.

Talladega-Fannin soils (red-yellow podzolic lithosols) overlie the southernmost portions of the Appalachian Mountain Province. Parent materials are metamorphics, including schists, micas, and quartz. These soils are predominantly rocky and severely eroded, and support subsistence agriculture and successively poorer timber yields.

The Piedmont Province of Alabama is overlain by soils of the Cecil-Appling Association (red-yellow podzolic). These soils were apparently quite fertile before excessive erosion took a heavy toll. Diversified agriculture is still supported in this area through continued application of chemical fertilizers. Underlying substrata are igneous or metamorphic and usually acid, consisting primarily of granites, gneisses and schists. Soils in some parts of the Piedmont are derived from more mafic rocks, which characteristically give rise to Davidson-Mecklenburg-Iredell soils (Alabama Department of Agriculture and Industries, 1953).

The Cretaceous Black Belt area of central Alabama is typified by Sumter-Vaiden soils (rendzina); the parent material is Selma Chalk (marl). These soils are clayey and heavy, sticky when wet and hard when dry. High temperatures and relatively low summer rainfall, coupled with soil conditions, lead to characteristic annual drought situations in the upland areas of the Black Belt. A preponderance of the acreage is now in pasture. Incidentally, this area of the state was apparently named for the predominant color of its soils, and not of its human populational majority, as has sometimes mistakenly been maintained.

The Red Hills and Tuscaloosa formation have given rise to Susquehanna-Savannah-Ruston and Norfolk-Ruston soils (red-yellow podzols) characterized by red to gray surface soils and red subsoils. These soils have developed over largely unconsolidated materials and vary from each other chiefly in texture. Some of the Red Hills soils appear to be derived from calcareous clays and marls. Norfolk Sand is rare in Alabama, although isolated occurrences have been reported (K. E. Landers, personal communication, 1967).

Greenville-Magnolia soils (red-yellow podzols) overlie a portion of extreme southeastern Alabama. These soils are typically deeper than other Red Hills soils and possess greater percentages of fine materials throughout their profiles. Erosion has proceeded quite severely in these soils, a notable example being the "Little Grand Canyon" of southwestern Georgia. These and soils of the preceding Associations support varied agricultural activities.

Extreme southern Alabama (Holocene) is characterized by water related soils such as Leon-Bladen, which are predominantly ground water podzols. Many soils in this Association commonly display an organic hardpan and are mediacid to strongly acid. In Alabama, these soils have remained largely wooded; much of this area is also swampy.

Significant alluvial deposits occur along the channels and terraces of the major rivers. These areas are usually timbered, except in the Tennessee Valley, where extensive flood control has rendered flood risk negligible, and the areas are thus safe for farming.

For more detailed information concerning the extent of Soil Associations and Series in Alabama, the reader is referred to Alabama Department of Agriculture and Industries (1953) and to soil surveys of individual counties.

CLIMATE

Annual mean temperatures measured in Alabama range from just under 60° F on the northern Cumberland Plateau to more than 67° F near the Gulf of Mexico (United States Department of Agriculture, 1941; United States Department of Commerce, n. d.). Absolute temperature minima range from near –20° F (northern Plateau) to just over 0° F (Gulf coast), while record maxima range between 100° F and 110° F over the state. Lowest temperatures generally occur from

TABLE 1. Summary of climatological data from selected stations in the major geological divisions of Alabama. Temperatures are in °F; precipitation in inches. See section on "Climate" for detailed localities of the stations.

Station	Month												Average or extreme	Mean frost-free season (days)
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.		
Mean maximum temperature														
Decatur (22)[a]	51.6	53.4	63.7	73.2	82.0	89.1	91.4	90.2	85.5	74.1	62.1	52.2	72.4	220
St. Bernard (22)	54.5	56.8	64.5	73.4	81.9	89.3	90.2	89.7	85.2	76.3	62.9	54.4	73.3	198
Talladega (21)	56.6	58.6	67.6	75.4	83.5	90.0	91.8	91.3	87.3	76.7	65.6	56.2	75.0	216
Auburn (22)	59.8	61.6	67.9	75.3	84.1	90.7	90.9	90.3	86.9	79.4	67.1	59.5	76.1	229
Troy (20)	61.1	63.0	69.4	77.0	85.3	91.3	91.3	90.8	87.3	79.4	67.7	61.1	77.1	244
Bay Minette (14)	65.2	67.2	71.5	78.5	85.6	90.8	90.9	91.4	87.4	81.1	71.3	65.5	78.9	292
Mean minimum temperature														
Decatur (22)	35.6	36.1	42.3	51.0	60.0	68.4	71.0	70.2	64.0	52.4	41.5	36.2	52.4	
St. Bernard (20)	33.1	33.8	39.6	47.4	55.8	64.3	67.3	66.4	60.2	48.6	37.6	32.9	48.9	
Talladega (20)	36.8	37.0	42.6	49.7	57.9	66.1	68.8	68.0	62.5	50.7	40.5	36.2	51.4	
Auburn (22)	39.7	40.0	45.2	52.1	60.2	67.7	69.8	69.2	64.7	54.7	44.0	39.1	53.9	
Troy (20)	41.0	41.9	46.8	53.5	61.2	68.0	69.9	69.2	64.9	54.8	44.2	40.8	54.7	
Bay Minette (14)	43.8	44.8	49.9	55.6	64.0	70.2	71.7	71.8	67.4	56.8	46.9	43.4	57.2	
Highest temperature														
Decatur (22)	78	80	88	91	99	107	106	107	103	97	86	78	107	
St. Bernard (21)	79	79	85	90	96	103	110	105	102	93	86	80	110	
Talladega (21)	80	81	88	97	98	109	107	107	103	96	86	80	109	
Auburn (21)	81	81	89	94	98	107	106	104	100	96	90	80	107	
Troy (20)	83	83	88	94	99	105	107	104	101	95	89	81	107	
Bay Minette (14)	85	82	89	94	100	102	103	101	98	93	88	82	103	
Lowest temperature														
Decatur (22)	–3	3	12	26	39	51	52	54	40	28	3	10	–3	
St. Bernard (20)	–16	–7	10	23	34	44	50	49	37	23	2	4	–16	
Talladega (20)	–5	2	10	25	35	45	51	46	39	23	5	9	–5	
Auburn (22)	7	9	13	27	37	51	57	56	42	25	9	13	7	
Troy (20)	10	10	19	29	39	55	59	55	44	28	12	14	10	
Bay Minette (14)	14	10	18	34	45	54	58	60	45	32	19	18	10	
Mean precipitation														
Decatur (22)	5.93	5.50	6.08	4.29	3.04	3.34	4.53	3.88	3.01	2.41	3.95	5.03	50.99	
St. Bernard (21+)	5.71	5.78	6.21	4.27	3.16	3.80	5.06	4.40	2.75	3.41	4.11	5.42	54.08	
Talladega (22)	4.66	5.47	6.56	4.66	3.39	4.49	5.11	4.50	2.71	2.64	3.16	5.17	52.52	
Auburn (22)	4.62	4.84	6.79	4.92	3.45	3.77	5.04	5.05	3.28	1.99	3.57	5.08	52.40	
Troy (21+)	4.90	4.37	7.27	5.58	3.97	3.31	6.13	6.18	3.69	1.56	3.56	4.84	55.36	
Bay Minette (16+)	5.15	3.96	8.45	6.23	5.23	4.91	8.72	6.34	6.26	2.60	3.89	5.02	66.76	

[a] Numbers of years on which records are based are given in parentheses.

December through February, while highs for the year usually occur in June through August. Proximity to the Gulf coast exerts a moderating effect on temperature extremes and heightens annual precipitation totals.

Annual mean precipitation is generally 50 or more inches statewide, approaching 70 inches near the Gulf coast and 55 inches on the Cumberland Plateau. Two peaks of precipitation are discernible, occurring in March and July. There is some tendency for the early spring peak to be more sustained inland, whereas the summer peak becomes much more accentuated toward the Gulf of Mexico. This latter phenomenon appears to be due primarily not to periods of heavy precipitation associated with tropical storms, but owes its occurrence to diurnal shower activity along the coast.

During the seasons of most active air mass movement, one of the principal breeding areas for cyclonic disturbances is in the northern Gulf of Mexico. Precipitation patterns in southern Alabama are influenced by this factor. Also, topography of the Appalachian System in northern Alabama acts as an effective orographic trigger, resulting in higher precipitation totals there than in the interior lowlands.

Table 1 is a sampling of climatological data from selected stations in the major geological divisions of the state. Decatur is in the Highland Rim Province, St. Bernard on the Cumberland Plateau, Talladega in the Valley and Ridge, Auburn on the Piedmont, Troy in the mid-Coastal Plain, and Bay Minette is on the lower Coastal Plain (near Mobile) not far from the Gulf coast.

Alabama Vegetation, an Annotated Catalogue

Among the portrayers of the vegetation of areas including Alabama are Harshberger (1911), Shantz and Zon (1924), Weaver and Clements (1938), Braun (1950), Kuchler (1964), and Knapp (1965). Of these treatments, Knapp appears to have arrived closest to the actual situation in the categories of vegetation he represents as well as their spatial extents and relationships to each other. It is worth noting, however, that Knapp's concepts appear to represent essentially those of Braun as modified by Kuchler.

Major Categories of Alabama Vegetation

- Eastern Deciduous Forest
  - Mixed mesophytic forest
  - Oak-hickory forest complex
- Coastal Plain Mixed Forest
  - Southern mixed forest
  - Swamp forest complex
- Prairie–Forest Mosaic
- Southeastern Coniferous Forest
  - Pine–oak forest
  - Pine–oak savanna
- Maritime Strand Complex

In spite of the limitations inherent in treating the vegetation in an area the size of Alabama, it seems appropriate to draft an original portrayal of the major vegetational types of Alabama (see Figure 2). The treatment presented here is, of course, based largely on the prior interpretations of previous workers and

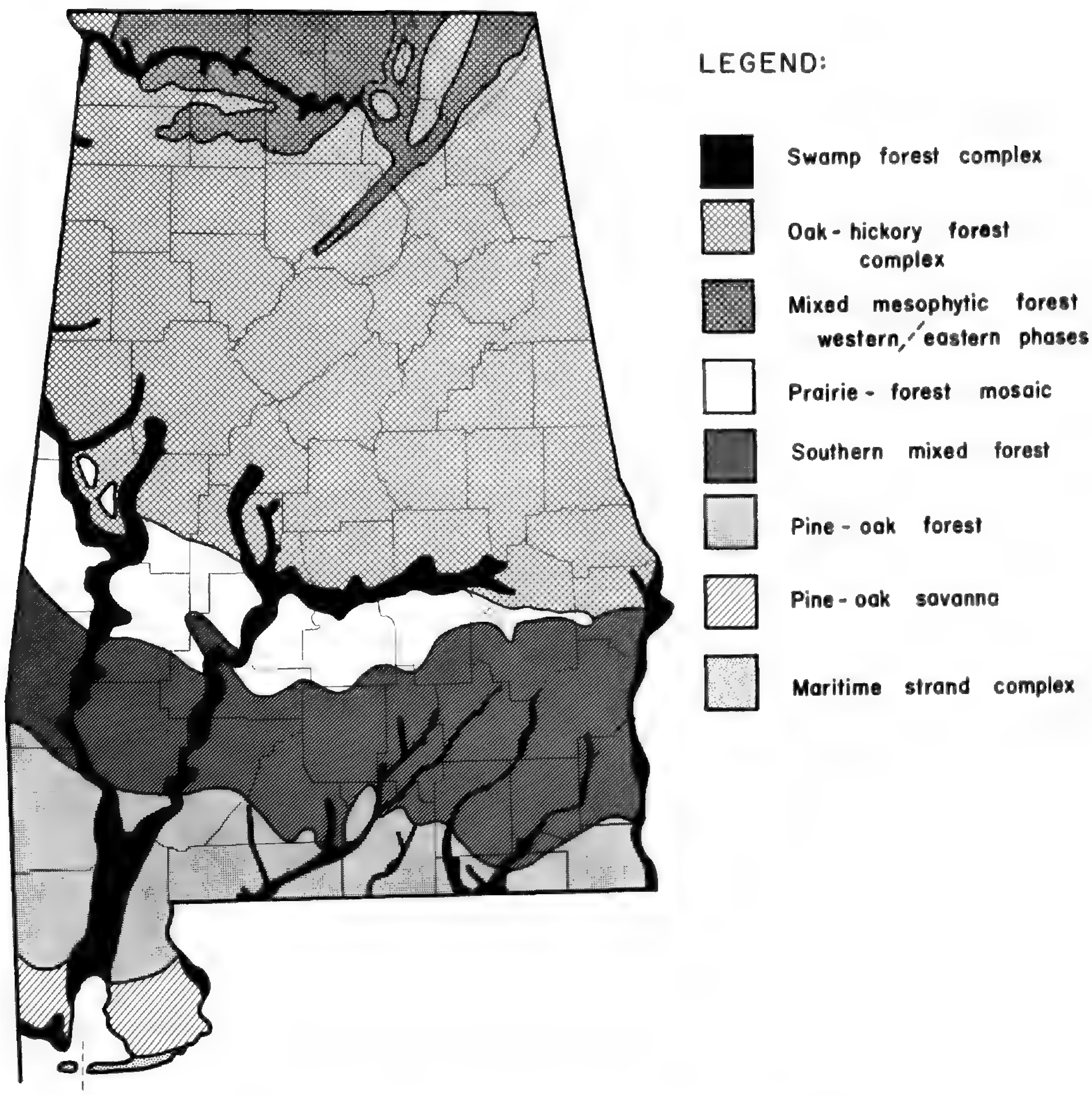


FIGURE 2. Estimated potential natural vegetation of Alabama.

represents an attempt to integrate these treatments with the extensive and detailed field experience accumulated during this study.

The following is an annotated catalogue of noteworthy vegetational types in Alabama, together with references indicating the treatments which have been most influential in guiding the present synthesis.

MIXED MESOPHYTIC FOREST

Characteristic taxa:

Woody:

Quercus alba, Q. rubra, Q. muehlenbergii, Ulmus rubra, U. americana, U. serotina, Carya ovata, Fraxinus americana subspp., *Castanea dentata* (formerly), *Robinia pseudo-acacia, Acer saccharum* subspp., *A. rubrum, Nyssa sylvatica, Liquidambar styraciflua, Tilia americana* sens. lat., *Fagus grandifolia, Magnolia acuminata, Liriodendron tulipifera, Aristolochia tomentosa,* *Smilax tamnoides, Juglans cinerea, J. nigra.* (*Betula, Tsuga, Cladrastis, Aesculus octandra*, rare.)

Herbaceous:

Many, including *Orchis specabilis, Hydrophyllum canadense, Erigenia bulbosa, Pachysandra procumbens, Asarum canadense, Polemonium reptans*, and *Aplectrum hyemale.*

Occurrence: Slopes of Cumberland Plateau and Highland Rim, including southward extension of Sequatchie Valley; northeastern part of state.

Comment: Small differences in topography are mirrored by significant shifts in vegetational patterns. Here, in the southernmost portions of its range, mixed mesophytic forests become largely confined to optimal, calcareous sites.

Principal source: Braun (1950).

OAK-HICKORY FOREST

Characteristic taxa:

Quercus alba, Q. rubra, Q. velutina, Q. muehlenbergii, Q. stellata, Q. marilandica, Q. falcata, Q. prinus, Carya cordiformis, C. ovata, Liquidambar styraciflua, Pinus taeda, P. palustris, P. virginiana, P. echinata, Fraxinus americana subspp., *Nyssa sylvatica, Robinia pseudo-acacia, Castanea dentata* (formerly), *Oxydendrum arboreum, Ceanothus americanus.*

Occurrence: Widely distributed in northern and central parts of state, and on mesic sites in Coastal Plain.

Comment: Varies widely in composition over its range, and is sometimes termed oak-hickory-pine forest.

Principal sources: Oosting (1942), Braun (1950).

SOUTHERN MIXED FOREST

Characteristic taxa:

Canopy: *Fagus grandifolia, Magnolia grandiflora, M. acuminata, Quercus alba, Q. nigra, Q. falcata, Q. rubra, Q. velutina, Q. laurifolia, Carya tomentosa, C. glabra, Acer saccharum* subspp., *Liquidambar styraciflua, Liriodendron tulipifera, Nyssa sylvatica.*

Understory: *Magnolia tripetala, M. macrophylla, Hamamelis virginiana, Oxydendrum arboreum, Illicium floridanum, Ilex opaca, Osmanthus americanus.*

Occurrence: Ravines in Red Hills, Lime Hills and Marl regions (the latter two of Harper, 1928) in southern part of state; also ravines bordering floodplains of larger streams of Coastal Plain. Higher elevations throughout its range are typically occupied by (less mesic) oak-hickory or pine-oak forest.

Comment: Most of the dominants point to a strong relationship between these forests and (ancestral?) mixed mesophytic forests.

Principal sources: Monk (1965), Quarterman and Keever (1962).

SWAMP FOREST

Characteristic taxa:

Taxodium distichum, Nyssa sylvatica, N. aquatica, Quercus prinus, Q. lyrata, Q. phellos, Carya aquatica, Populus deltoides, Platanus occidentalis, Carpinus caroliniana, Planera aquatica, Forestiera acuminata, Brunnichia ovata, Sabal minor, Sebastiania ligustrina.

Occurrence: Along major streams in the Coastal Plain.

Comment: Habitat preferences are complex.

Principal sources: Harper (1907), Penfound (1952).

PRAIRIE-FOREST MOSAIC

Characteristic taxa:

Andropogon scoparius, A. gerardii, Sorghastrum nutans, Quercus stellata, Q. falcata, Q. marilandica, Q. durandii, Q. macrocarpa (rare), *Juniperus virginiana, Liquidambar styraciflua, Ulmus alata, Carya* spp., and other typical prairie and prairie-forest border taxa.

Occurrence: Central part of state, from Sumter to Russell counties.

Comment: The source of perennial interest and debate as a putative disjunct from the main body of tall grass prairie; its original aspect seems to have been of patches of grassland of varying size, interspersed with oak-hickory forest. The principal geological substrate, Selma Chalk, appears to have been important in maintaining the vegetation.

Principal sources: Bartram (1791), Harper (1943), Jones and Patton (1966), Maginness (1967).

PINE-OAK FOREST

Characteristic taxa:

Pinus palustris, Quercus laevis, Q. incana, Q. stellata var. *margaretta, Q. marilandica, Cnidoscolus stimulosus, Stillingia sylvatica, Baptisia tinctoria, Stipulicida setacea.*

Occurrence: Upland sites in the Coastal Plain and adjacent provinces, principally south of the Black Belt and Red Hills.

Comment: Vegetation mapped in this category (Figure 2) has been greatly altered since settlement by Europeans. In its area of best development, the original vegetation (on upland sites) apparently consisted of extensive open forests of longleaf pine, with few other woody taxa except in areas experiencing infrequent fire. In eastern Georgia and the Carolinas, the extant range of *Pinus palustris* is usually taken to be spatially equivalent to the original forests. This correlation cannot be assumed in Alabama, since longleaf pine shows wider ecological amplitude there. Control of fire has led to higher percentages of hardwood dominants throughout the range of this vegetation type.

Principal sources: Wells (1928), Garren (1943).

PINE-OAK SAVANNA

Characteristic taxa:
Pinus elliottii, P. palustris, Serenoa repens, Quercus virginiana, Q. myrtifolia, Myrica cerifera, Ilex glabra, Hypericum spp., and many typical herbs.

Occurrence: Low uplands on the southernmost portions of the Coastal Plain.

Comment: Corresponds to meso-hydrophytic forest of Pessin (1933). Fire seems to be an important factor in maintaining the physiognomy and flora of this community.

Principal source: Pessin (1933).

MARITIME STRAND

Characteristic taxa:
Quercus virginiana, Q. myrtifolia, Q. chapmanii, Pinus clausa (east of Mobile Bay only), *Juniperus virginiana, Ceratiola ericoides, Serenoa repens, Ilex vomitoria, Uniola paniculata, Iva* spp., *Croton punctatus, Ipomoea stolonifera, Solidago pauciflosculosa, Opuntia* spp.; *Spartina alterniflora, Distichlis spicata, Juncus roemerianus.*

Occurrence: The barrier peninsulas and islands of Baldwin and Mobile counties in the extreme southern part of the state.

Comment: Three major community complexes are usually distinguished on the maritime strand of the southeastern United States, exclusive of southern Florida. These are marsh (brackish and salt), dune, and maritime forest. A canopy predominantly of *Quercus virginiana* typifies the maritime forest. The distribution of maritime forests and the various dune communities is strongly influenced by factors relating to their proximity to open salt water. All of these communities are mapped as a single complex in Figure 2.

Principal sources: Bourdeau and Oosting (1959), Kuchler (1964), Kurz (1942), Laessle (1958), Penfound (1952), Stallard (1950), Wells (1939).

FLORISTICS

It is possible to categorize the modes of occurrence of many Alabama woody plants and—to an extent—relate their distributions within Alabama to their wider distributions. Explanations of these distributional categories follows. Sources of the data which form the bases for these generalizations are indicated in the introduction to this paper.

Taxa which may be termed as outer Coastal Plain in overall affinity occur in extreme southern Alabama. Most of these plants have centers of distribution in northern Florida and southeastern Georgia. In Alabama, most appear to be confined to sediments of Miocene age or younger. Some of these plants are widespread over these sediments, while others appear to occur only in rather restricted habitats over these substrata. Some outer Coastal Plain plants seem to be strictly confined to even younger Pleistocene or Holocene sediments. Included in this category are the following taxa:

Polygonella polygama (Vent.) Engelm. & Gray
Quercus virginiana Miller
Quercus pumila Walter
Quercus chapmanii Sargent
Quercus myrtifolia Willd.
Myrica inodora Bartram
Taxodium distichum var. *nutans* (Aiton) Sweet
Pinus clausa (Chapman) Vasey
Serenoa repens (Bartram) Small
Smilax auriculata Walter
Ilex amelanchier Curtis
Ceratiola ericoides Michaux
Gaylussacia mosieri Small
Kalmia hirsuta Walter
Pieris phillyreifolia (Hooker) DC.
Vaccinium myrsinites Lam.
Conradina canescens (T. & G.) Gray
Satureja coccinea (Nuttall) Benth.
Cinnamomum camphora (L.) Nees & Eberm.
Chamaecyparis thyoides (L.) BSP.
Stillingia aquatica Chapman
Chrysobalanus oblongifolius Michaux
Crataegus aestivalis (Walter) T. & G.
Sageretia minutiflora (Michaux) Trel.
Populus heterophylla L.
Cissus incisa (Nuttall) Des Moulins
Daubentonia punicea (Cav.) DC.
Hypericum fasciculatum Lam.
Hypericum cistifolium Lam.
Hypericum suffruticosum P. Adams & N. Robson
Rhododendron viscosum var. *serrulatum* (Small) Ahles
Borrichia frutescens (L.) DC.
Iva frutescens L.
Iva imbricata Walter
Viburnum obovatum Walter
Decodon verticillatus (L.) Ell.
Cliftonia monophylla (Lam.) Sargent

Several of the outer Coastal Plain plants have been of phytogeographical interest because of close relatives in the southwestern United States or in Mexico. Various interpretations have been advanced regarding the origins of plants of the eastern Gulf of Mexico area (Neill, 1957; James, 1961).

Some woody plants of Alabama appear to occur throughout the Coastal Plain and are mainly confined to that province. This category includes the following:

Myrica cerifera L.
Halesia diptera Ellis
Magnolia grandiflora L.
Brunnichia ovata (Walter) Shinners
Ilex vomitoria Aiton
Pinus glabra Walter
Persea borbonia (L.) Spreng.
Osmanthus americanus (L.) Gray
Sebastiania ligustrina (Michaux) Muell-Arg.
Cyrilla racemiflora L.

In addition to those above, a substantial number of taxa of woody plants are primarily confined to the Coastal Plain but are not really widespread there, possibly due to the relatively high geological diversity of this province in Alabama. For instance, plants of *Baccharis halimifolia* L. and *Bumelia lanuginosa* (Michaux) Persoon appear to become much rarer in the western Coastal Plain in Alabama than they are eastward.

Other plants that have centers of distribution in the Coastal Plain of the southeastern United States seem to show significant extensions into more northern provinces in Alabama. This is probably a rather common occurrence in the southeastern United Staes, but certification of this fact awaits more complete data from adjacent states. Plants in this grouping are listed below. Many of them display range extensions into the Highland Rim (HR) or Valley and Ridge (VR) Provinces. See the introduction to the keys to families (p. 122) for an explanation of the abbreviations.

Trachelospermum difforme (Walter) Gray (VR, CuP, HR)
Ampelopsis arborea (L.) Koehne (VR, HR)
Taxodium distichum (L.) Richard (P, VR, HR)
Styrax americana Lam. (P, VR)
Sabal minor (Jacquin) Persoon (VR)
Quercus stellata var. *margaretta* (Ashe) Sargent (VR, CuP)
Quercus incana Bartram (CuP)
Magnolia virginiana L. (P, VR)
Quercus prinus L. (= *michauxii*) (HR, CuP)
Quercus laurifolia Michaux (P, CuP)
Quercus lyrata Walter (HR)
Smilax smallii Morong (VR)
Smilax laurifolia L. (VR)
Pinus palustris Miller (AM, CuP)
Sorbus arbutifolia (L.) Heynhold (CuP, AM, HR)
Gelsemium sempervirens (L.) Aiton f. (P, CuP)
Nyssa aquatica L. (HR, CuP)
Carya aquatica (Michaux f.) Nuttall (HR)

Quite often, it seems that these plants are those which occur in conjunction with Coastal Plain river swamps and display range extensions northward on the (calcareous) alluvial soils along the Coosa and Tennessee Rivers. This suggests that there may be some correspondence of these habitats, at least in Alabama, or that perhaps some compensating mechanisms may be operative in the northward habitats. Also suggested indirectly is the possibility that (at least) the Valley and Ridge Province might serve as a significant avenue for migration.

As one would expect, there are several plants with centers of distribution in the northeastern United States which also occur in Alabama and which tend to become confined to the Cumberland Plateau and Appalachian Mountain Provinces as they occur southward. A listing of these includes the following plants:

Acer saccharum ssp. *nigrum* (Michaux f.) Desmarais
Corylus americana Walter
Betula lenta L.
Chimaphila maculata (L.) Pursh
Tsuga canadensis (L.) Carr.

There is also a group of woody plants with centers of distribution in the southern Appalachians. These reach their southern limits on the same physiographic areas as those in the previous group. They include:

Hypericum stragalum P. Adams & N. Robson
Pinus virginiana Miller
Stewartia ovata (Cav.) Weatherby
Physocarpus opulifolius (L.) Maxim.
Fothergilla major (Sims) Lodd

Pyrularia pubera Michaux
Rhododendron catawbiense Michaux
Rhododendron arborescens (Pursh) Torrey
Rhododendron minus Michaux
Diervilla sessilifolia Buckley *sens. lat.*
Hydrangea arborescens subsp. *discolor* (Ser.) McCl.
Celastrus scandens L.
Vaccinium pallidum L.
Corylus cornuta Marshall

There is a relatively small group of woody plants which displays distributional patterns centered in the Piedmont or southernmost Appalachian Mountains (and the Ozarks, in one case). This group is here designated as of perimontane affinity and includes the following:

Lonicera flava Sims (also in Ozarks)
Prunus serotina subsp. *hirsuta* (Ell.) McVaugh
Ribes curvatum Small
Amorpha schwerini Schneider
Rhododendron flammeum (Michaux) Sargent
Quercus georgiana Curtis

Certain plants which are characteristic of mixed mesophytic forests as defined by Braun (1950) reach southern extremes on calcareous sites in Alabama, as do mixed mesophytic forests (see section on Alabama Vegetation). These taxa characteristically display centers of distribution west of the Blue Ridge. *Aesculus octandra* Marshall is a characteristic dominant of Braun's eastern phase of mixed mesophytic forest; *Fraxinus quadrangulata* Michaux and *Ulmus serotina* Sargent show strong affinities to western phases of this forest type. *Cladrastis lutea* (Michaux f.) K. Koch is typical of both eastern and western phases of mixed mesophytic forest.

A small group of lower Southeastern woody plants with centers of occurrence in Alabama is recognizable. Among these are *Illicium floridanum* Ellis, *Hydrangea quercifolia* Bartram and *Aesculus parviflora* Walter, all highly celebrated plants.

Several of the woody plants included in this treatment represent previous escapes that have now become naturalized. Some of these have spread widely. The following list includes plants widely naturalized, but does not include incidental escapees.

Carya illinoensis (Wang.) K. Koch
Maclura pomifera (Raf.) Schneider (possibly native also)
Lonicera japonica Thunberg
Ailanthus altissima (Miller) Swingle
Melia azedarach L.
Ligustrum sinense Loureiro
Pueraria lobata (Willd.) Ohwi
Paulownia tomentosa (Thunberg) Steudel
Albizia julibrissin Durazzini

Some woody plants of wide distribution within the eastern United States or North America apparently become less and less common southward, until they are quite rare or altogether absent near the Gulf Coast. This group includes:

Quercus prinoides var. *acuminata* (Michaux) Gleason
Acer negundo L.
Quercus rubra L.
Quercus shumardii Buckley
Quercus velutina Lam.

Oxydendrum arboreum (L.) DC.
Hydrangea arborescens L. *sens. lat.*
Cercis canadensis L.
Fraxinus americana L. *sens. lat.*
Rhus glabra L.

A considerable number of native woody plants is widespread over Alabama; they probably occur in every county. These plants are also of widespread occurrence in the southeastern United States, and some are common over a wider range.

Fagus grandifolia Ehrhart
Quercus alba L.
Quercus falcata Michaux
Quercus marilandica Muenchh.
Quercus nigra L.
Quercus phellos L.
Quercus stellata Wang.
Hamamelis virginiana L.
Liquidambar styraciflua L.
Hypericum hypericoides (L.) Crantz
Carya tomentosa (Poiret) Nuttall
Sassafras albidum (Nuttall) Nees
Smilax bona-nox L.
Smilax glauca Walter
Phoradendron serotinum (Raf.) Johnston
Morus rubra L.
Nyssa sylvatica Marshall
Pinus taeda L.
Platanus occidentalis L.
Arundinaria gigantea (Walter) Muhl.
Prunus angustifolia Marshall
Prunus serotina Ehrhart
Salix nigra Marshall
Tilia americana L.
Ulmus alata Michaux
Cocculus carolinus (L.) DC.
Celtis occidentalis L.
Vitis rotundifolia L.
Callicarpa americana L.
Acer rubrum L.
Rhus copallina L.
Rhus radicans L.
Ilex opaca Aiton
Alnus serrulata (Aiton) Willd.
Betula nigra L.
Carpinus caroliniana Walter
Ostrya virginiana (Miller) K. Koch
Campsis radicans (L.) Seemann
Sambucus canadensis L.
Euonymus americanus L.
Juniperus virginiana L.
Diospyros virginiana L.
Vaccinium arboreum Marshall
Vaccinium stamineum L.
Cephalanthus occidentalis L.

The most noted plants in Alabama are the rare ones, several of which are near-endemics. Alabama's interesting rarities include *Quercus macrocarpa* Michaux, *Cotinus obovatus* Raf., *Andrachne phyllanthoides* (Nuttall) Mueller, *Neviusia alabamensis* Gray, *Croton alabamensis* Smith, *Schisandra glabra* (Brickell) Rehder, *Dirca palustris* L., and *Myrica inodora* Bartram. Herbs in this category include *Oenothera grandiflora* Bartram and *Croomia pauciflora* (Nuttall) Torrey.

Quercus macrocarpa is associated with oak-parkland (or "prairie") vegetation in Alabama, as it is in the midwestern United States. A single population is known in Alabama, near Snowdoun, Montgomery County (Harper, 1942), though the plant should also be looked for particulary in the southern portions of Perry and Hale Counties and also in Sumter and Greene Counties. It seems unlikely that *Q. macrocarpa* does not or has not occurred in some of these other areas in Alabama, in view of the recurrence of the habitat.

Cotinus obovatus Raf. occurs east of the Mississippi River only on the Highland Rim–Cumberland Plateau interface near the Tennessee River in northeastern Alabama and adjacent Tennessee (Franklin County). Localized yet large populations of *Cotinus* appear to be always associated with *Mirabilis albida* (Walter) Heimerl and to occur only over Bangor Limestone (as noted by Harper, 1928). The eastern population series is disjunct from populations in northern Arkansas, extreme southern Missouri, and extreme eastern Oklahoma, particularly in the White River watershed. In this western area, plants of *Cotinus* occur over an analogous (or homologous) limestone stratum, though they are also known from sandstone strata (G. L. Tucker, personal communication, 1967). The Alabama populations reproduce substantially from seed, as well as by layering.

Andrachne phyllanthoides (Nuttall) Mueller was first collected in Alabama in 1966 (Clark, 1967), after it was discovered by Mrs. Blanche E. Dean along a tributary of the Black Warrior River on the Cumberland Plateau. This is the first population of the plant known from east of Arkansas. Although it appears to reproduce readily by layering, it is not known whether or not the plant reproduces from seed in Alabama.

Neviusia alabamensis Gray apparently occurs only in Alabama and Arkansas. The widely scattered Alabama populations evidently are in habitats over calcareous strata. This plant reproduces extensively by asexual means; it is aggressively soboliferous.

Croton alabamensis Smith has been the subject of a doctoral dissertation (Farmer, 1962). It is known only from Coffee County, Tennessee (near Tullahoma) and from Bibb and Tuscaloosa Counties, Alabama, where it occurs on the Cumberland Plateau–Coastal Plain interface. Its closest morphological relative appears to be South American. This plant reproduces extensively in isolated populations by both sexual and asexual means (Farmer, 1962). It apparently is restricted to shales and calcareous strata.

Schisandra glabra (Brickell) Rehder apparently occurs over calcareous clays or marls in the western "Red Hills" of Alabama. It is sporadic (and relictual) throughout the Southeast (Duncan, 1967), often on similar sites.

Dirca palustris L. also occurs sporadically over circumneutral or basic soils in the Southeast.

Myrica inodora Bartram has been noted above under the category of plants of the outer Coastal Plain. It occurs only in creek swamps from western Florida through southern Alabama into eastern Mississippi. Its nearest morphological relative in the Nearctic occurs on the west coastal area of the United States (Baird, 1968). Other than the fact that its distribution is pericoastal in an area of high moisture availability, its distribution represents an enigma.

Minuartia alabamensis McCormick, Bozeman & Spongberg, recently described, is known only from two granitic outcrops in the upper Piedmont (McCormick, Bozeman & Spongberg, 1971). *Oenothera grandiflora* Bartram evidently occurs only in the Tombigbee River drainage. *Croomia pauciflora* (Nuttall) Torrey is apparently confined to calcareous sites from the Appalachicola River bluffs in northwestern Florida northward sporadically into the Valley and Ridge Province of Alabama (and Georgia?). In the few populations observed, reproduction appeared to be entirely by means of stolons.

Certain interesting similarities are displayed by the distributions of several of the rare plants above. First, most appear to be at least facultatively asexual. Also, most apparently are restricted to sites which might be expected to offer optimal nutritional possibilities, *i.e.* calcareous sites. Most seem closely associated in their occurrences to a major drainage or drainages. At least two, *Croton alabamensis* and *Cotinus obovatus*, occur primarily on major physiographic boundaries. Several of the above rarities also occur only in association with the southern Cumberland Plateau and its analogues (or, indeed, homologues) the Ouachita Plateau and southern Ozarks. These observations suggest that the present distributions of these plants may be related fairly directly to processes which have shaped and disrupted major physiographic features in the past. Several of these species are also excellent illustrations of the known and expected behavior of many rare plants, *i.e.* restriction to optimal sites and population maintenance by facultative asexuality in relictual habitats.

KEYS TO THE WOODY PLANTS OF ALABAMA, WITH AN ANNOTATED CATALOGUE

Taxa in this treatment are listed by family, generally following the phyletic treatment proposed by Radford, Ahles and Bell (1968). Infrafamilial taxa are arranged alphabetically. Flowering and fruiting seasons are included. (Flowering season is listed first; then fruiting season. If flowering and fruiting are continuous, no semicolon separates the seasons; if only one season is listed, flowering and fruiting may both be expected then.)

As much as possible, a conscious effort has been made to list the common names of plants as they are used in Alabama.

Synonymy is listed from the treatments of Mohr (1901), Harper (1928), Small (1933), and Radford, Ahles and Bell (1968). These authors are hereinafter abbreviated M, H, S, and RAB, respectively.

Distribution is given by abbreviation of physiographic provinces, *i.e.* Coastal Plain (CP), Piedmont (P), Appalachian Mountain (AM), Cumberland Plateau (CuP), Valley and Ridge (VR), and Highland Rim (HR). Since the outer Coastal Plain of Alabama constitutes such a distinctive subprovince with respect to its plants, reference is made to it by the abbreviation OCP.

Plants apparently collected for the first time in Alabama during this study include *Veratrum parviflorum* Michaux, *Ilex amelanchier* Curtis, *Amorpha schwerini* Schneider, *Hibiscus syriacus* L., *Rhus typhina* L., *Andrachne phyllanthoides* (Nuttall) Mueller, *Castanea sativa* Miller and *Pyrularia pubera* Michaux. The first specimens of *Minuartia alabamensis* McCormick, Bozeman & Spongberg to be available may have been collected during this study, in 1967 (McCormick, Bozeman & Spongberg, 1971). *Rhododendron flammeum* (Michaux) Sargent has apparently been recognized as such for the first time in Alabama.

A specimen of *Viburnum obovatum* Walter collected by Sidney McDaniel and forwarded to the writer after field work for this study was concluded is evidently the first documentation of this plant in Alabama.

FIGURE 3. County index map of Alabama. (Source: U. S. Department of Commerce, Bureau of the Census, County boundaries as of April 1, 1960.)

The writer considers the presence of 437 taxa of woody plants in 177 genera and 74 families as verifiable in Alabama. The presence of all of these but a very small number (noted individually as they appear in the following text) is based on specimens. Dots in counties on included distributional maps are based on specimens; blank maps are included for taxa whose presence is claimed by reliable reports, but for which no specimens have been seen by the writer. Documented records are also included from Duncan (1967), Hardin (1957), and from correspondence with W. P. Adams (*Hypericum*) and E. W. Chester (*Halesia*). The names and locations of the counties of Alabama are shown in Figure 3.

KEYS TO FAMILIES OF WOODY PLANTS OF ALABAMA

Plant a vine; climbing by twining, tendril-like leaf rachises, or by roots, or trailing on ground or other support .... KEY 1

Plant a shrub or tree; habit various, but not climbing on other support or trailing on ground 1

1. Stem thick and fleshy, pad-like; nodes bearing glochidia .... 50. CACTACEAE
1. Stem not thick and fleshy, not pad-like; nodes not bearing glochidia 2
    2. Stem bearing ochreae at nodes .... 17. POLYGONACEAE
    2. Stem not bearing ochreae at nodes, or stem not evident 3

3. Leaves flabelliform, margin lacerate .... 5. Arecaceae
3. Leaves not flabelliform, or margin not lacerate, or leaves absent 4
    4. Leaves linear, acicular or subulate 5
        5. Leaves lance- or scale-like .... 3. Cupressaceae
        5. Leaves linear or needle-like 6
            6. Perianth present; fruit a drupe or capsule 7
                7. Flowers bisexual; fruit a capsule .... 49. Hypericaceae
                7. Flowers unisexual; fruit a drupe .... 58. Empetraceae
            6. Perianth absent; fruiting structure composed of woody scales (*i.e.* a cone) 8
                8. Leaves in fascicles, evergreen .... 1. Pinaceae
                8. Leaves alternate or spiralled, evergreen or deciduous 9
                    9. Leaves deciduous; bark stringy .... 2. Taxodiaceae
                    9. Leaves evergreen; bark roughened to smoothish .... 1. Pinaceae
    4. Leaves not linear, needle-like, or scale-like, or leaves absent 10
        10. Leaves or leaf-scars opposite or subopposite .... KEY 2
        10. Leaves or leaf-scars alternate .... KEY 3

KEY 1

Woody Vines

1. Leaves both opposite and compound 2
    2. Leaflets entire, 2 per leaf .... 71. Bignoniaceae
    2. Leaflets toothed or lobed, 3 or more per leaf 3
        3. Leaflets 3 per leaf .... 18. Ranunculaceae
        3. Leaflets 5 or more per leaf .... 71. Bignoniaceae
1. Leaves either alternate or simple 4
    4. Leaves alternate 5
        5. Leaves compound 6
            6. Leaves palmately compound; leaflets more than three .... 44. Vitaceae
            6. Leaves pinnately compound 7
                7. Leaflets three 8
                    8. Flower actinomorphic; fruit a drupe .... 35. Anacardiaceae
                    8. Flower zygomorphic; fruit a legume .... 30. Fabaceae
                7. Leaflets more than 3 9
                    9. Leaves decompound .... 44. Vitaceae
                    9. Leaves once compound .... 30. Fabaceae
        5. Leaves simple 10
            10. Leaves evergreen, or partially so 11
                11. Plant with tendrils .... 6. Liliaceae
                11. Plant lacking tendrils 12
                    12. Leaves entire .... 59. Ericaceae
                    12. Leaves lobed or toothed 13
                        13. Leaves lobed .... 54. Araliaceae
                        13. Leaves toothed .... 59. Ericaceae
            10. Leaves deciduous 14
                14. Plant with tendrils 15
                    15. Tendrils terminating branches .... 17. Polygonaceae
                    15. Tendrils from nodes 16
                        16. Tendrils arising with leaves, from petiolar sheaths .... 6. Liliaceae
                        16. Tendrils arising opposite leaves .... 44. Vitaceae
                14. Plant without tendrils 17
                    17. Leaf venation palmate 18
                        18. Inflorescence paniculate; fruit fleshy .... 19. Menispermaceae
                        18. Inflorescence solitary, rarely two flowers to an axil; fruit a capsule .... 16. Aristolochiaceae
                    17. Leaf venation pinnate 19
                        19. Inflorescence terminal 20
                            20. Leaf margin serrate .... 38. Celastraceae
                            20. Leaf margin entire, or occasionally sinuate .... 43. Rhamnaceae

19. Inflorescence axillary 21
21. Leaf bases cordate .... 16. Aristolochiaceae
21. Leaf bases cuneate; rarely truncate 22
22. Leaf margin entire or remotely dentate .... 23. Schisandraceae
22. Leaf margin serrate .... 38. Celastraceae
4. Leaves opposite 23
23. Vine climbing by means of adventitious roots .... 26. Saxifragaceae
23. Vine climbing by twining stem 24
24. Corolla zygomorphic; fruit a berry .... 73. Caprifoliaceae
24. Corolla actinomorphic; fruit a follicle or capsule 25
25. Naked peduncle of axillary inflorescence more than 1 cm long; fruit a follicle .... 66. Apocynaceae
25. Bracted peduncle of axillary inflorescence less than 1 cm long; fruit a capsule .... 65. Loganiaceae

KEY 2

Shrubs or Trees; Leaves Opposite

1. Leaves absent at anthesis 2
2. Stamens 5 or more; ovary conspicuously lobed .... 40. Aceraceae
2. Stamens 2; ovary not lobed .... 64. Oleaceae
1. Leaves present at anthesis, or leaves present 3
3. Leaves compound 4
4. Leaves palmately compound .... 41. Hippocastanaceae
4. Leaves pinnately compound 5
5. Leaflets lobed .... 40. Aceraceae
5. Leaflets serrate, not lobed 6
6. Inflorescence terminal; fruit a berry or drupe .... 73. Caprifoliaceae
6. Inflorescence axillary; fruit not a berry or drupe 7
7. Leaves 3-foliolate; fruit bladder-like, inflated .... 39. Staphyleaceae
7. Leaves more than 3-foliolate; fruit a samara .... 64. Oleaceae
3. Leaves simple 8
8. Stems and leaves succulent .... 74. Asteraceae
8. Stems and leaves not succulent 9
9. Flowers and fruit in heads, or compact head-like cymes 10
10. Bracts subtending inflorescence large, conspicuous, whitened, not imbricate, not resembling leaves; fruit a drupe .... 56. Cornaceae
10. Bracts subtending inflorescences either greatly resembling leaves or imbricate; fruit not fleshy 11
11. Corolla lobes 4; fruit 2-seeded .... 72. Rubiaceae
11. Corolla lobes 5; fruit 1-seeded .... 74. Asteraceae
9. Flowers not in heads or compact head-like cymes 12
12. Leaves lobed 13
13. Ovary inferior; linear stipules present .... 73. Caprifoliaceae
13. Ovary superior; linear stipules absent .... 40. Aceraceae
12. Leaves not lobed 14
14. Leaf margin entire 15
15. Plant entirely green; parasitic on stems of deciduous woody plants .... 15. Loranthaceae
15. Plant not green throughout; not parasitic on stems of deciduous woody plants 16
16. Leaf bases cordate 17
17. Stamens 4; capsule less than 5 cm long .... 70. Scrophulariaceae
17. Stamens 2; capsule more than 6 cm long .... 71. Bignoniaceae
16. Leaf bases not cordate 18
18. Leaves granular-farinose beneath .... 65. Loganiaceae
18. Leaves pubescent to glabrous beneath, but not granular-farinose 19

19. Leaves acuminate to abruptly acuminate — 20
    20. Corolla lobes 5 or less, or corolla lacking; fruit a drupe or drupe-like — 21
        21. Flowers unisexual; corolla lacking; fruit more than 1 cm in diameter — 14. SANTALACEAE
        21. Flowers bisexual; corolla present; fruit less than 1 cm in diameter — 22
            22. Inflorescence axillary — 53. LYTHRACEAE
            22. Inflorescence terminal — 23
                23. Stamens 5; leaves involute — 73. CAPRIFOLIACEAE
                23. Stamens 4; leaves not involute — 56. CORNACEAE
    20. Perianth lobes more than 10, undifferentiated; fruit not drupe-like 24. CALYCANTHACEAE
19. Leaves obtuse to acute, not acuminate — 24
    24. Leaf venation penniparallel — 66. APOCYNACEAE
    24. Leaf venation not penniparallel — 25
        25. Stamens 10 or more; fruit a capsule — 49. HYPERICACEAE
        25. Stamens 2–5; fruit a berry, drupe, or of nutlets enclosed by calyx — 26
            26. Ovary inferior; stamens 5 — 73. CAPRIFOLIACEAE
            26. Ovary superior; stamens 4 or less — 27
                27. Corolla lobes 4; fruit a drupe — 64. OLEACEAE
                27. Corolla lobes 5; fruit of nutlets enclosed by calyx — 68. LAMIACEAE

14. Leaf margin not entire — 28
    28. Leaves with occasional large teeth confined to distal half of blade — 68. LAMIACEAE
    28. Leaves regularly crenate, serrate, or dentate, at least distally — 29
        29. Inflorescence axillary — 30
            30. Tips of branchlets pubescent — 31
                31. Corolla apopetalous or lacking; flowers unisexual; leaves crenate to serrate — 64. OLEACEAE
                31. Corolla gamopetalous; flowers bisexual; leaves coarsely serrate-dentate — 67. VERBENACEAE
            30. Tips of branchlets glabrous — 32
                32. Twigs distinctly greenish — 38. CELASTRACEAE
                32. Twigs distinctly brownish — 64. OLEACEAE
        29. Inflorescence terminal — 33
            33. Ovary partially or wholly inferior — 34
                34. Stamens 5; sepals 5, linear or less than 1 mm long — 73. CAPRIFOLIACEAE
                34. Stamens more than 10; sepals 4, lanceolate to ovate, more than 2 mm long — 26. SAXIFRAGACEAE
            33. Ovary superior — 35
                35. Stamens 4; fruit of 4 nutlets — 67. VERBENACEAE
                35. Stamens 5; fruit drupe-like, but separating into 3 nutlets — 43. RHAMNACEAE

KEY 3

SHRUBS OR TREES; LEAVES ALTERNATE

1. Leaves compound, or absent at time pollen is shed — 2
    2. Leaves absent at time pollen is shed — 3

3. Corolla present 4
  4. Stamens awned .... 59. ERICACEAE
  4. Stamens awnless 5
    5. Corolla apopetalous, or essentially so .... 35. ANACARDIACEAE
    5. Corolla gamopetalous, urceolate .... 59. ERICACEAE
3. Corolla absent, or perianth undifferentiated 6
  6. Elongate, catkin-like cones present .... 2. TAXODIACEAE
  6. Elongate cones and catkins absent 7
    7. Stamens more than 10 .... 29. ROSACEAE
    7. Stamens less than 10 .... 12. ULMACEAE

2. Leaves present 8
  8. Leaves decompound 9
    9. Stem spiny 10
      10. Leaflets, at least some, more than 2 cm broad .... 54. ARALIACEAE
      10. Leaflets less than 2 cm broad .... 30. FABACEAE
    9. Stem not spiny 11
      11. Terminal or ultimate leaflets toothed or lobed .... 33. MELIACEAE
      11. Terminal or ultimate leaflets entire or crenulate .... 30. FABACEAE
  8. Leaves once compound 12
    12. Teeth of leaflets bearing a conspicuous green gland on the central under-surface of each tooth .... 32. SIMAROUBACEAE
    12. Teeth of leaflets lacking conspicuous glands on their under-surfaces, or leaflets not toothed 13
      13. Leaves trifoliolate, or palmately compound 14
        14. Stem spiny 15
          15. Petioles winged; midrib of leaflets not spiny .... 31. RUTACEAE
          15. Petioles wingless; midrib of leaflets often retrorsely spiny .... 29. ROSACEAE
        14. Stem not spiny 16
          16. Mature leaves conspicuously glandular above .... 31. RUTACEAE
          16. Mature leaves eglandular above 17
            17. Leaflets obtuse, mucronate .... 30. FABACEAE
            17. Leaflets acuminate, not mucronate 18
              18. Leaves trifoliolate .... 35. ANACARDIACEAE
              18. Leaves 4- or more-foliolate .... 44. VITACEAE
      13. Leaves pinnately compound, with predominantly more than 3 leaflets .. 19
        19. Leaflets entire 20
          20. Inflorescence axillary; leaflets obtuse to emarginate .... 30. FABACEAE
          20. Inflorescence terminal; leaflets acute to acuminate .... 42. SAPINDACEAE
        19. Leaflets toothed or lobed 21
          21. Terminal leaflets of some leaves lobed 22
            22. Fruit a follicle; corolla much shorter than calyx .... 18. RANUNCULACEAE
            22. Fruit a drupe; corolla longer than calyx .. 35. ANACARDIACEAE
          21. Terminal leaflets not lobed 23
            23. Stamens more than 10, not borne in a catkin; fruit fleshy, not a nut, drupe or capsule .... 29. ROSACEAE
            23. Stamens 10 or less or male inflorescence a catkin; fruit a drupe, capsule or nut 24
              24. Terminal leaflets entire .... 35. ANACARDIACEAE
              24. Terminal leaflets serrate 25
                25. Leaflets spotted with large, sessile glands .... 31. RUTACEAE
                25. Leaflets lacking glands .... 9. JUGLANDACEAE

1. Leaves simple 26
  26. Flowers and fruits in heads .... 74. ASTERACEAE
  26. Flowers and fruits not in heads 27
    27. Leaf venation parallel, not netted 28

28. Leaf bearing indurate, sharp mucro (capable of piercing flesh), or leaf margin fraying into filamentous threads .... 6. LILIACEAE
28. Leaf lacking indurate mucro, and margin entire .... 4. POACEAE
27. Leaf venation netted, or vein single 29
29. Plant in fruit (for plants in flower, see p. 130) 30
30. Inflorescence terminal 31
31. Leaf margins entire, sometimes undulate 32
32. Fruit a drupe, or drupe-like 33
33. Leaves acuminate 34
34. Flowers imperfect; calyx lobes more than 1 mm long; fruit more than 1 cm broad .... 14. SANTALACEAE
34. Flowers perfect; calyx lobes less than 0.5 mm long; fruit less than 1 cm broad .... 56. CORNACEAE
33. Leaves obtuse to retuse, sometimes mucronate 35
35. Inflorescence branches plumose, with trichomes exceeding 1 mm in length .... 35. ANACARDIACEAE
35. Inflorescence densely tomentose, not plumose .... 29. ROSACEAE
32. Fruit capsular or follicular 36
36. Fruit an aggregate of follicles 37
37. Follicles borne in a single whorl; receptacle not elongate .... 21. ILLICIACEAE
37. Follicles spiralled on an elongate receptacle .... 20. MAGNOLIACEAE
36. Fruit a capsule 38
38. Leaves acuminate 39
39. Fruit 3 times or more as long as broad, pubescent .... 59. ERICACEAE
39. Fruit less than 2 times as long as broad, glabrous .... 34. EUPHORBIACEAE
38. Leaves retuse, obtuse or acute 40
40. Leaves and twigs heavily vested with silvery, peltate scales .... 34. EUPHORBIACEAE
40. Leaves and twigs not vested with peltate scales, vestiture various 41
41. Plant creeping .... 59. ERICACEAE
41. Plant not creeping 42
42. Capsule disintegrating with dehiscence; seed one per locule .... 34. EUPHORBIACEAE
42. Capsule remaining intact after dehiscence; seeds several to many per locule 43
43. Capsule 3 or more times longer than broad .... 59. ERICACEAE
43. Capsule less than twice as long as broad .... 53. LYTHRACEAE
31. Leaf margins serrate, dentate, crenate or lobed 44
44. Fruit a cone-like aggregate of samaras .... 20. MAGNOLIACEAE
44. Fruit not an aggregate of samaras 45
45. Inflorescence a catkin, sometimes appearing woody .... 10. BETULACEAE
45. Inflorescence not a catkin 46
46. Inflorescence adnate basally to a single, conspicuous bract .... 45. TILIACEAE
46. Inflorescence not adnate to a single, basal bract 47
47. Fruit a berry or drupe 48
48. Ovary inferior or partially so 59. ERICACEAE
48. Ovary superior .... 43. RHAMNACEAE
47. Fruit follicular or capsular 49

49. Fruit of follicles .... 29. ROSACEAE
49. Fruit a capsule 50
50. Fruit one per inflorescence 51
51. Sepals pubescent, more than 1 cm long; pedicel much shorter than capsule .... 48. THEACEAE
51. Sepals glabrous or glandular, less than 0.5 cm long; pedicel much longer than capsule .... 59. ERICACEAE
50. Fruit 2–many in an inflorescence 52
52. Adaxial leaf surface of two contrasting colors (variegated) .... 59. ERICACEAE
52. Adaxial leaf surface not of two contrasting colors 53
53. Capsule 2–3 valved 54
54. Fruit pubescent 55
55. Capsule depressed apically and somewhat lobed .... 57. CLETHRACEAE
55. Capsule not depressed apically 56
56. Fruit columnar, not beaked; stigma persistent .... 26. SAXIFRAGACEAE
56. Fruit ovoid, abruptly beaked; stigmata deciduous .... 27. HAMAMELIDACEAE
54. Fruit not pubescent .... 43. RHAMNACEAE
53. Capsule 4–5 valved 57
57. Sepals densely pubescent; trichomes stellate .... 46. MALVACEAE
57. Sepals glabrous or pubescent; trichomes, if present, not stellate .... 59. ERICACEAE
30. Inflorescence axillary 58
58. Fruit a legume .... 30. FABACEAE
58. Fruit not a legume 59
59. Fruit of achenes or nutlets enclosed by fleshy calyces in in multiple fruits .... 13. MORACEAE
59. Fruit not of achenes or nutlets enclosed by fleshy calyces in multiple fruits 60
60. Twigs, leaves and inflorescences heavily vested with silvery scales .... 52. ELAEAGNACEAE
60. Twigs, leaves and inflorescences not vested with silvery scales 61

61. Axillary buds entirely enclosed by pulvinus 62
62. Leaves lobed .... 28. PLATANACEAE
62. Leaves entire .... 51. THYMELAEACEAE
61. Axillary buds not entirely enclosed by pulvinus 63
63. Fruit or fruiting structure burr-like 64
64. Leaves lobed 65
65. Fruit a spherical multiple of 2-valved capsules, without a basal cup .... 27. HAMAMELIDACEAE
65. Fruit not a multiple of capsules, but enclosed by a basal cup .... 11. FAGACEAE
64. Leaves serrate or dentate, not lobed 66
66. Fruit spiny or prickly .... 11. FAGACEAE
66. Fruit not spiny or prickly, irregularly lobed .... 12. ULMACEAE
63. Fruit or fruiting structure not burr-like 67
67. Fruit with irregular projections or lobes .... 12. ULMACEAE
67. Fruit without irregular projections or lobes 68
68. Fruit an aggregate of separate pistils, or solitary and remnants or scars of aborted ovaries evident 69
69. Leaves serrate, often lobed .... 29. ROSACEAE
69. Leaves entire, not lobed .... 22. ANNONACEAE
68. Fruit a single pistil or of several united pistils, not of several apocarpous pistils 70
70. Fruit enclosed by a basal cup .... 11. FAGACEAE
70. Fruit not enclosed by a basal cup .... KEY 4
29. Plant in flower 71
71. Flowers imperfect 72
72. Flowers, at least one sex, in spherical heads or spiny involucres 73
73. Staminate heads racemose, the pistillate heads at the base 74
74. Leaf scars completely encircling the buds .... 28. PLATANACEAE
74. Leaf scars not encircling the buds .... 27. HAMAMELIDACEAE
73. Staminate heads not racemose; pistillate flowers variously arranged 75
75. Plant monoecious, with pistillate and staminate flowers in separate inflorescences .... 11. FAGACEAE
75. Plant dioecious, or plant monoecious with pistillate and staminate flowers in the same head 76
76. Stamens 5 or more .... 55. NYSSACEAE
76. Stamens 4 or absent .... 13. MORACEAE
72. Flowers not in spherical heads 77
77. Inflorescence terminal 78
78. Plant monoecious .... 34. EUPHORBIACEAE
78. Plant dioecious 79
79. Ovary inferior .... 14. SANTALACEAE
79. Ovary superior 80
80. Sepals or petals, or both, present 81
81. Flowers in cymes or cymules 25. LAURACEAE
81. Flowers in catkins .... 7. SALICACEAE
80. Sepals and petals absent .... 7. SALICACEAE

77. Inflorescences axillary 82
82. Corolla white or pinkish 83
83. Corolla lobes united for less than ⅓ of their lengths, corolla rotate .... 37. AQUIFOLIACEAE
83. Corolla lobes united for more than ½ of their lengths, corolla urceolate .... 61. EBENACEAE
82. Corolla greenish, brownish, yellow, or absent 84
84. Plant dioecious 85
85. Inflorescences in the axils of new leaves, or calyx present 86
86. Stamens 5 or more; pistil absent 87
87. Inflorescence pedunculate .... 55. NYSSACEAE
87. Inflorescence sessile .... 62. SYMPLOCACEAE
86. Stamens 4 or pistil present .... 13. MORACEAE
85. Inflorescences in axils of leaves of preceding year; calyx absent 88
88. Leaves evergreen, irregularly or remotely toothed .... 8. MYRICACEAE
88. Leaves deciduous, regularly serrate .... 7. SALICACEAE
84. Plant monoecious 89
89. Perianth lobes evident, more than 1 mm long; inflorescence never a catkin 90
90. Ovary pubescent; perianth undifferentiated .... 12. ULMACEAE
90. Ovary glabrous; perianth differentiated into calyx and corolla .... 34. EUPHORBIACEAE
89. Perianth lobes less than 1 mm long or absent; inflorescence often a catkin 91
91. Pistillate and staminate flowers in catkins, or not in catkins and the pistillate flowers terminal .... 10. BETULACEAE
91. Pistillate flowers not in catkins, or in catkins and not terminal .... 11. FAGACEAE
71. Flowers perfect 92
92. Inflorescence terminal 93
93. Corolla absent, or perianth undifferentiated 94
94. Stamens less than 10 95
95. Leaves almost fully expanded at anthesis .... 14. SANTALACEAE
95. Leaves absent at anthesis .... 12. ULMACEAE
94. Stamens more than 10 .... 27. HAMAMELIDACEAE
93. Corolla and calyx both present and discernible 96
96. Stamens 2 times or less the number of calyx lobes 97
97. Ovary inferior 98
98. Corolla apopetalous .... 56. CORNACEAE
98. Corolla gamopetalous .... 59. ERICACEAE
97. Ovary superior 99
99. Adaxial leaf surface of two contrasting colors .... 59. ERICACEAE
99. Adaxial leaf surface not of two contrasting colors 100
100. Corolla gamopetalous .... 59. ERIACEAE
100. Corolla apopetalous 101
101. Leaves entire 102
102. Pedicels plumose .... 35. ANACARDIACEAE
102. Pedicels glabrous 103

103. Leaves less than 1 cm long .... 43. RHAMNACEAE
103. Leaves more than 1 cm long .... 36. CYRILLACEAE
101. Leaves crenate or serrate 104
104. Stamens twice the number of calyx lobes .... 57. CLETHRACEAE
104. Stamens equal to the number of calyx lobes 105
105. Sepals pubescent .... 26. SAXIFRAGACEAE
105. Sepals glabrous .... 43. RHAMNACEAE
96. Stamens more than twice the number of calyx lobes .. 106
106. Inflorescence adnate to a conspicuous, basal bract .... 45. TILIACEAE
106. Inflorescence not adnate to a conspicuous, basal bract 107
107. Flower solitary, rarely 2 together 108
108. Sepals stellate-pubescent 46. MALVACEAE
108. Sepals not stellate-pubescent, but simply pubescent .... 48. THEACEAE
107. Flowers in racemes, panicles, corymbs, or axillary fascicles 109
109. Sepals densely stellate-pubescent .... 46. MALVACEAE
109. Sepals glabrous to pubescent, but not stellate-pubescent 110
110. Style 1 111
111. Sepals densely pubescent; shrub less than 0.5 m tall .... 29. ROSACEAE
111. Sepals glabrous; shrub or tree more than 1 m tall .... 53. LYTHRACEAE
110. Styles several .... 29. ROSACEAE
92. Inflorescence axillary 112
112. Petals absent, or perianth undifferentiated 113
113. Leaves, twigs and calyces vested with silvery, peltate scales .... 52. ELAEAGNACEAE
113. Leaves, twigs, and calyces not vested with peltate scales, or leaves absent 114
114. Leaves lobed 115
115. Inflorescence paniculate; ovary stipitate; sepals more than 2 mm long 47. STERCULIACEAE
115. Inflorescence capitate, racemose, umbellate, or solitary; ovary sessile; sepals less than 2 mm long .... 55. NYSSACEAE
114. Leaves not lobed, or leaves absent 116
116. Calyx synsepalous 117
117. Corolla absent .... 51. THYMELAEACEAE
117. Corolla present .... 59. ERICACEAE
116. Calyx aposepalous or lacking 118
118. Calyx less than 1 mm long .... 55. NYSSACEAE
118. Calyx more than 1 mm long 119
119. Stamens more than 10 .... 29. ROSACEAE

119. Stamens less than 10 120
120. Ovary laterally flattened, 2-notched apically .. 12. ULMACEAE
120. Ovary terete, not apically notched .... 35. ANACARDIACEAE
112. Corolla and calyx both present and discernible 121
121. Inflorescence adnate to a conspicuous basal bract .... 45. TILIACEAE
121. Inflorescence not adnate to a conspicuous basal bract .. 122
122. Sepals or calyx lobes 3 123
123. Petals 3; leaves evergreen .... 25. LAURACEAE
123. Petals 6 or more; leaves deciduous .... 22. ANNONACEAE
122. Sepals or calyx lobes more than 3 124
124. Ovary partially or entirely inferior 125
125. Stamens more than twice the number of corolla lobes .... 62. SYMPLOCACEAE
125. Stamens twice or fewer than twice the number of corolla lobes 126
126. Corolla gamopetalous; anthers poricidal .... 59. ERICACEAE
126. Corolla apopetalous; anthers septicidal .... 26. SAXIFRAGACEAE
124. Ovary superior 127
127. Petals united, at least basally 128
128. Stamens 5, or more and the same number as the corolla lobes 129
129. Staminodia petaloid .... 60. SAPOTACEAE
129. Staminodia absent 130
130. Corolla rotate .... 37. AQUIFOLIACEAE
130. Corolla salverform .... 69. SOLANACEAE
128. Stamens 8 or more, more numerous than the corolla lobes .. 131
131. Stamens twice as many as the corolla lobes 132
132. Anthers opening by slits their entire lengths 133
133. Petals united for ½ their lengths .... 61. EBENACEAE
133. Petals united for less than ⅛ their lengths .... 63. STYRACACEAE
132. Anthers opening by pores or slits at the ends .... 59. ERICACEAE
131. Stamens 3 or more times as many as the corolla lobes 134
134. Flowers on a leafless portion of

branch; petals united only at base ...... 62. SYMPLOCACEAE
134. Flowers in leaf axils of new growth; petals united for more than ½ their lengths 61. EBENACEAE
127. Petals separate 135
135. Corolla zygomorphic, papilionaceous .... 30. FABACEAE
135. Corolla neither zygomorphic nor papilionaceous 136
136. Corolla more than 2.5 cm broad 137
137. Style enclosed by a staminal tube .... 46. MALVACEAE
137. Style or styles not enclosed by a staminal tube 48. THEACEAE
136. Corolla less than 2.5 cm broad 138
138. Petals 4 .... 27. HAMAMELIDACEAE
138. Petals 5 or more .. 139
139. Stamens equal to the number of corolla lobes .... 37. AQUIFOLIACEAE
139. Stamens twice or more the number of petals or corolla lobes .. 140
140. Stamens twice the number of petals or corolla lobes .... 63. STYRACACEAE
140. Stamens more than twice the number of petals .. 29. ROSACEAE

KEY 4

From lead 70, KEY 3

1. Fruit fleshy; a drupe, drupelets, berry or pome 2
2. Ovary inferior 3
3. Fruit several-seeded, a berry or pome 4
4. Fruit a pome .... 29. ROSACEAE

4. Fruit a berry 5
5. Leaves lobed .... 26. SAXIFRAGACEAE
5. Leaves serrate, not lobed .... 59. ERICACEAE
3. Fruit 1-seeded; a drupe or nut 6
6. Calyx lobes 5 .... 62. SYMPLOCACEAE
6. Calyx absent .... 55. NYSSACEAE
2. Ovary superior 7
7. Leaves entire 8
8. Calyx lacking or not persistent on fruit 9
9. Leaves acuminate, cordate .... 34. EUPHORBIACEAE
9. Leaves obtuse, not cordate .... 51. THYMELAEACEAE
8. Calyx present at base of fruit 10
10. Fruit several-seeded 11
11. Fruit on spur branches .... 60. SAPOTACEAE
11. Fruit not on spur branches 12
12. Calyx more than 1 cm broad .... 61. EBENACEAE
12. Calyx less than 1 cm broad 13
13. Drupelets less than 5 per fruit .... 43. RHAMNACEAE
13. Seeds more than 10 per fruit .... 69. SOLANACEAE
10. Fruit 1-seeded 14
14. Fruit on spur branches .... 60. SAPOTACEAE
14. Fruit not on spur branches .... 25. LAURACEAE
7. Leaves not entire 15
15. Lower leaves opposite .... 67. VERBENACEAE
15. All leaves alternate 16
16. Drupelets several per fruit 17
17. Fruit lobed .... 43. RHAMNACEAE
17. Fruit unlobed .... 37. AQUIFOLIACEAE
16. Drupe 1 per fruit 18
18. Leaves lobed .... 25. LAURACEAE
18. Leaves not lobed 19
19. Inflorescence adnate basally to a conspicuous bract .... 45. TILIACEAE
19. Inflorescence not adnate to a conspicuous basal bract 20
20. Fruit pubescent or granular 21
21. Fruit thickly appressed-pubescent with stellate trichomes .... 63. STYRACACEAE
21. Fruit granular, waxy, not vested with stellate trichomes .... 8. MYRICACEAE
20. Fruit not pubescent or granular 22
22. Leaves strongly oblique, cuneate to truncate .... 12. ULMACEAE
22. Leaves symmetrical, cuneate to attenuate .... 29. ROSACEAE
1. Fruit dry; a capsule, achene, nut, utricle or samara 23
23. Leaves lobed 24
24. Fruit 1–3-seeded, glabrous .... 47. STERCULIACEAE
24. Fruit many-seeded, thickly stellate-pubescent .... 46. MALVACEAE
23. Leaves not lobed 25
25. Leaves entire 26
26. Fruit granular, waxy .... 8. MYRICACEAE
26. Fruit not granular and waxy 27
27. Fruit dehiscent .... 59. ERICACEAE
27. Fruit indehiscent .... 36. CYRILLACEAE
25. Leaves serrate or cuneate 28
28. Fruit a capsule 29
29. Seeds with a coma; leaves acuminate .... 7. SALICACEAE
29. Seeds devoid of coma; leaves not acuminate 30
30. Capsule beaked .... 27. HAMAMELIDACEAE
30. Capsule not beaked .... 48. THEACEAE
28. Fruit not a capsule 31

31. Leaves cordate or obliquely cordate 32
    32. Inflorescence adnate to a conspicuous basal bract; fruit a nut-like drupe .... 45. TILIACEAE
    32. Inflorescence not adnate to a basal bract; fruit a samara .... 12. ULMACEAE
31. Leaves cuneate to attenuate 33
    33. Surface of fruit granular, waxy, not stellate-pubescent nor winged .... 8. MYRICACEAE
    33. Surface of fruit either stellate-pubescent or winged .... 63. STYRACACEAE

1. PINACEAE

1. Leaves fasciculate .... 1. *Pinus*
1. Leaves borne singly .... 2. *Tsuga*

1. *Pinus* L., PINE

1. Fascicular sheaths averaging more than 2 cm long .... 5. *P. palustris*
1. Fascicular sheaths averaging less than 2 cm long 2
    2. Bark of 1-year-old twigs, branches, and upper trunk smooth, not exfoliating .... 4. *P. glabra*
    2. Bark of 1-year-old twigs, branches, and upper trunk obviously cracked, roughened, readily exfoliating 3
        3. Leaves predominantly more than 1 dm long 4
            4. Leaves, at least some, in fascicles of 2; upper portion of distal end of cone scale shiny 5
                5. Cone turbinate, serotinous .... 6. *P. serotina*
                5. Cone oblong-conical, opening promptly when mature .... 3. *P. elliottii*
            4. Leaves all in fascicles of 3; upper portion of distal end of cone scale not shiny .... 7. *P. taeda*
        3. Leaves predominantly less than 1 dm long 6
            6. Leaves entirely in fascicles of 3 7
                7. Cone turbinate, serotinous .... 6. *P. serotina*
                7. Cone oblong-conical, opening promptly when mature .... 7. *P. taeda*
            6. Leaves in fascicles of 2 and 3 8
                8. Leaves strongly twisted, or cone scale prickles indurate, stout, recurved 9
                    9. Bark of young twigs reddish; seed subovoid .... 8. *P. virginiana*
                    9. Bark of young twigs gray to tan; seed subtriangular .... 1. *P. clausa*
                8. Leaves not strongly twisted, or cone scale prickle weak, slender, straight .... 1. *P. clausa*, 2. *P. echinata*

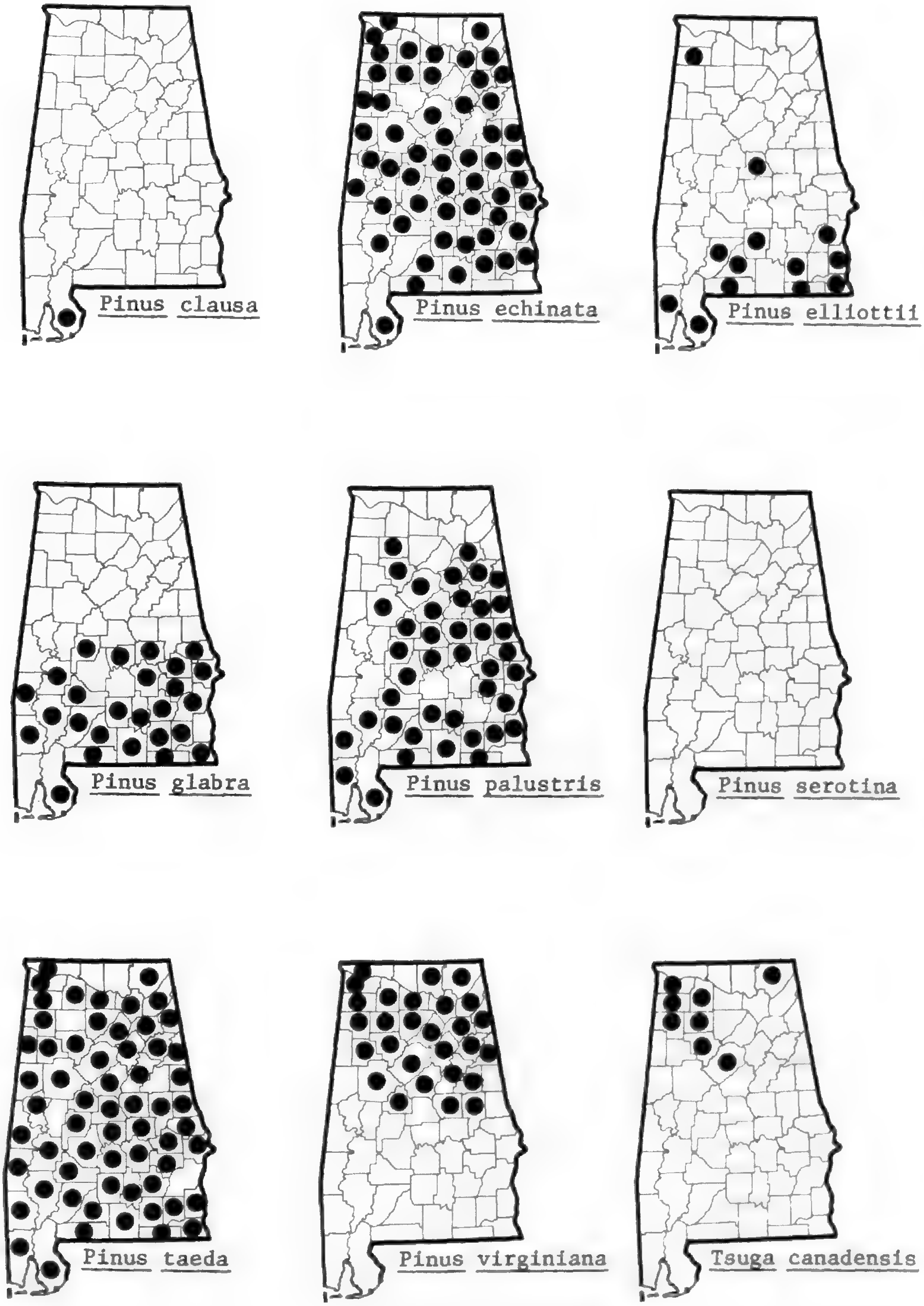
In Alabama there are no characteristics known to the writer which will enable one to separate consistently *Pinus echinata* from *P. clausa*, since the western race of *P. clausa* (constituting the only population of this species in Alabama) does not bear serotinous cones. It is interesting to speculate that the "open cone" race of *P. clausa* might have arisen as a result of introgression with *P. echinata*, or that populations of *P. echinata* may have given rise to *P. clausa* by the development of serotiny.

1. *P. clausa* (Chapman) Vasey, SAND P., FLORIDA SPRUCE P. Spring; fall. Beaches, dunes, rare; OCP. *P. clausa* (Engelm.) Sarg.—M, H; *P. clausa* (Engelm.) Vasey—S.

2. *P. echinata* Miller, SHORT-LEAF P. Spring; fall. Old fields, woods, throughout, but rare in HR and southwest Alabama.

3. *P. elliottii* Engelm., SLASH P. Spring; fall. Low woods, savannas; OCP and occasionally escaping from plantings northward. *P. heterophylla* (Ell.) Sudw.—M; *P. palustris* Mill.—S.

1. PINACEAE



Pinus clausa

Pinus echinata

Pinus elliottii

Pinus glabra

Pinus palustris

Pinus serotina

Pinus taeda

Pinus virginiana

Tsuga canadensis

4. *P. glabra* Walter, SPRUCE P. Spring; fall. Low woods, flood-plains; CP.

5. *P. palustris* Miller, LONG-LEAF P. Spring; fall. Upland woods, old fields; CP, CuP, AM, VR. *P. australis* Michx. f.—S.

6. *P. serotina* Michaux, POND P., BLACK P. Spring; fall. Low woods, creek swamps, rare. Reported from eastern CP by Harper (1928), Dean (1961), and Radford, Ahles and Bell (1968).

7. *P. taeda* L., LOBLOLLY P. Spring; fall. Woods and fields, throughout; rare in HR.

8. *P. virginiana* Miller, VIRGINIA P., SCRUB P., NIGGER P. Spring; fall. Upland fields and woods, xeric slopes; CuP, AM, VR.

2. *Tsuga* (Endl.) Carr., HEMLOCK

1. *T. canadensis* (L.) Carr., HEMLOCK, SPRUCE PINE. Spring; fall. Mesic slopes and ravines; CuP.

2. TAXODIACEAE

1. *Taxodium* Richard, CYPRESS

1. *T. distichum* (L.) Richard. Spring; fall.

1. Leaves distichous .... *T. distichum* var. *distichum*
1. Leaves appressed to twigs, or strongly ascending .... *T. distichum* var. *nutans*

T. distichum (L.) Richard var. *distichum*, BALD C., SWAMP C., RIVER C. Swamps, river margins; throughout CP and rare in HR, VR, P.

T. distichum var. *nutans* (Aiton) Sweet, POND C. Swamps, ponds; OCP. *T. distichum imbricaria* (Nutt.) Sudw.—M; *T. ascendens* Brongn.—S, H, RAB.

3. CUPRESSACEAE

1. Plant bisexual, monoecious; mature pistillate cone leathery or woody; seeds winged .... 1. *Chamaecyparis*
1. Plant unisexual, plants dioecious; mature pistillate cone baccate; seeds wingless .... 2. *Juniperus*

1. *Chamaecyparis* Spach, WHITE CEDAR

1. *C. thyoides* (L.) BSP. Spring; fall. Low woods, creek swamps, rare; OCP.

2. *Juniperus* L., RED CEDAR

1. *J. virginiana* L. Spring; fall. Habitats various; throughout. *Sabina virginiana* (L.) Antoine—S; *Sabina silicicola* Sm.—S; *J. barbadensis* L.—M; *J. silicicola* (Sm.) Bail.—RAB.

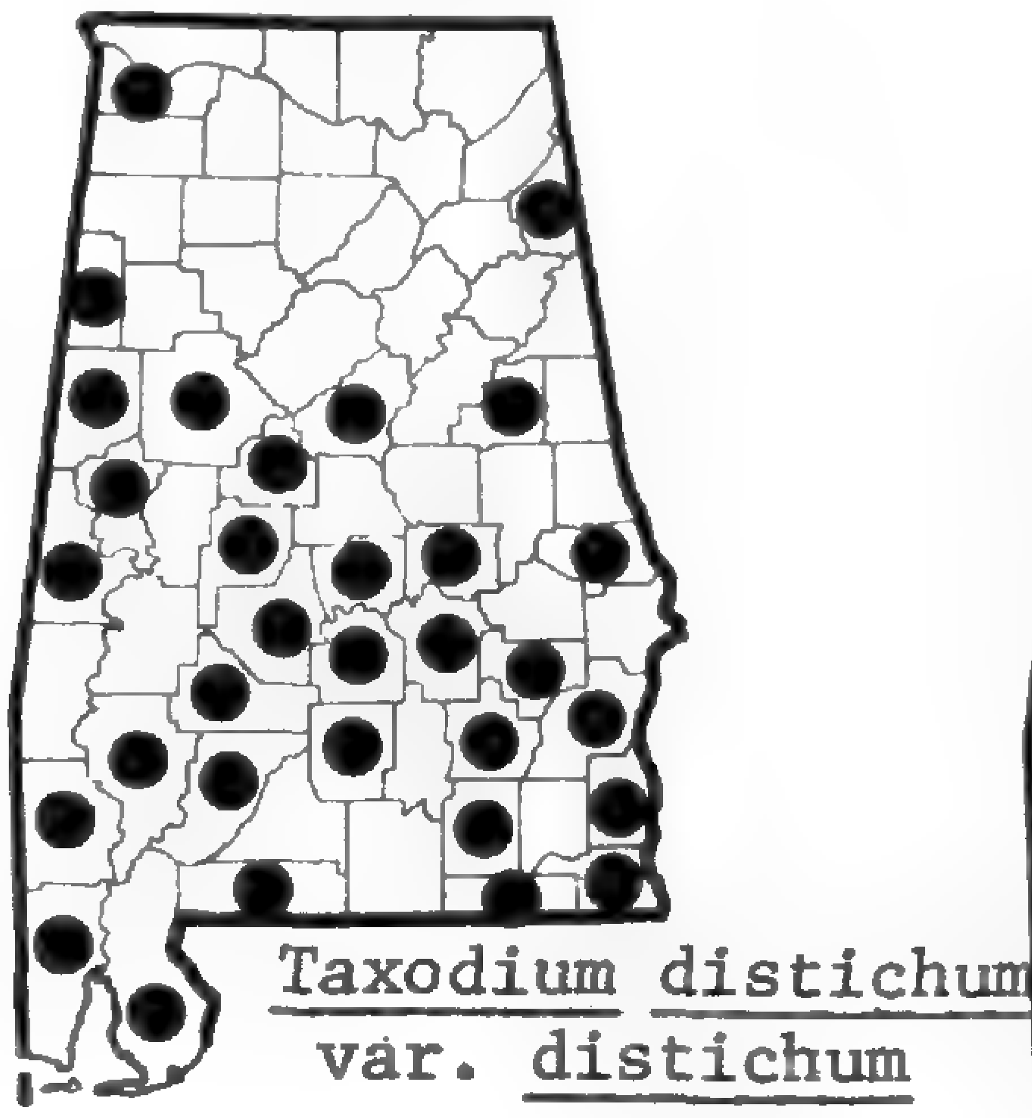
4. POACEAE

1. Culm terete or subterete above node .... 1. *Arundinaria*
1. Culm distinctly flattened on one side above node .... 2. *Phyllostachys*

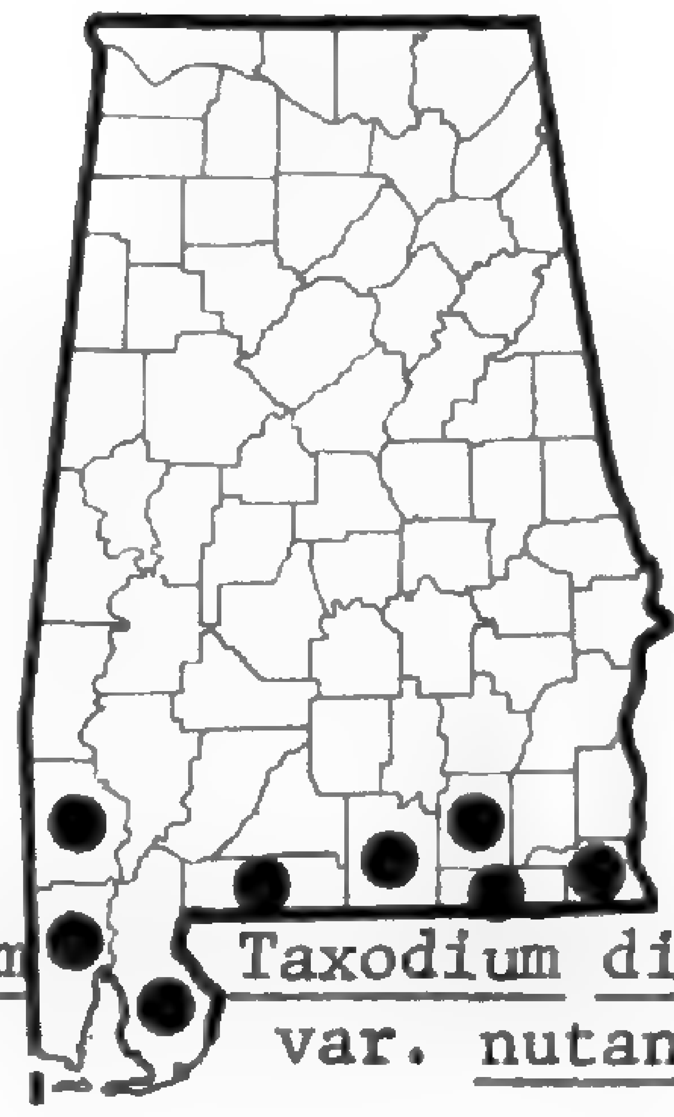
1. *Arundinaria* Michaux, CANE

1. *A. gigantea* (Walter) Muhl. Spring. Ravines, mesic and dry slopes, alluvial

2. TAXODIACEAE

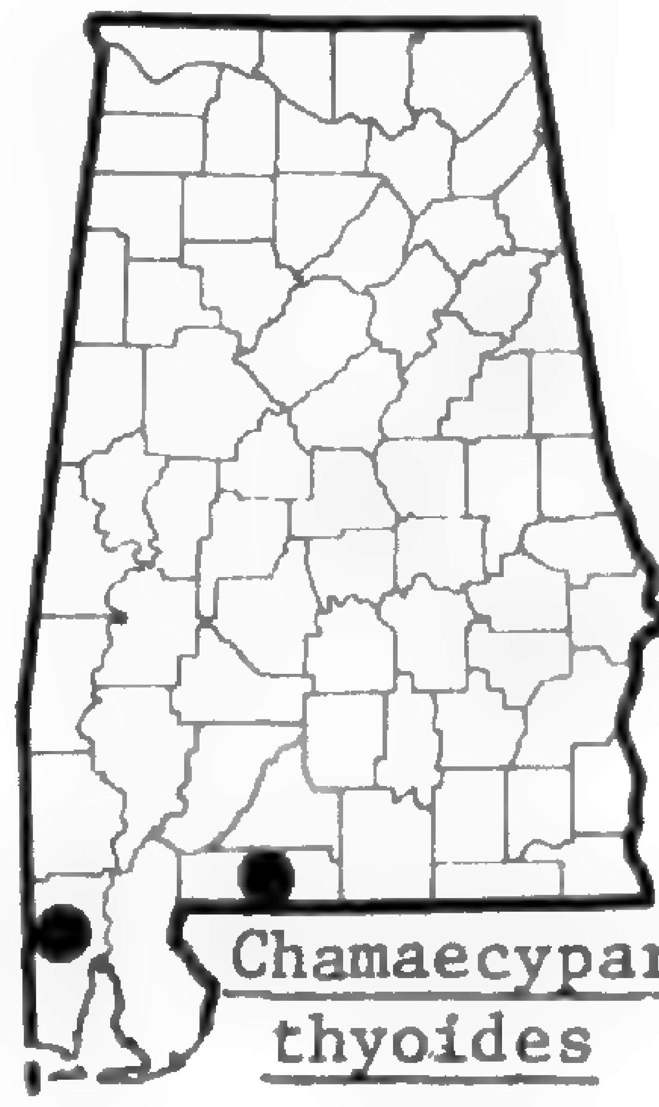


Taxodium distichum var. distichum

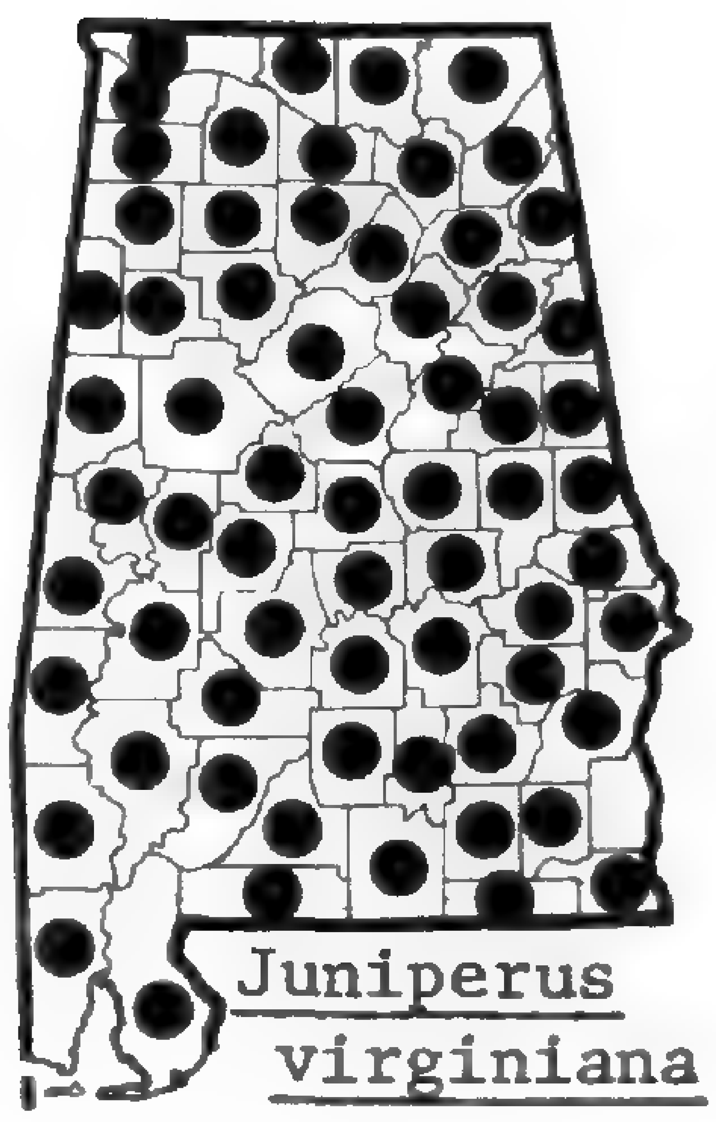


Taxodium distichum var. nutans

3. CUPRESSACEAE

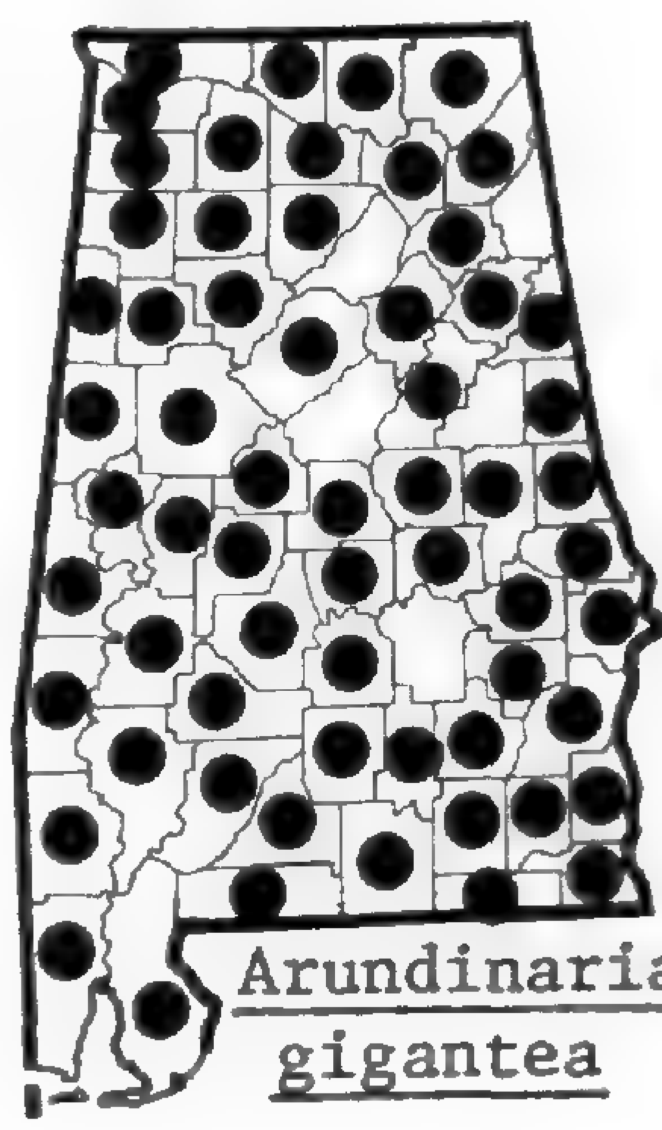


Chamaecyparis thyoides

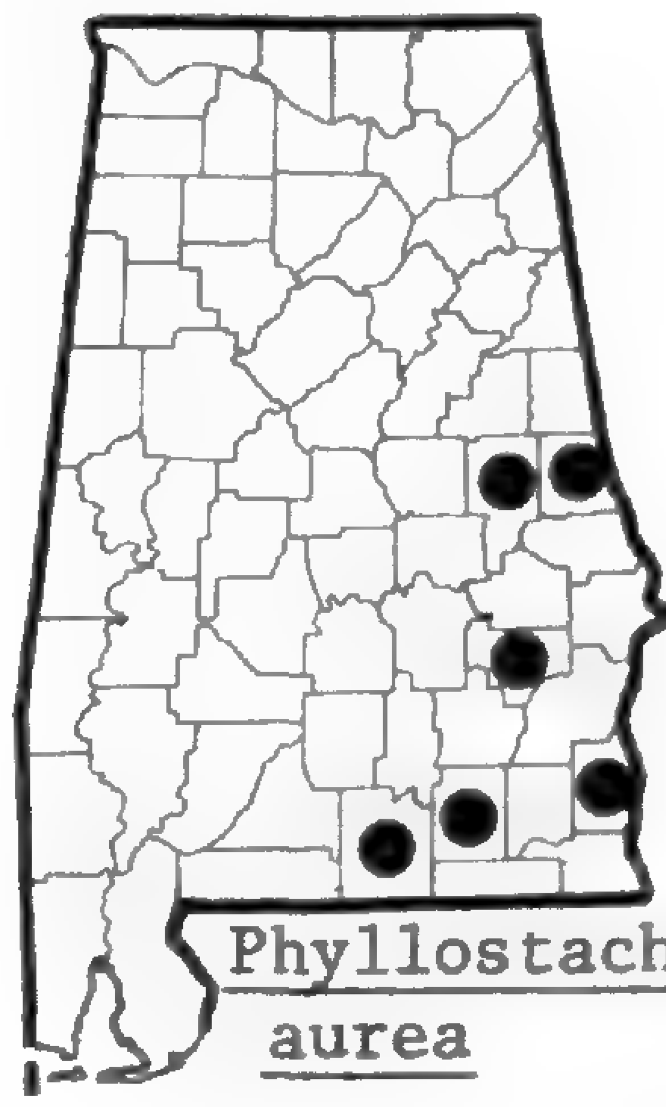


Juniperus virginiana

4. POACEAE

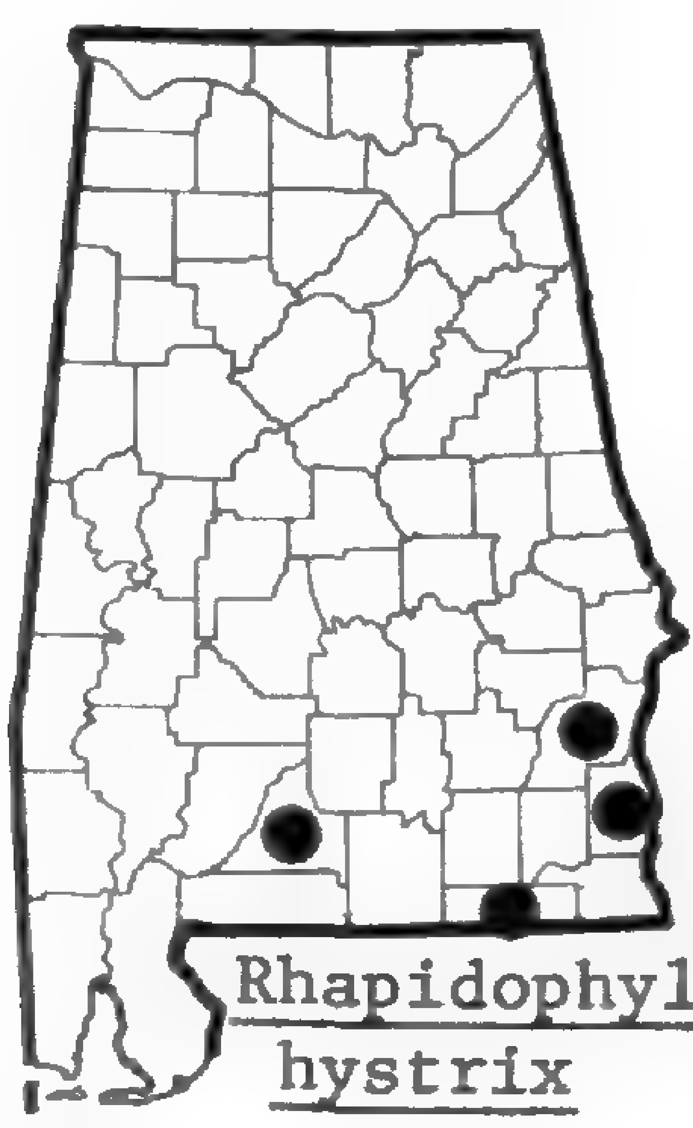


Arundinaria gigantea

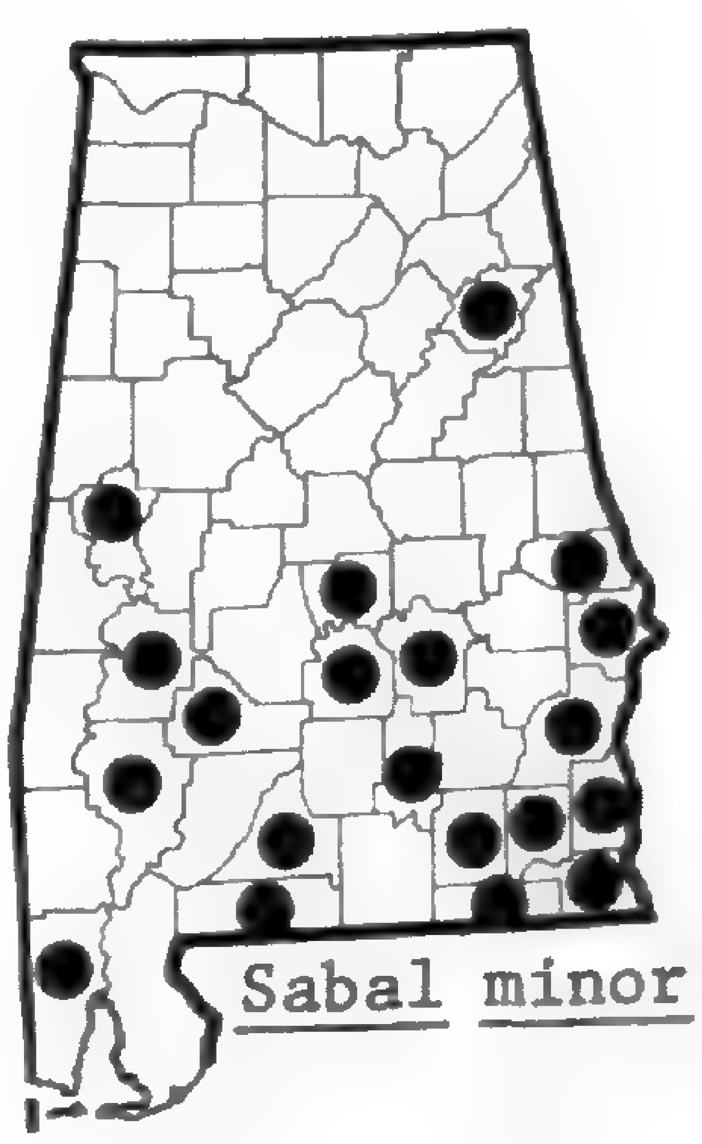


Phyllostachys aurea

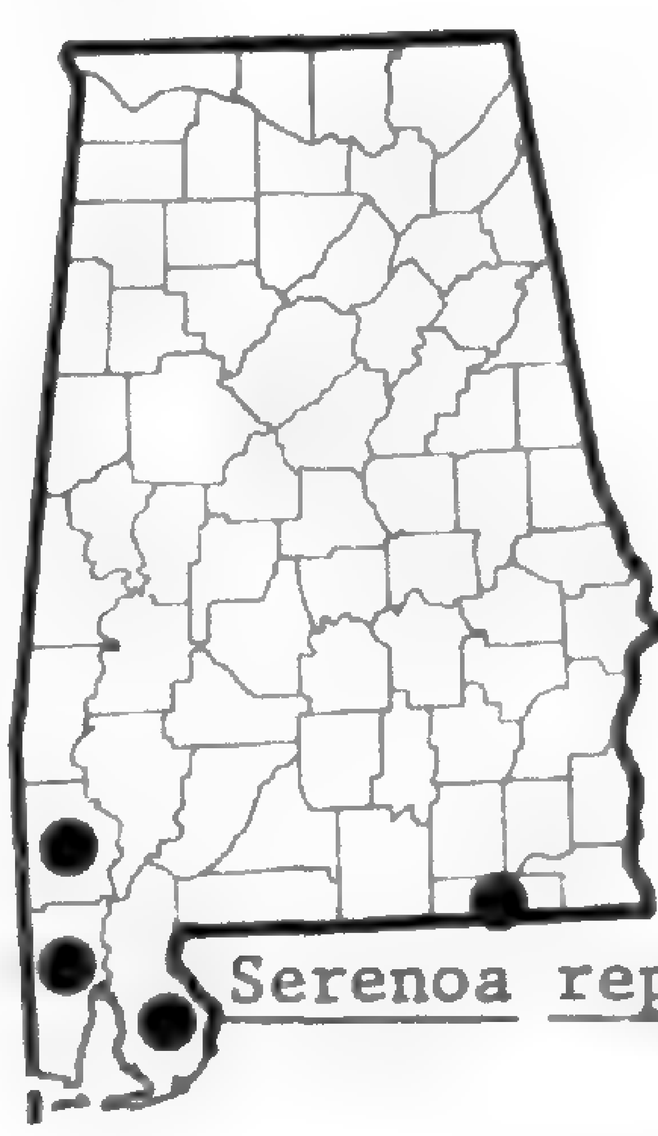
5. ARECACEAE



Rhapidophyllum hystrix



Sabal minor



Serenoa repens

woods; throughout. *A. gigantea* (Walt.) Chap.—M; *A. tecta* (Walt.) Muhl.—M, S, H; *A. macrosperma* Michx.—H.

2. *Phyllostachys* Sieb. & Zucc.

1. *P. aurea* Riv. Flowers, fruit not seen. Planted for fishpoles and escaping, scattered localities mostly in CP.

5. Arecaceae

1. Petiole coarsely serrate .... 3. *Serenoa*
1. Petiole not coarsely serrate 2
  2. Leaves silvery-scurfy beneath; leaf sheaths armed with stout spines .. 1. *Rhapidophyllum*
  2. Leaves glabrous beneath; leaf sheaths unarmed .... 2. *Sabal*

1. *Rhapidophyllum* Wendland & Drude, Needle-Palm

1. *R. hystrix* (Pursh) Wendland & Drude. Flowers, fruits not seen. Swamp forests, rich ravines, rare; principally CP, and more common southeastward.

2. *Sabal* Adanson, Palmetto

1. *S. minor* (Jacquin) Persoon, Dwarf P. Late spring–summer; fall. Alluvial woods; CP and rare in VR. *S. minus* (Jacq.) Pers.—M; *S. minor* Jacq.—H.

3. *Serenoa* Hooker, Saw Palmetto

1. *S. repens* (Bartram) Small. Late spring–summer; fall. Low pinelands, savannas, sand ridges and dunes; OCP. *S. serrulata* (Michx.) Benth. & Hook.—M, H.

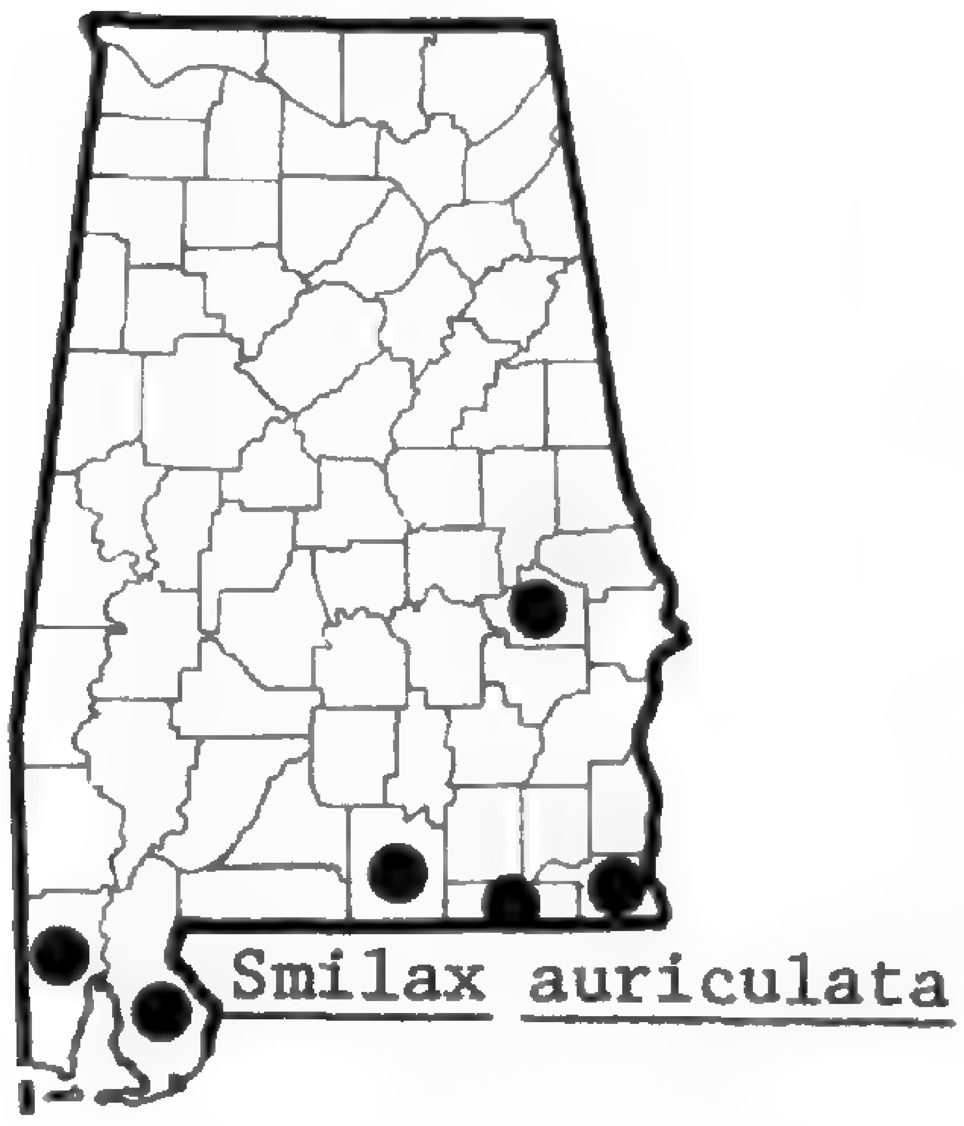
6. Liliaceae

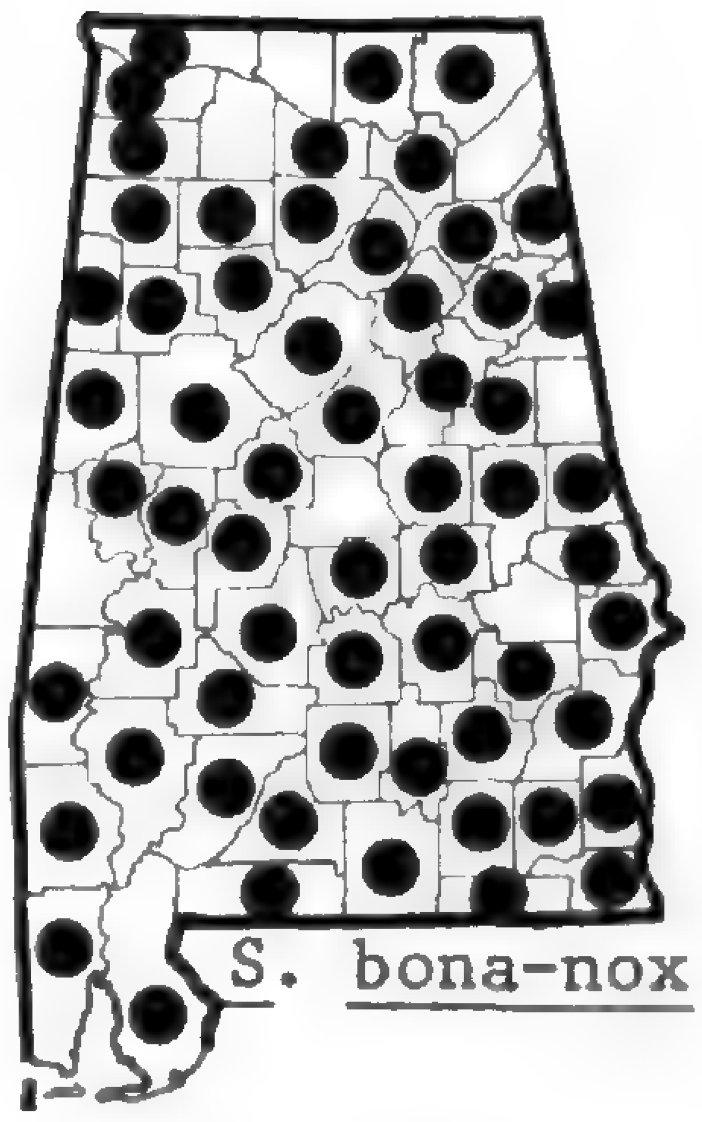
1. Leaves less than 1.5 dm long; inflorescences axillary .... 1. *Smilax*
1. Leaves more than 1.5 dm long; inflorescence terminal .... 2. *Yucca*

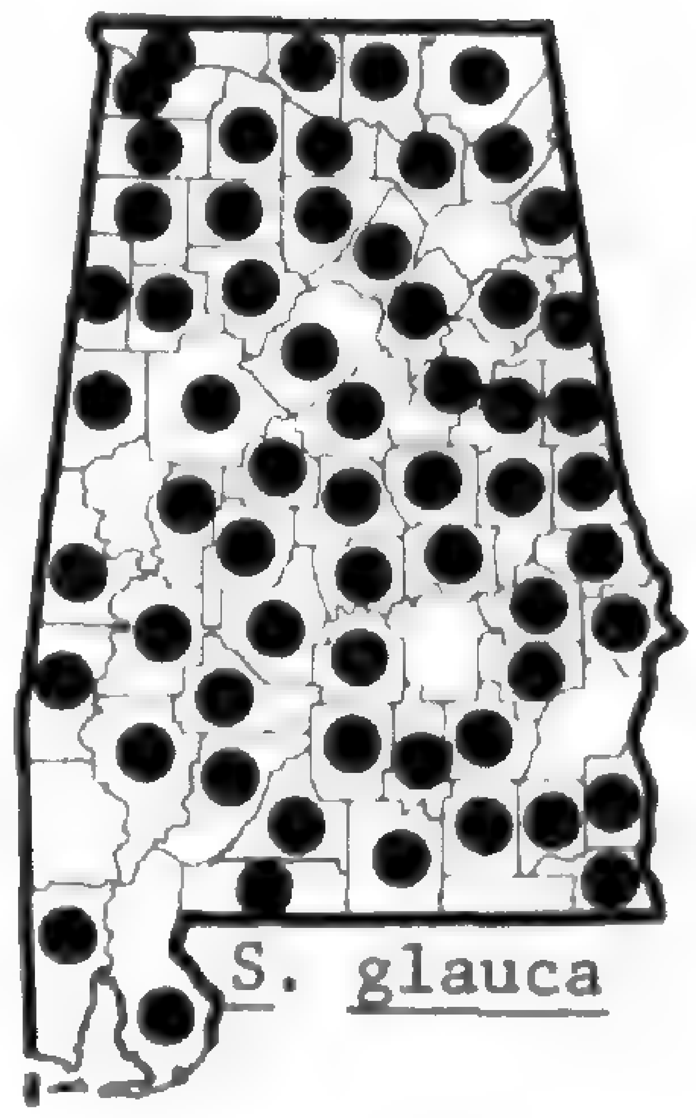
1. *Smilax* L.

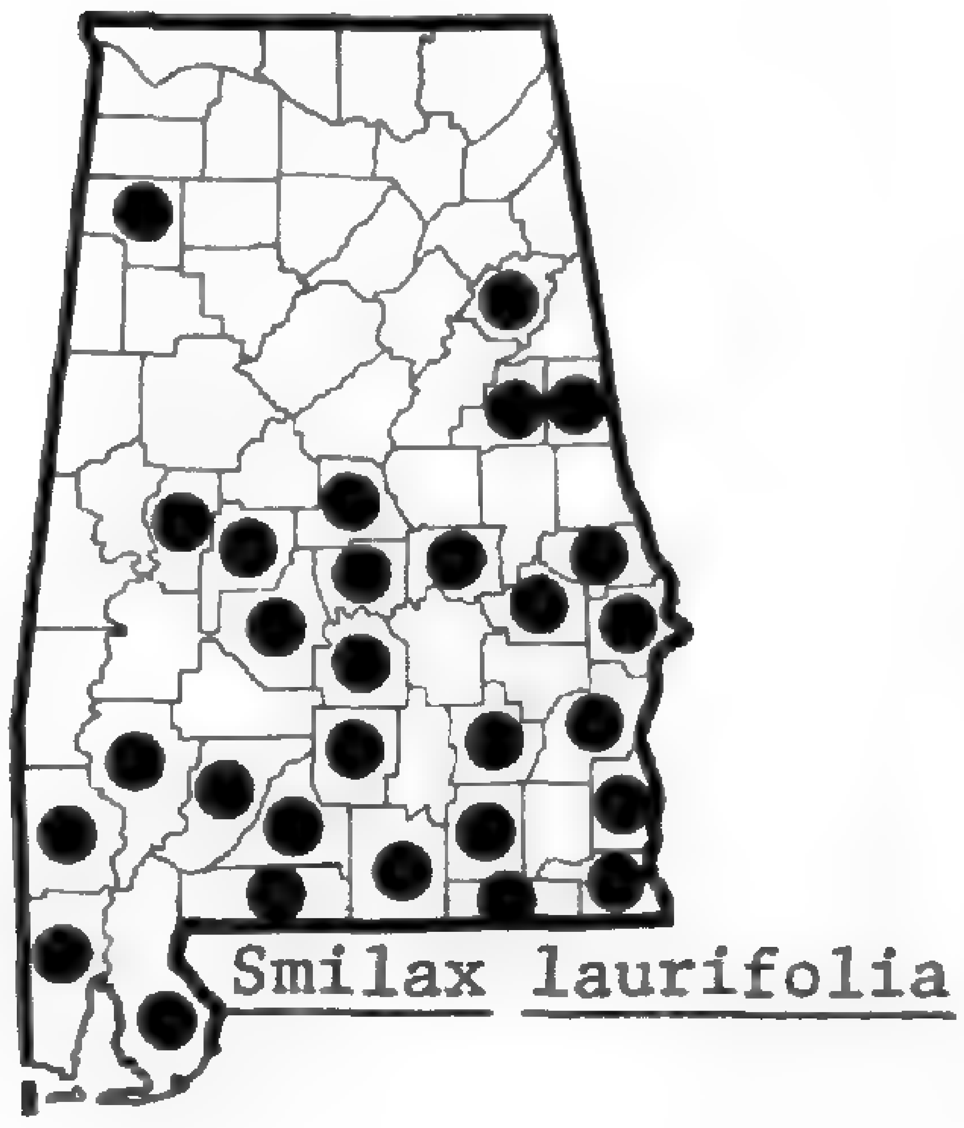
1. Stems and lower surfaces of leaves densely pubescent .... 5. *S. pumila*
1. Stems and lower surfaces of leaves glabrous or glabrate, sometimes scurfy 2
  2. Leaves glaucous beneath, distinctly grayish to whitish .... 3. *S. glauca*
  2. Leaves green beneath (or drying black), non-glaucous 3
    3. Fruit red or reddish 4
      4. Leaves deciduous; peduncle distinctly flattened .... 9. *S. walteri*
      4. Leaves evergreen; peduncle terete or subterete .... 7. *S. smallii*
    3. Fruit black or bluish-black 5
      5. Fruit maturing in second season; leaves oblong to narrowly elliptic, exauriculate, entire .... 4. *S. laurifolia*
      5. Fruit maturing in first season; leaves ovate, often auriculate, or margins spinulose or erose 6
        6. Peduncles more than 1.5 times as long as the petioles of subtending leaves 7
          7. Leaf margins thin, erose; stems hispid or unarmed .... 8. *S. tamnoides*
          7. Leaf margins hyaline-thickened, often spinulose; stems thorny .... 2. *S. bona-nox*
        6. Peduncles 1.5 times or less as long as the petioles of subtending leaves 8
          8. Leaf margins thin .... 6. *S. rotundifolia*
          8. Leaf margins hyaline-thickened 9

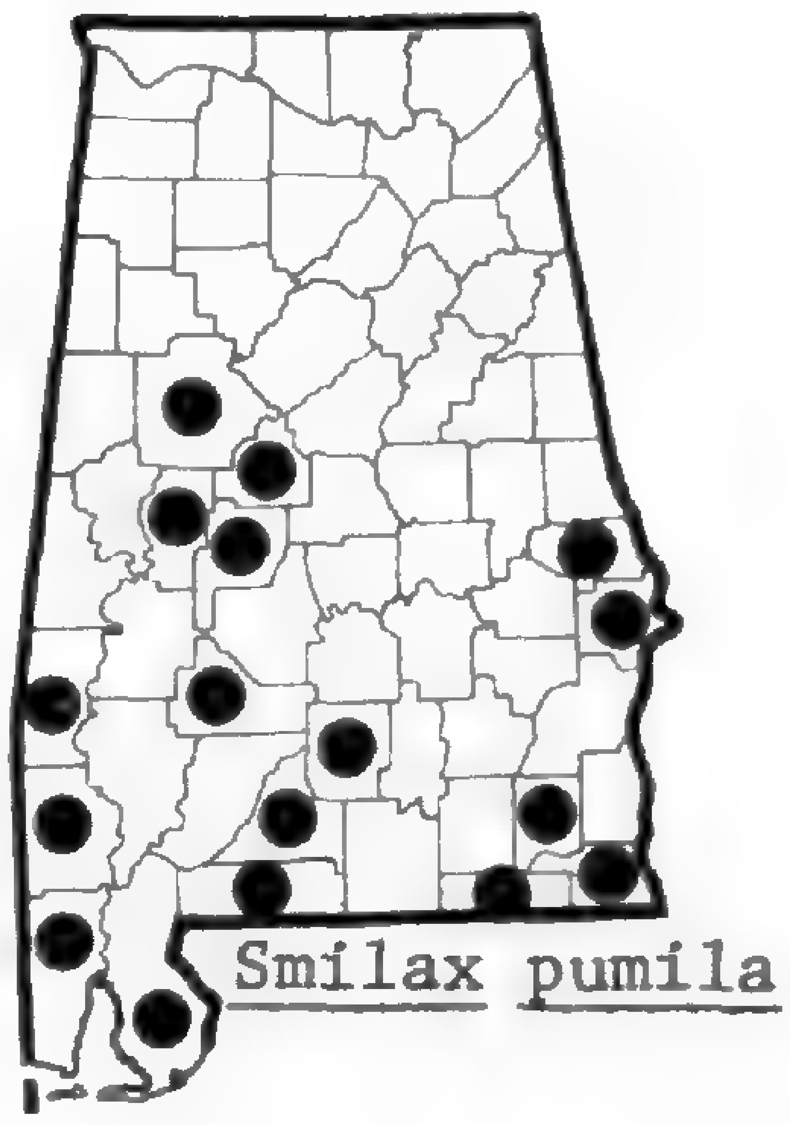
6. LILIACEAE

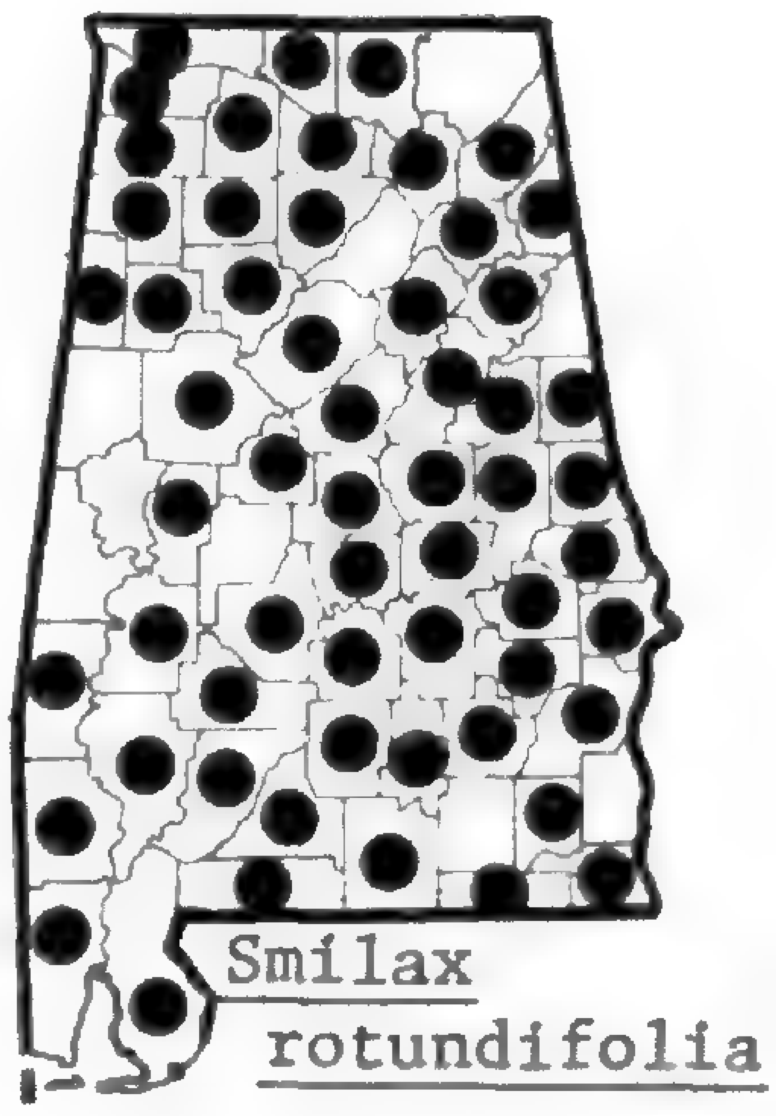

Smilax auriculata

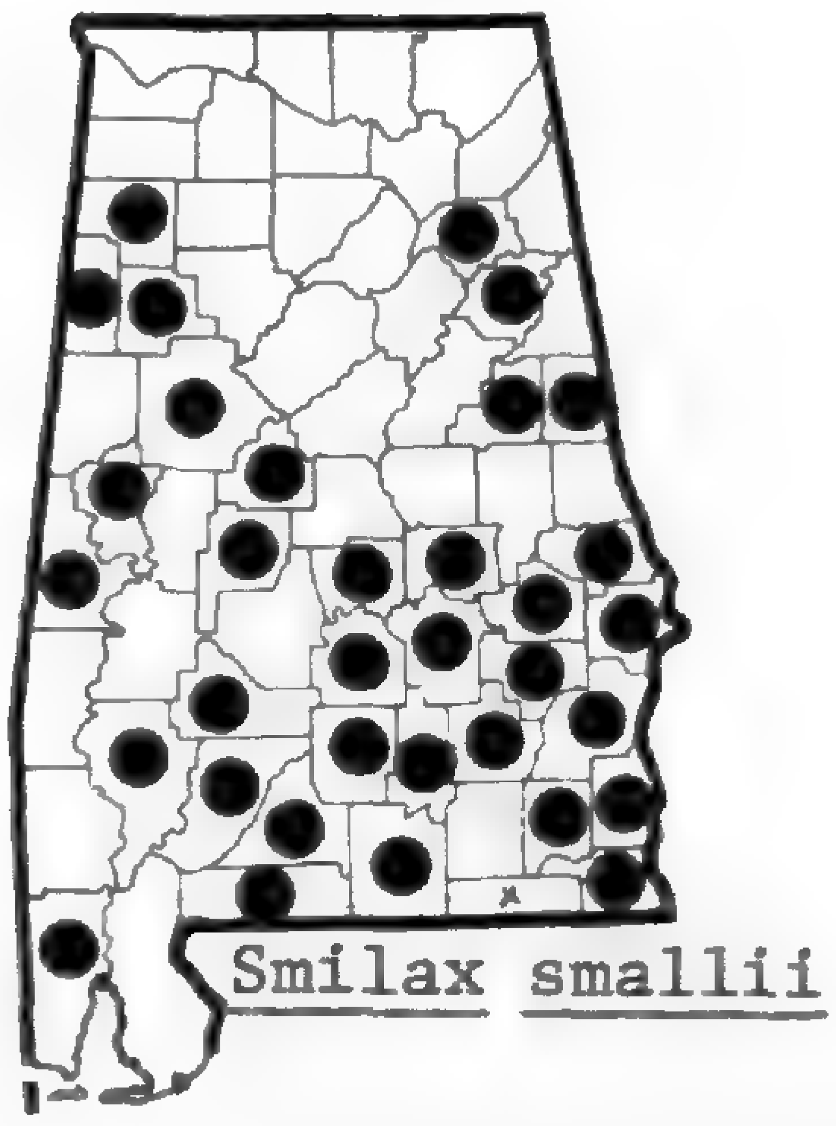

S. bona-nox

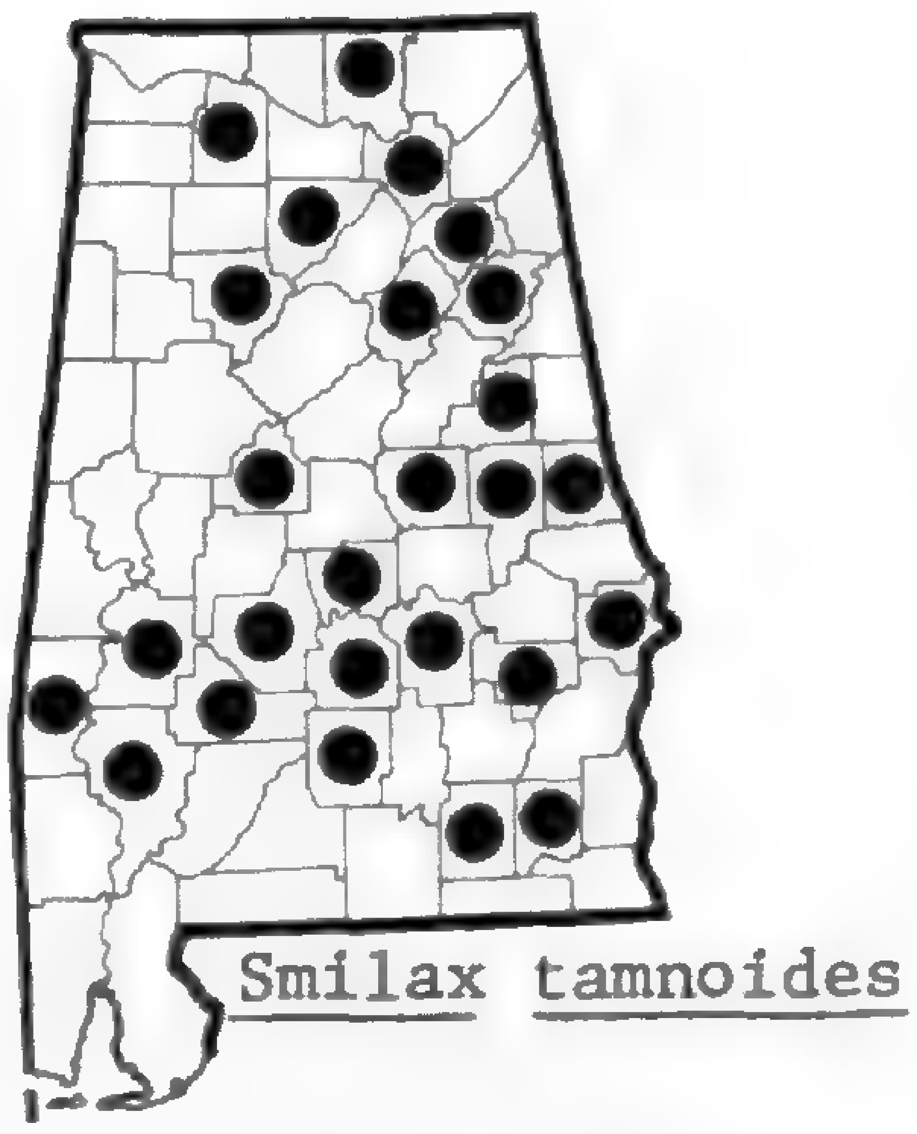

S. glauca

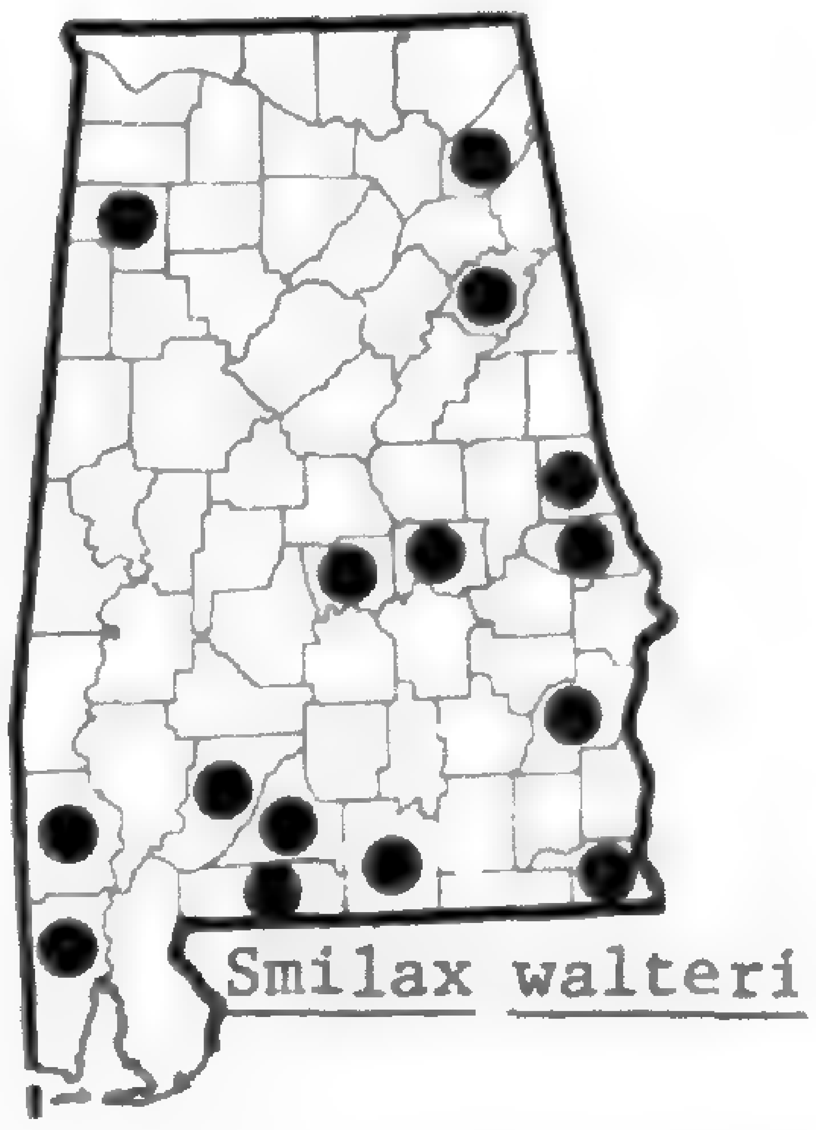

Smilax laurifolia


Smilax pumila


Smilax rotundifolia


Smilax smallii


Smilax tamnoides


Smilax walteri

9. Petioles subtending peduncles less than 8 mm long ...... 1. *S. auriculata*
9. Petioles subtending peduncles more than 8 mm long ...... 2. *S. bona-nox*

1. *S. auriculata* Walter, SAND BAMBOO-BRIER. Spring–summer; fall–winter. Sandy woods, dunes; principally OCP.

2. *S. bona-nox* L., BAMBOO-BRIER. Spring; fall. Habitats various; throughout.

3. *S. glauca* Walter. Spring; fall. Habitats various; throughout.

4. *S. laurifolia* L., BAMBOO. Summer; fall. Seepages, bogs, ditches, swamp ecotones; principally CP, but rare in P, AM, VR.

5. *S. pumila* Walter. Fall; spring. Sandy woods; CP and southern P.

6. *S. rotundifolia* L. Spring; fall. Deciduous woods, thickets, fencerows; throughout.

7. *S. smallii* Morong. Late spring-summer; spring. Low woods, seepages, thickets; CP, P, VR. *S. lanceolata* L.—M, H, S.

8. *S. tamnoides* L. Spring; fall. Alluvial and mesic woods, often over calcareous substrata; throughout. *S. hispida* Muhl.—S, RAB.—The application of *S. hispida* Muhl. is apparently based upon plants from north of the Coastal Plain, which generally display smaller foliage and are more densely armed. Coastal Plain plants generally occur in semialluvial habitats, which may affect their more robust aspect.

9. *S. walteri* Pursh. Spring; fall. Ditches, seepages, low woods; CP, rare in P, VR.

2. *Yucca* L.

1. Leaf margins with filamentous threads ...... 2. *Y. filamentosa*
1. Leaf margins entire or serrate 2
   2. Leaf margins entire or scaberulous ...... 3. *Y. gloriosa*
   2. Leaf margins serrate ...... 1. *Y. aloifolia*

1. *Y. aloifolia* L., SPANISH DAGGER, SPANISH BAYONET. Spring; fall. Sandy deciduous woods, thickets; CP.

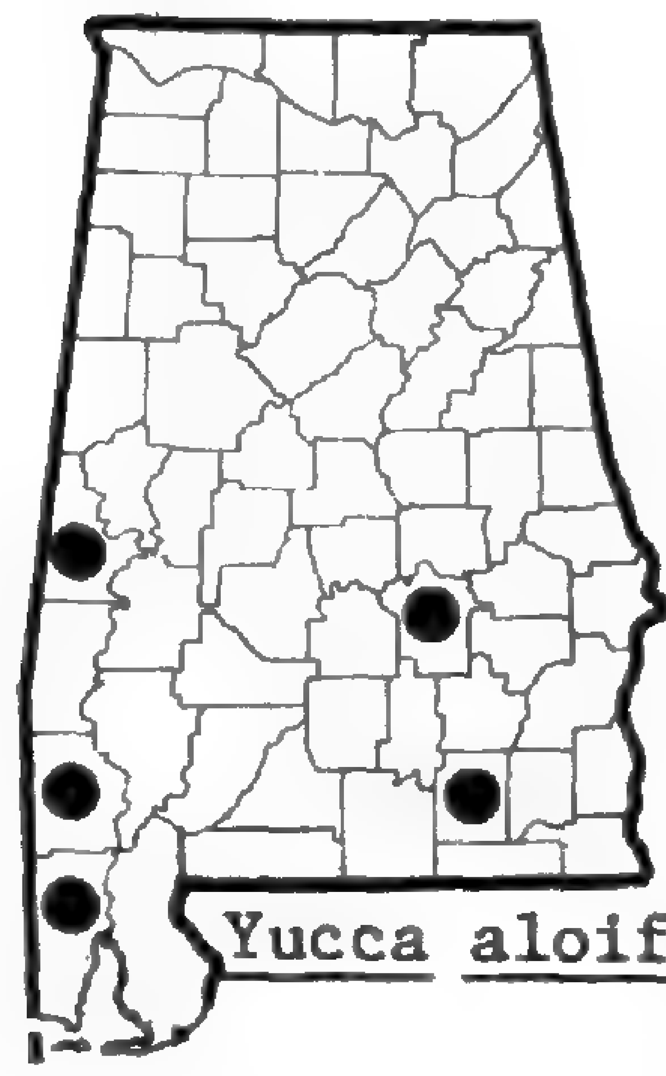
2. *Y. filamentosa* L. var. *smalliana* (Fernald) Ahles, BEARGRASS. Spring; summer–fall. Fields, fencerows, open woods; throughout. *Y. flaccida* Haw.—S.—Specimens of *Y. filamentosa* L. var. *filamentosa*, reported from Alabama, have not been seen by the writer.

3. *Y. gloriosa* L., SPANISH BAYONET. Spring–summer; fall. Fencerows, thickets, open woods; principally CP.

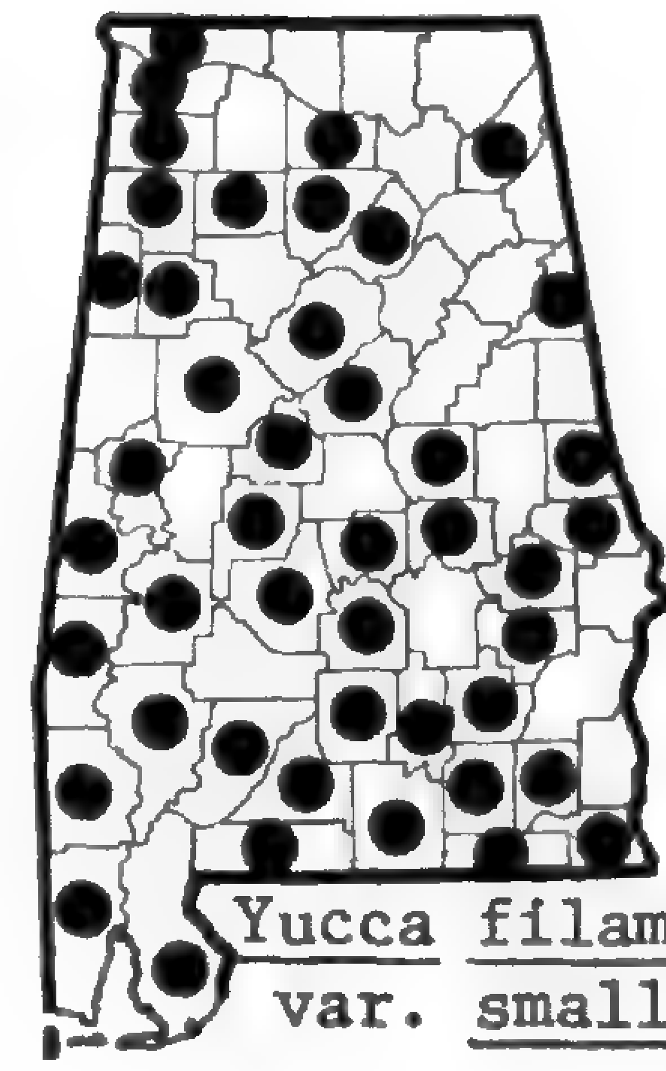
The three taxa listed above are all occasionally cultivated and are commonly persistent or rarely escaping. Alabama is considered as being within the range of *Yucca recurvifolia* Salisbury by Small (1933). Individuals with pliable leaves and winged capsules may be referable to this taxon.

7. SALICACEAE

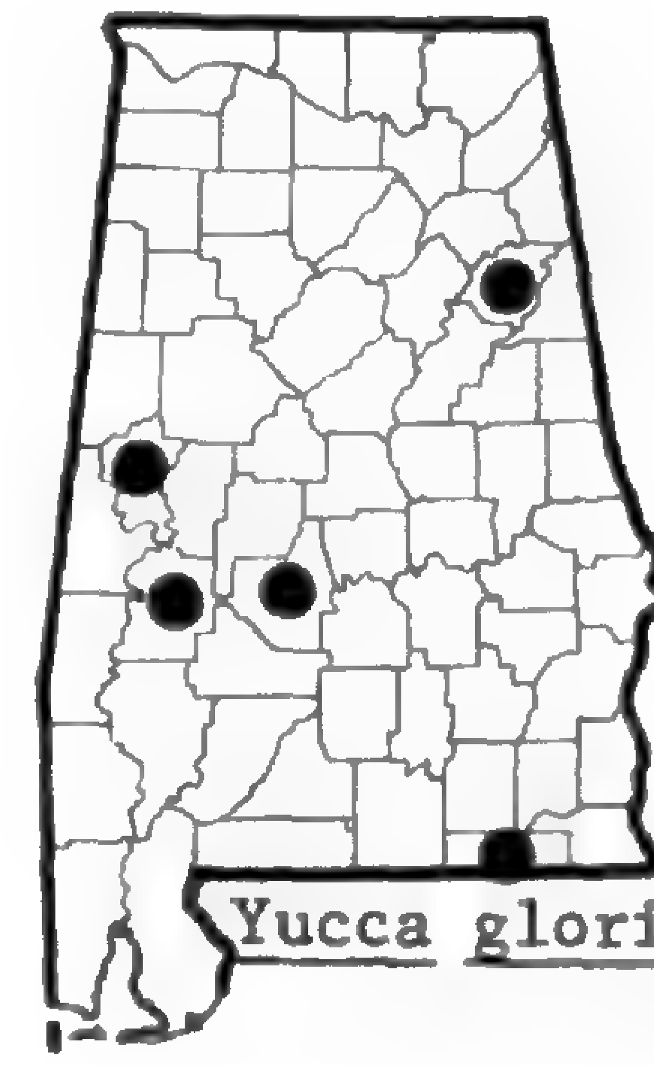
1. Catkin scales laciniate; stamens more than 10; buds with several scales; leaves usually less than 3 times as long as wide ...... 1. *Populus*
1. Catkin scales entire; stamens 10 or less; bud scale single; leaves usually more than 3 times as long as wide ...... 2. *Salix*



Yucca aloifolia



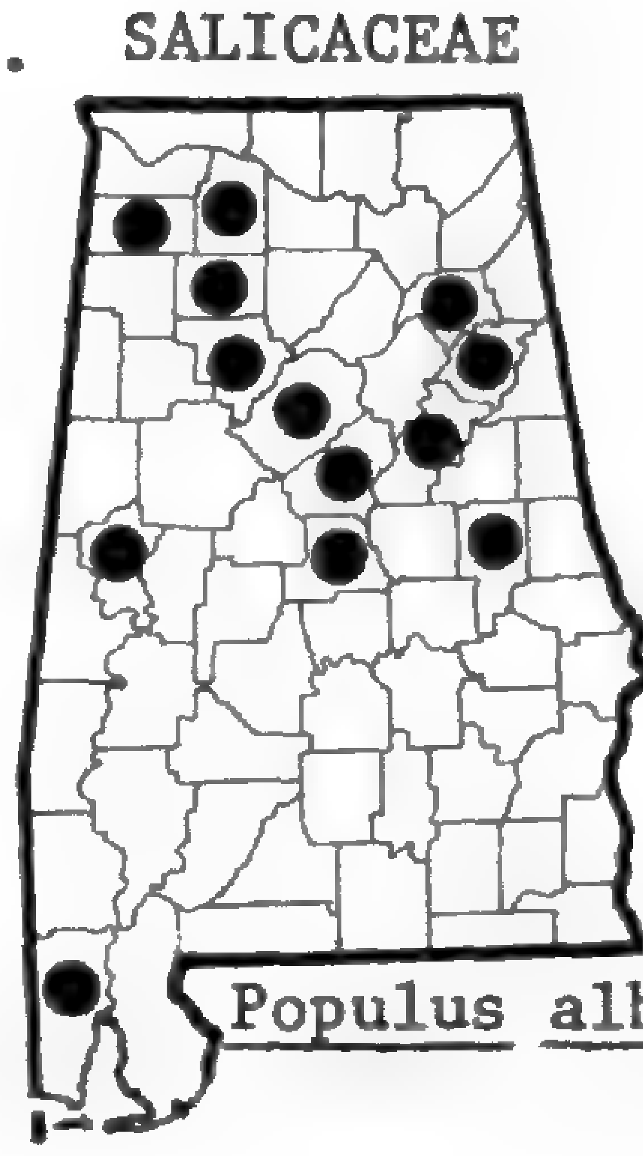
Yucca filamentosa var. smalliana



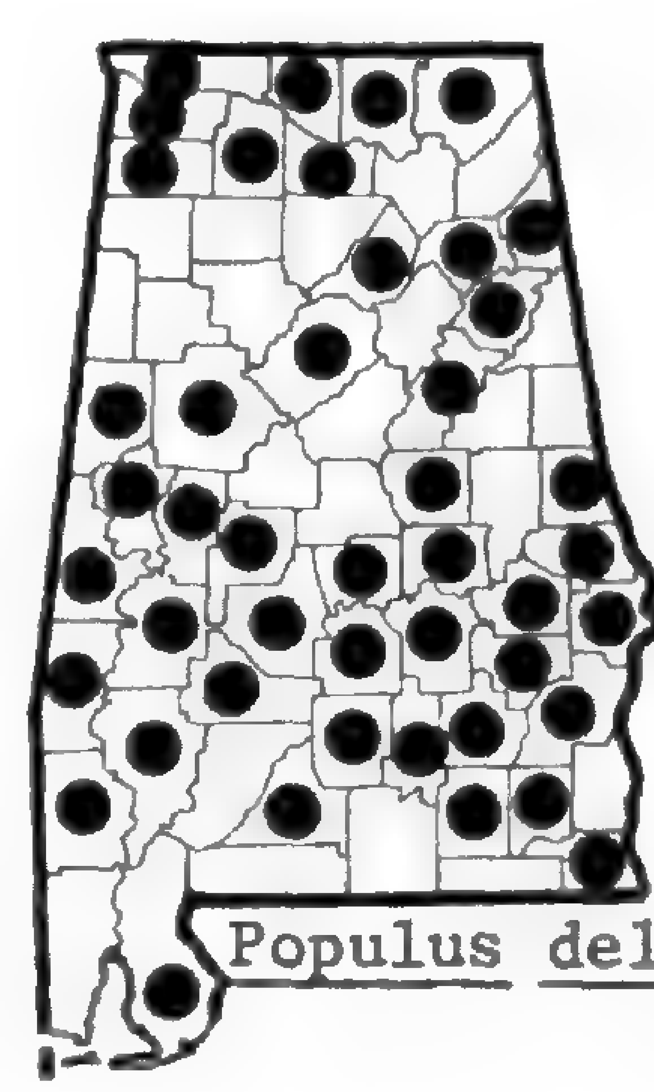
Yucca gloriosa

7. SALICACEAE

Yucca recurvifolia



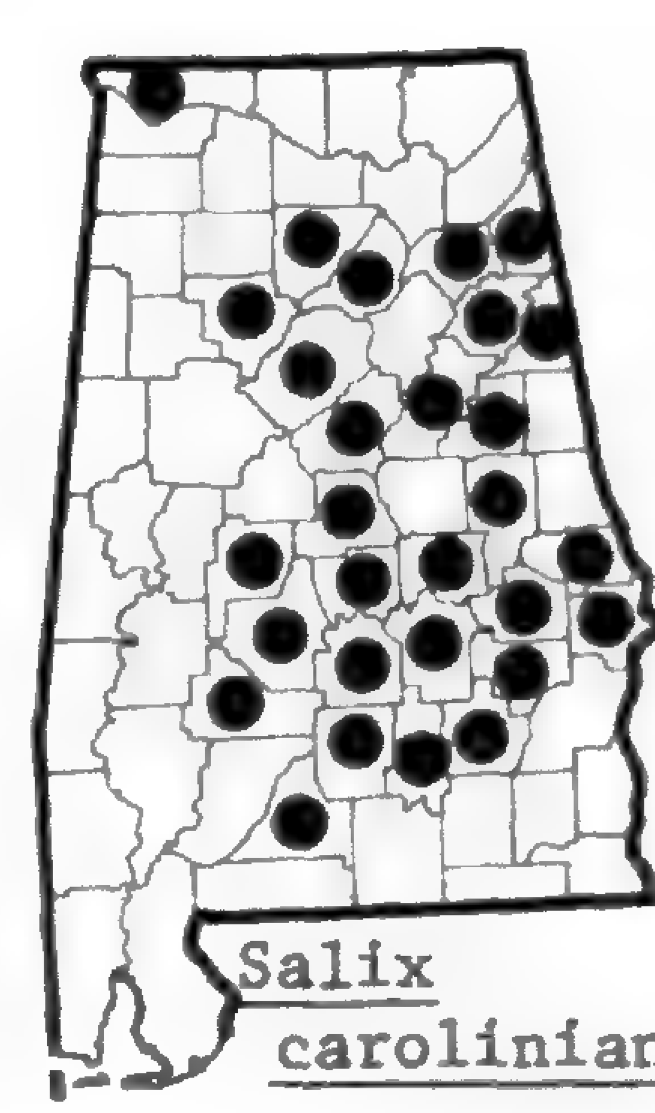
Populus alba



Populus deltoides

Populus heterophylla

Salix babylonica



Salix caroliniana

1. *Populus* L., Poplar

1. Petioles distinctly flattened .... 2. *P. deltoides*
1. Petioles terete or subterete 2
   2. Mature leaves white-tomentose or floccose beneath; capsule less than 5 mm long .... 1. *P. alba*
   2. Mature leaves not white-tomentose or floccose beneath; capsule more than 5 mm long .... 3. *P. heterophylla*

1. *P. alba* L., White P., Silver P. Spring. Thickets, fencerows, old homesites, frequently an asexual escape from planting; principally north of CP.

2. *P. deltoides* Marshall, Cottonwood. Spring. Streambanks, alluvial woods, river swamps; throughout, except rare on western CuP. Most frequent in circumneutral situations. *P. balsamifera* L.—S.

3. *P. heterophylla* L., Swamp Cottonwood. Spring. River swamps, rare; OCP.

Populus nigra L. var. *italica* DuRoi (Lombardy poplar) is rarely persistent from old stumps after cultivation.

2. *Salix* L., Willow

1. Capsule less than 2.5 mm long; branches quite pendulous; twigs whip-like .... 1. *S. babylonica*
1. Capsule more than 2.5 mm long; branches not decidedly pendulous; twigs not whip-like .. 2
   2. Leaves entire or nearly so, commonly revolute .... 3. *S. humilis*
   2. Leaves serrate to serrulate, erevolute 3
      3. Leaves and capsules sericeous; stamens 2 .... 5. *S. sericea*
      3. Leaves and capsules not sericeous; stamens 3 or more 4
         4. Leaves glaucous beneath .... 2. *S. caroliniana*
         4. Leaves green beneath .... 4. *S. nigra*

1. *S. babylonica* L., Weeping W. Spring. Rare escape to stream-banks, ditches, low open ground; CP, VR.

2. *S. caroliniana* Michaux. Spring. Open streambeds, ditches, throughout, but most common in central portions of Alabama.

3. *S. humilis* Marshall, Prairie W. Spring. Open, low ground, rare; CP, P, AM, CuP, HR.

4. *S. nigra* Marshall, Black W. Spring. Ditches, low ground and seepages; throughout.

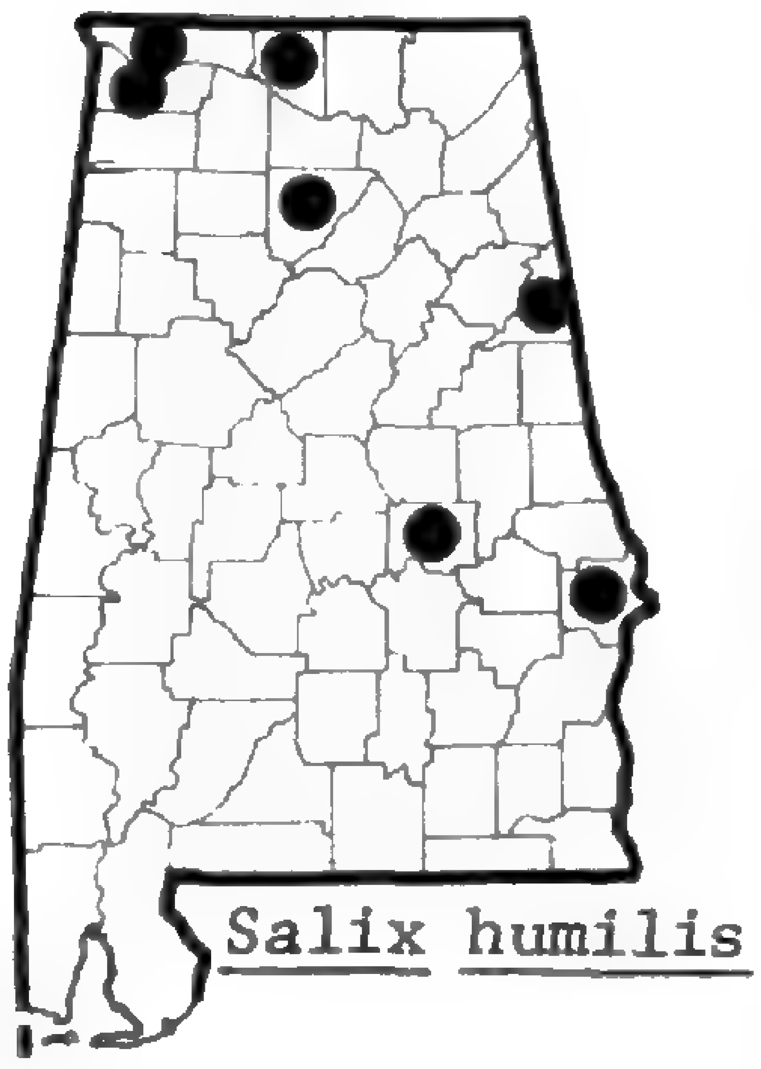
5. *S. sericea* Marshall, Silky W. Spring. Open seepages, rare; CP. HR. *S. wardi* Bebb—M.

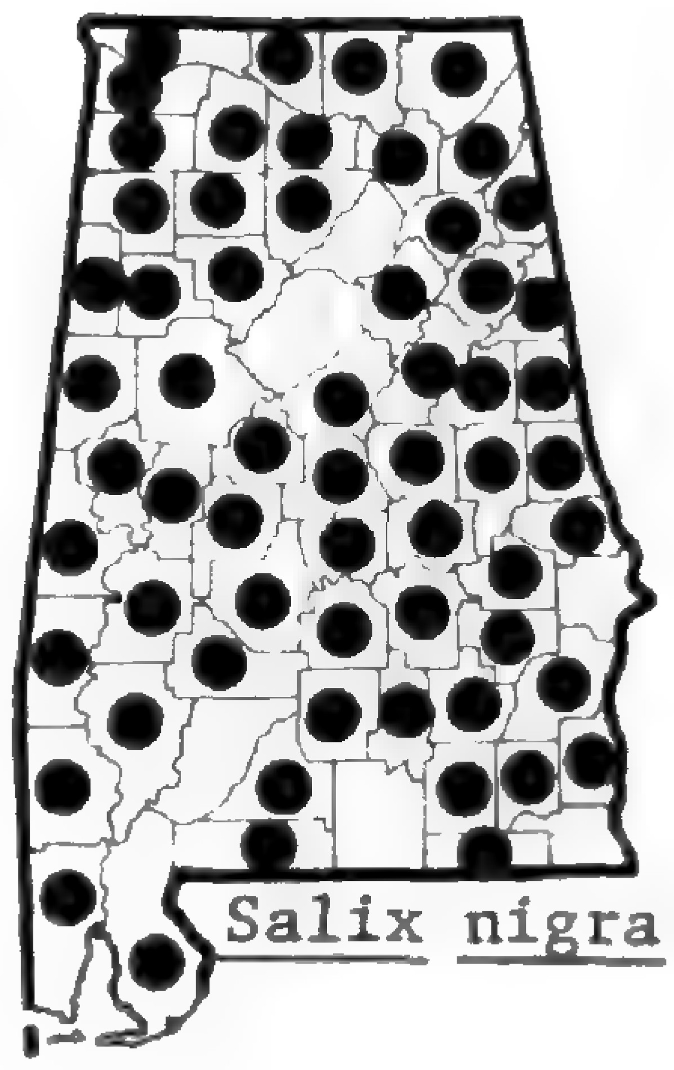
Further study is needed to determine the best status of *Salix marginata* Wimm. in Small (1933). This name may belong in synonymy with either *S. nigra* Marsh. or *S. caroliniana* Michx.

8. Myricaceae

1. *Myrica* L.

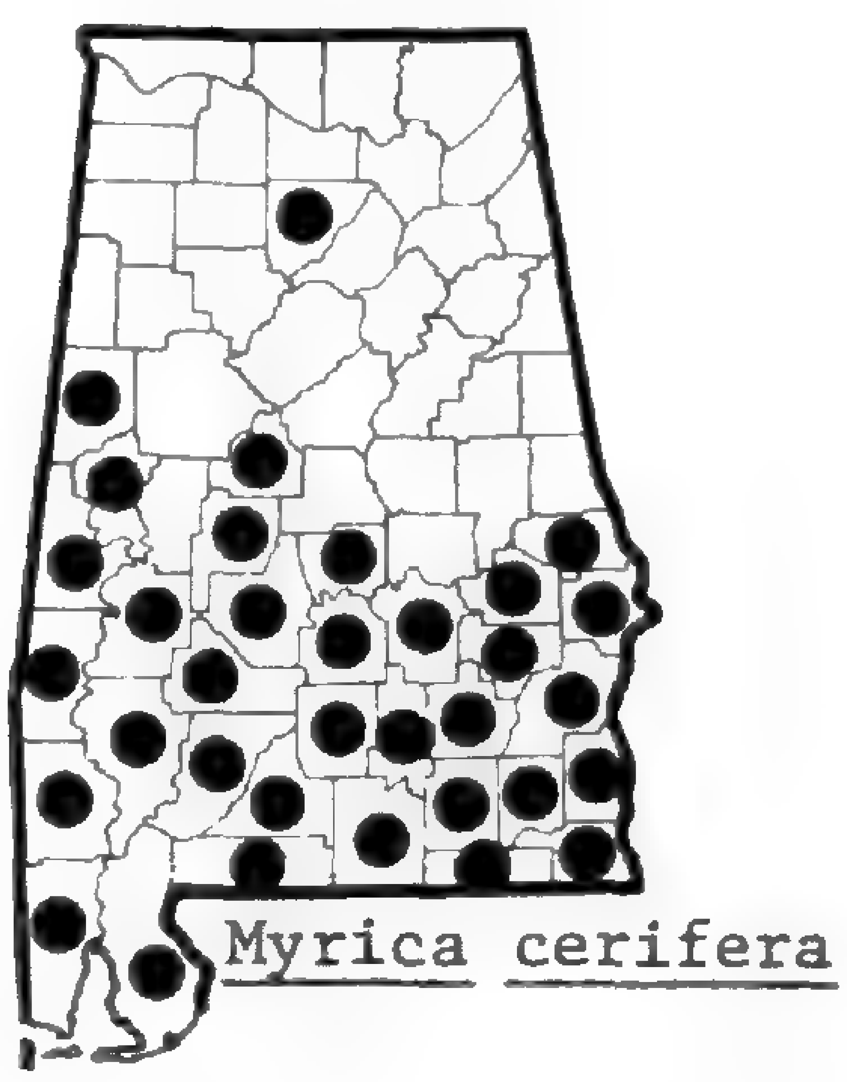
1. Staminate flowers with 8 or more stamens; pistils 1–3 in each bract axil; fruit more than 1 cm long .... 3. *M. inodora*
1. Staminate flowers with less than 7 stamens; pistil solitary in each bract axil; fruit less than 0.5 cm long 2

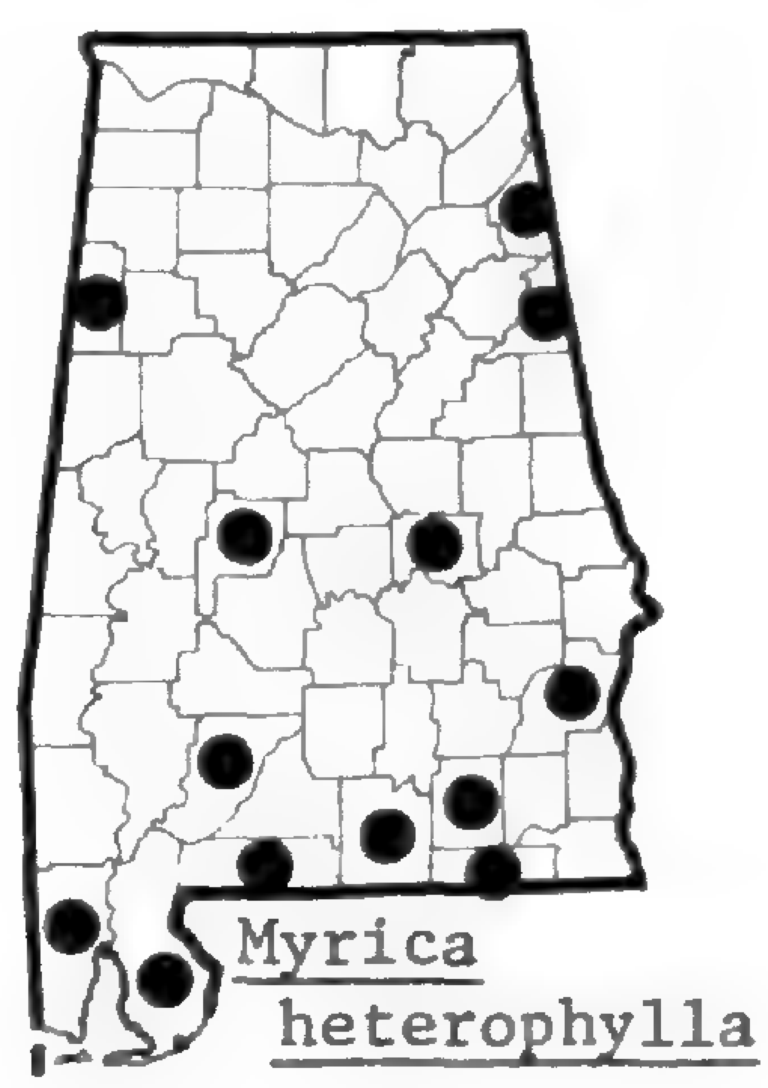

Salix humilis


Salix nigra


Salix sericea

8. MYRICACEAE


Myrica cerifera

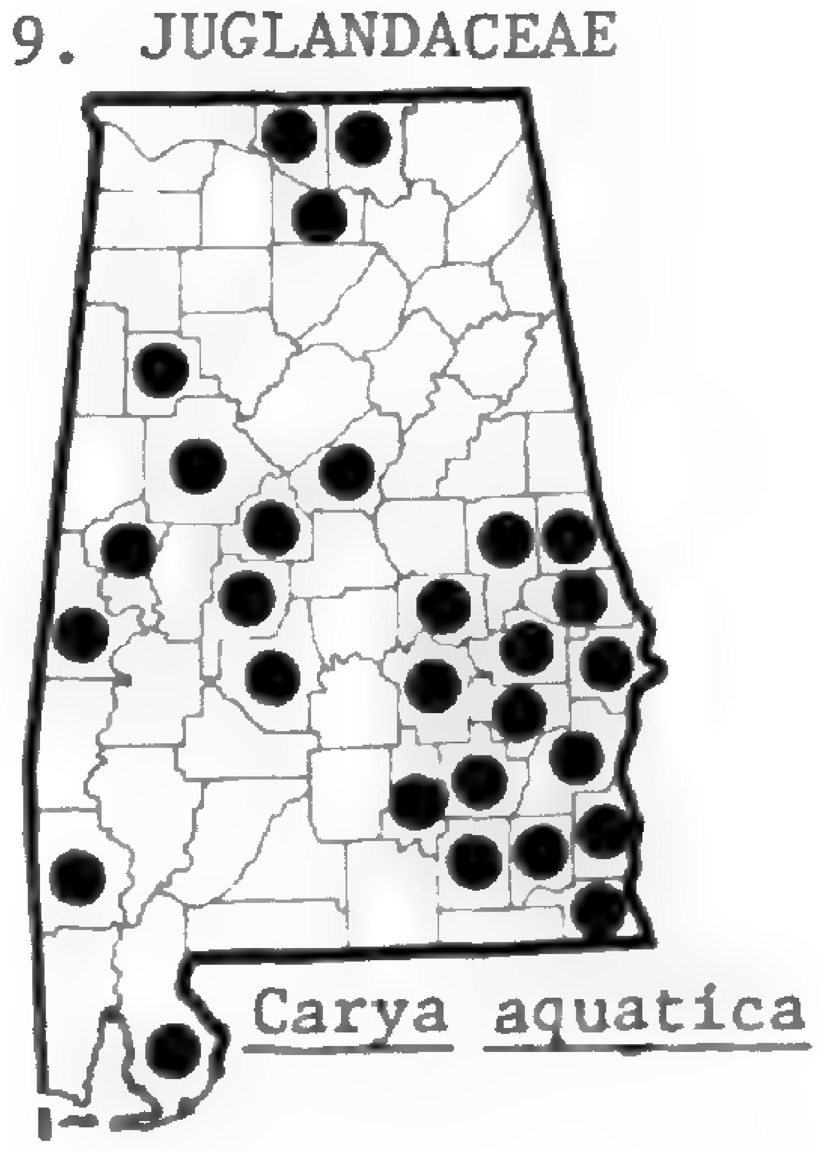

Myrica heterophylla

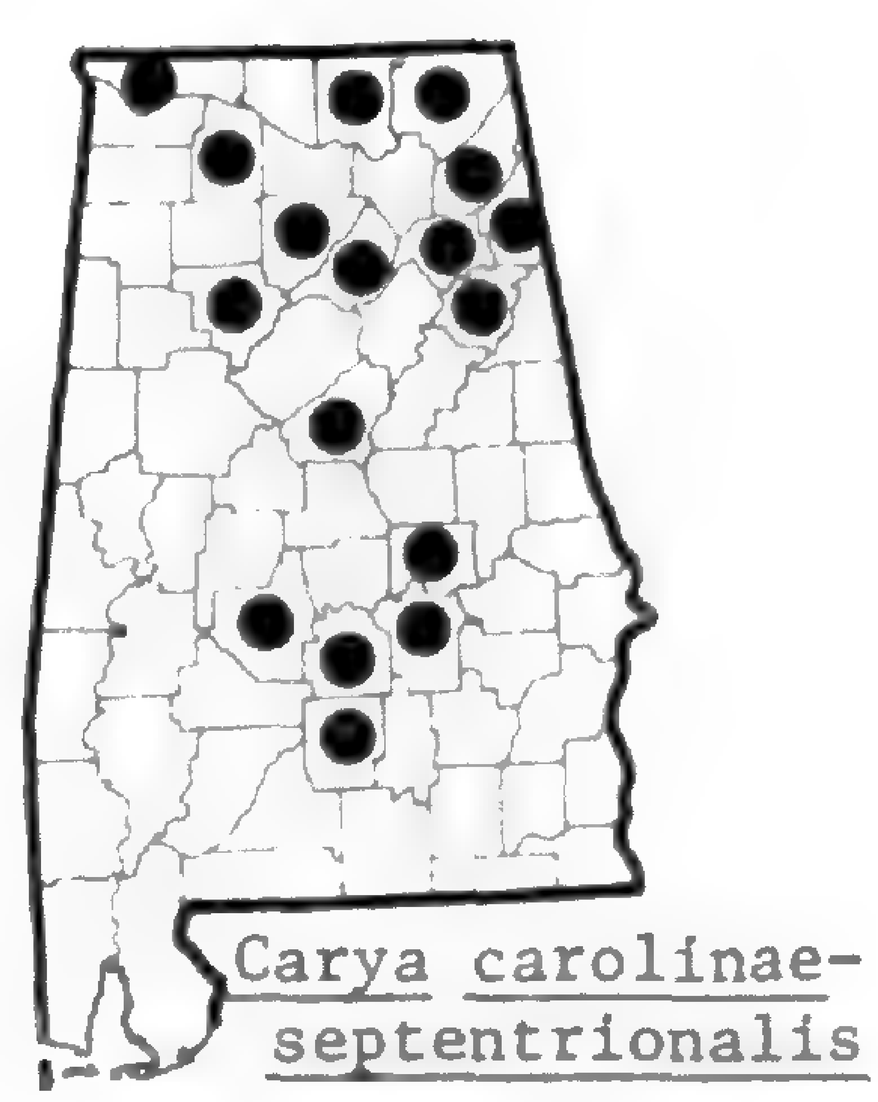

Myrica inodora

LEITNERIACEAE


Leitneria floridana

9. JUGLANDACEAE


Carya aquatica


Carya carolinae-septentrionalis

2. Glands on upper leaf surface very sparse or absent .... 2. *M. heterophylla*
2. Glands on upper leaf surface dense .... 1. *M. cerifera*

1. *M. cerifera* L., WAX MYRTLE. Spring; fall. Habitats various; CP, CuP (rare). *M. pumila* (Michx.) Sm.—M, H; *Cerothamnus ceriferus* (L.) Sm.—S; *C. pumilus* (Michx.) Sm.—S.

2. *M. heterophylla* Rafinesque, BAYBERRY. Spring; fall. Seepages, bogs, infrequent; CP, P, AM, VR. *M. carolinensis* Mill.—M, H; *Cerothamnus carolinensis* (Mill.) Tidest.—S.

3. *M. inodora* Bartram. Spring; fall. Seepages, creek swamps, rare; OCP. *Cerothamnus inodorus* (Bart.) Sm.—S.

LEITNERIACEAE

Leitneria floridana Chapman (CORKWOOD) has been listed by Dean (1961), but no specimens have been seen.

9. JUGLANDACEAE

1. Pith of twigs continuous; involucre dehiscent at maturity .... 1. *Carya*
1. Pith of twigs chambered; involucre indehiscent .... 2. *Juglans*

1. *Carya* Nuttall, HICKORY

1. Bud scales valvate 2
 2. Buds distinctly yellow .... 3. *C. cordiformis*
 2. Buds brownish 3
  3. Involucre smooth, or angled only distally 4
   4. Young twigs, buds and lower surfaces of leaves entirely covered with peltate scales .... 7. *C. myristicaeformis*
   4. Young twigs, buds and lower surfaces of leaves not entirely covered with peltate scales .... 5. *C. illinoensis*
  3. Involucre angled .... 1. *C. aquatica*
1. Bud scales imbricate 5
 5. Margins of young leaflets densely ciliate, older serrations ciliate or with persistent subterminal tufts of cilia 6
  6. Cilia on leaflet margins stellate, not densely tufted 7
   7. Buds and fruit glandular; peltate glands present beneath on leaflets .... 10. *C. pallida*
   7. Buds and fruit eglandular; abaxial glands of leaflets not peltate .. 11. *C. tomentosa*
  6. Cilia on leaflet margins simple, often densely tufted 8
   8. Terminal leaflet lanceolate or oblanceolate; fruit less than 3.5 cm long .... 2. *C. carolinae-septentrionalis*
   8. Terminal leaflet ovate or obovate; fruit more than 3.5 cm long .... 9. *C. ovata*
 5. Margins of young leaflets not densely ciliate, older leaf serrations lacking subterminal tufts of cilia 9
  9. Leaflets pubescent beneath, the pubescence not confined to the midrib or axils of the principal veins 10
   10. Abaxial leaflet pubescence simple .... 6. *C. laciniosa*
   10. Abaxial leaflet pubescence stellate 11
    11. Buds and fruit glandular; peltate glands present beneath on leaflets .... 10. *C. pallida*
    11. Buds and fruit eglandular; abaxial glands of leaflets not peltate .... 11. *C. tomentosa*
  9. Leaflets glabrous beneath, pubescence when present confined to vicinity of midrib or axils of principal veins 12
   12. Buds peltate-glandular .... 10. *C. pallida*
   12. Buds eglandular 13

13. Fruit obovoid, often stipitate; husk not splitting to base of fruit at maturity; leaves usually 5-foliolate .... 4. *C. glabra*
13. Fruit globose or obovoid, not stipitate; husk splitting to base of fruit at maturity; leaves usually 7-foliolate .... 8. *C. ovalis*

1. *C. aquatica* (Michaux f.) Nuttall, WATER H. Spring; fall. Alluvial woods, river swamps; principally CP, HR. *Hicoria aquatica* (Michx.) Britt.—M, H, S.

2. *C. carolinae-septentrionalis* (Ashe) Engler & Graebner, SCALY-BARK H. Spring; fall. Deciduous woods, more common over calcareous substrata; CP, P, VR, CuP, HR. *Hicoria carolinae-septentrionalis* (Michx.) Britt.—M, H, S.

3. *C. cordiformis* (Wang.) K. Koch, BITTERNUT H. Spring; fall. Rich or alluvial woods; CP, AM, VR, CuP, HR. *Hicoria minima* (Marsh.) Britt.—M; *H. cordiformis* (Wang.) Britt.—H, S.

4. *C. glabra* (Miller) Sweet, PIGNUT H. Spring; fall. Deciduous woods; CP, AM, VR, CuP. *Hicoria ashei* Sudw.—H; *H. glabra* (Miller) Britt.—M, H, S.

5. *C. illinoensis* (Wang.) K. Koch, PECAN. Spring; fall. Fence-rows, vacant lots, disturbed areas; principally CP. Possibly occurring naturally in the Black Belt (Harper, 1928). *Hicoria pecan* (Marsh.) Britt.—M, H, S.

6. *C. laciniosa* (Michaux f.) Loud., BIG SCALY-BARK H. Spring; fall. Rich woods, alluvial woods; CP, VR, CuP, HR. *Hicoria laciniosa* (Michx.) Sarg.—S.

7. *C. myristicaeformis* Michaux f., NUTMEG H. Spring; fall. Calcareous soil, rare; Black Belt of CP. *Hicoria myristicaeformis* (Michx.) Britt.—M, H, S.

8. *C. ovalis* (Miller) K. Koch, PIGNUT H. Spring; fall. Deciduous woods, very rare, but poorly collected; CuP. *Hicoria microcarpa* (Nutt.) Britt.—S.

9. *C. ovata* (Miller) K. Koch, SCALY-BARK H. Spring; fall. Mesic woods, low woods, alluvial woods, river swamps; throughout. *Hicoria ovata* (Mill.) Britt.—M, H, S.

10. *C. pallida* (Ashe) Engler & Graebner. Spring; fall. Dry or sandy woods; throughout. *Hicoria villosa* (Sarg.) Ashe—M; *H. pallida* Ashe—H, S.

11. *C. tomentosa* (Poiret) Nuttall, MOCKERNUT H., WHITE H., WHITE-HEART H. Spring; fall. Deciduous woods in various habitats; throughout. *Hicoria alba* (L.) Britt.—M, H, S.

2. *Juglans* L., WALNUT

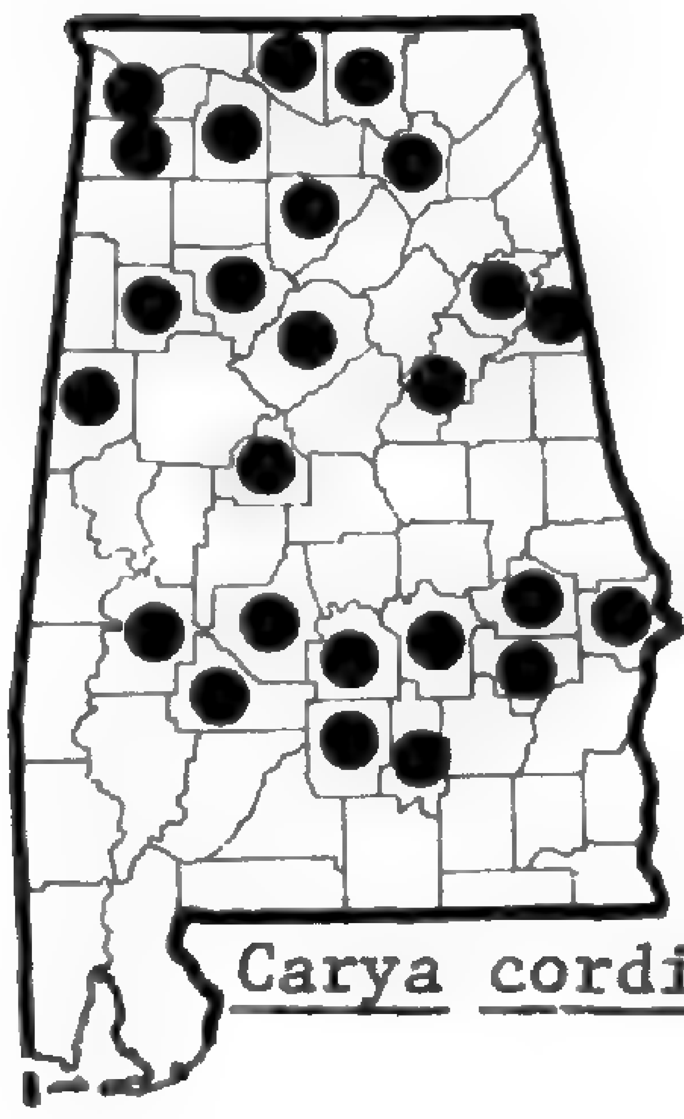
1. Pith dark brown; fruit elliptic, subcylindric or ovoid .... 1. *J. cinerea*
1. Pith cream-colored, tan or light brown; fruit subglobose .... 2. *J. nigra*

1. *J. cinerea* L., BUTTERNUT, WHITE W. Spring; fall. Rich deciduous woods, infrequent; CP (rare), CuP, HR. *Wallia cinerea* (L.) Alef.—S.

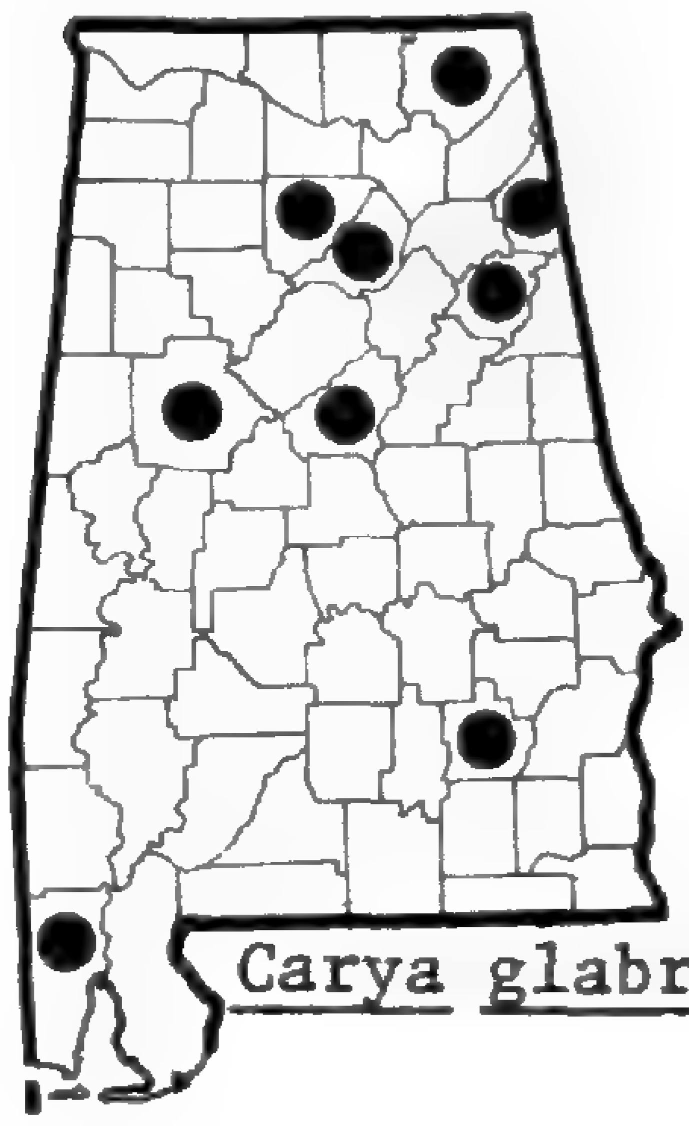
2. *J. nigra* L., WALNUT, BLACK W. Spring; fall. Rich woods; throughout. *Wallia nigra* (L.) Alef.—S.

10. BETULACEAE

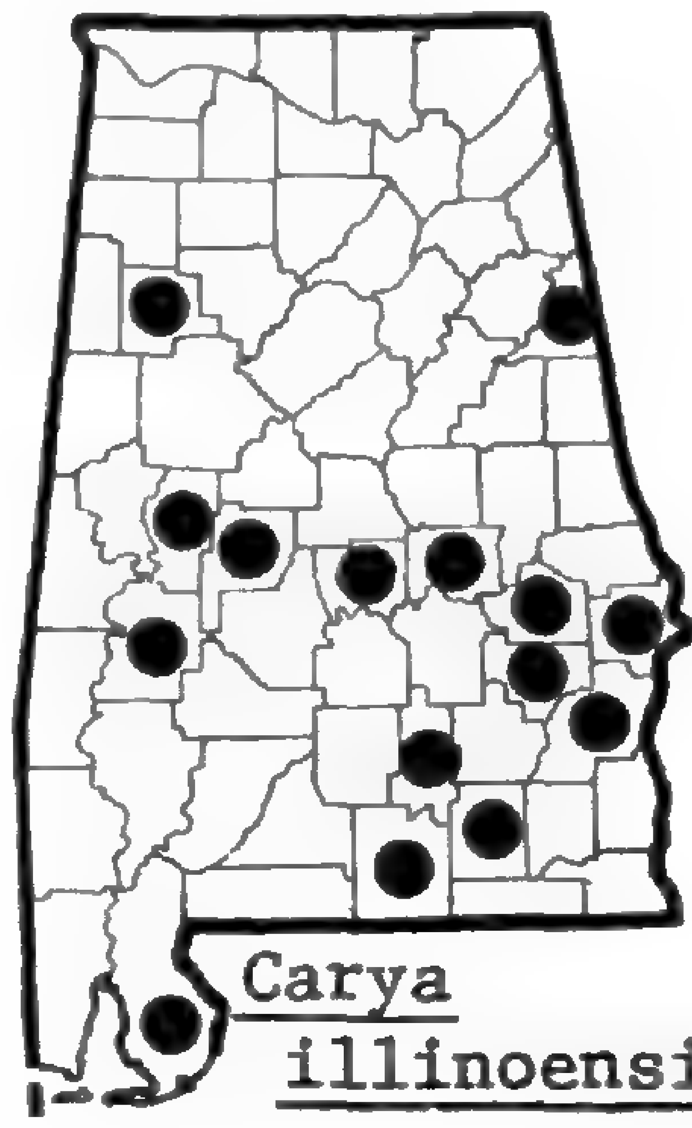
1. Fruiting pistillate bracts brownish or less than 5 mm long; calyx of staminate flower present 2
   2. Fruiting bracts woody; pistillate inflorescence persistent; stamens more than 2 .. 1. *Alnus*
   2. Fruiting bracts chartaceous; pistillate inflorescence disintegrating at maturity; stamens 2 .... 2. *Betula*
1. Fruiting pistillate bracts green, more than 5 mm long; calyx of staminate flower absent 3



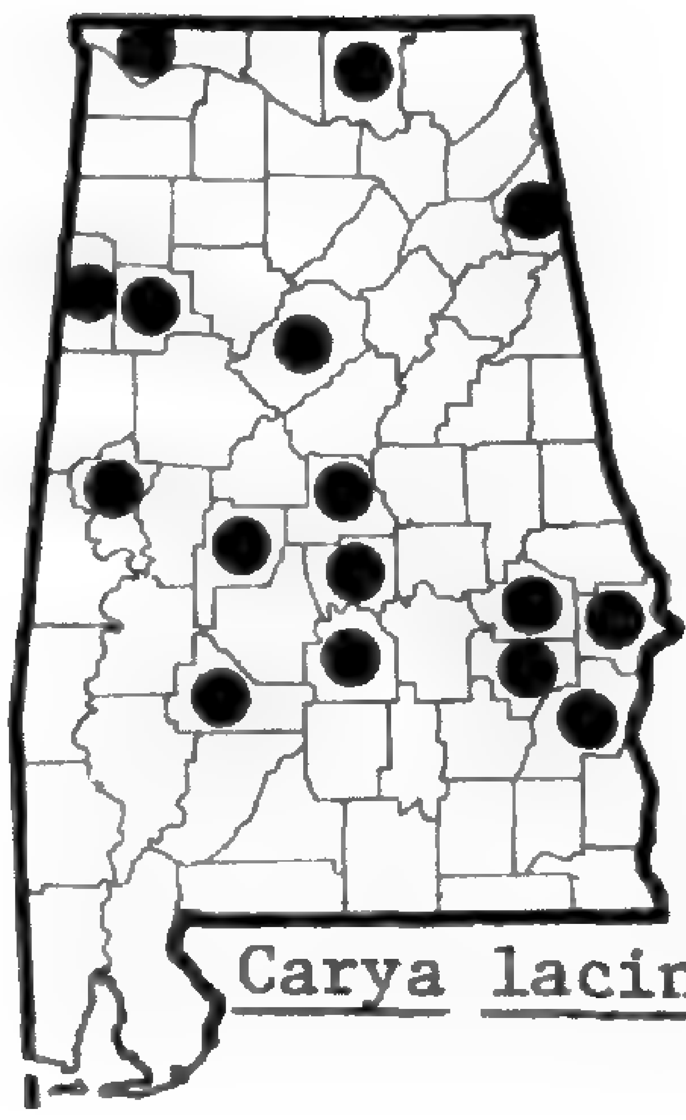
Carya cordiformis



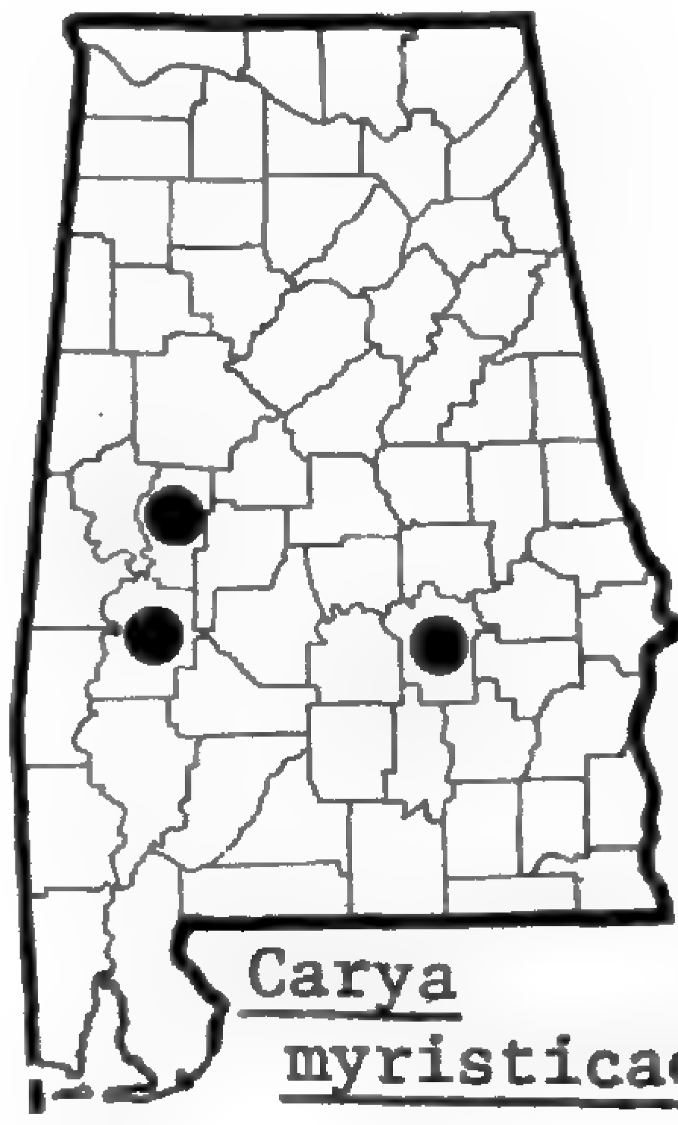
Carya glabra



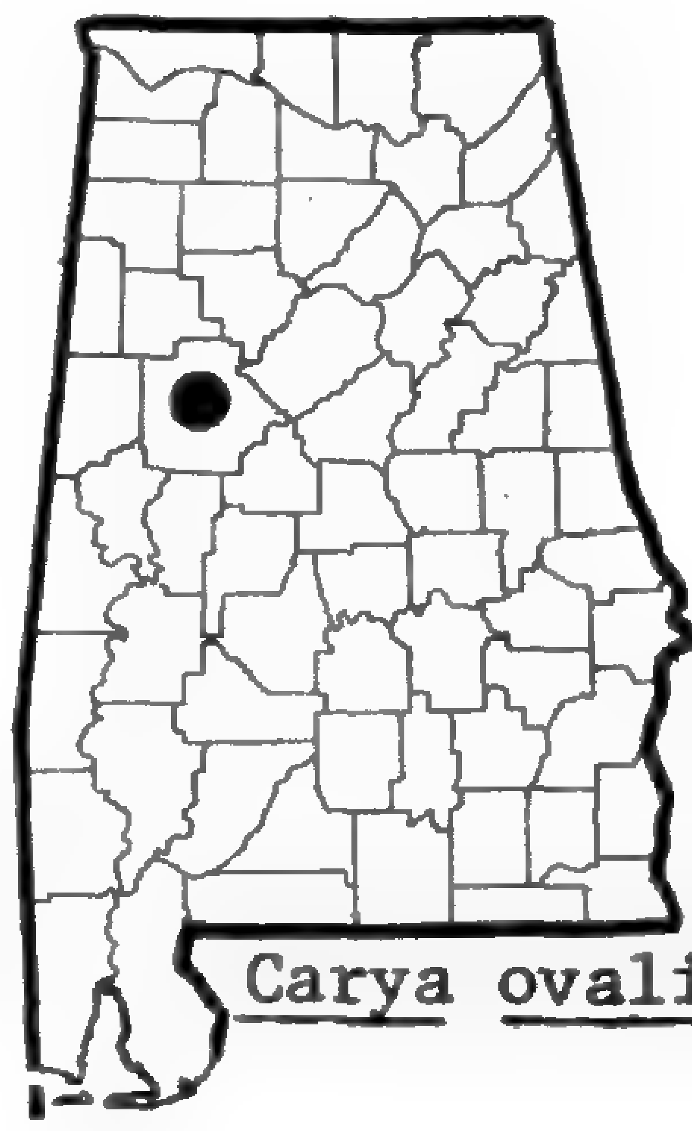
Carya illinoensis



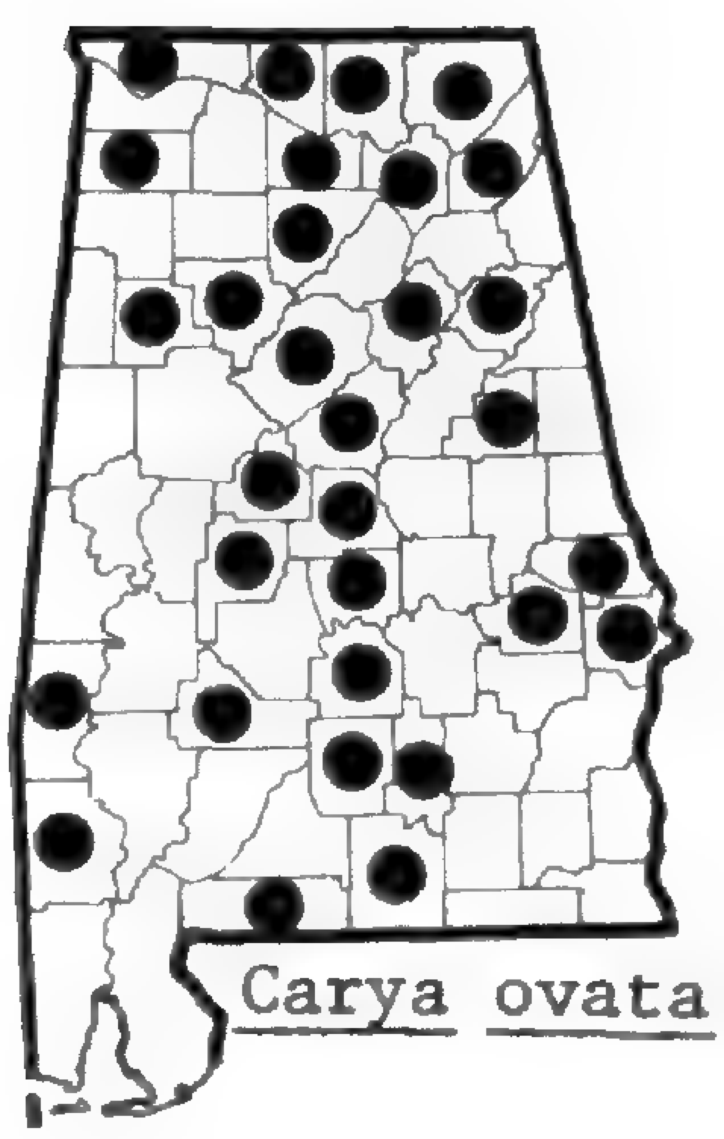
Carya laciniosa



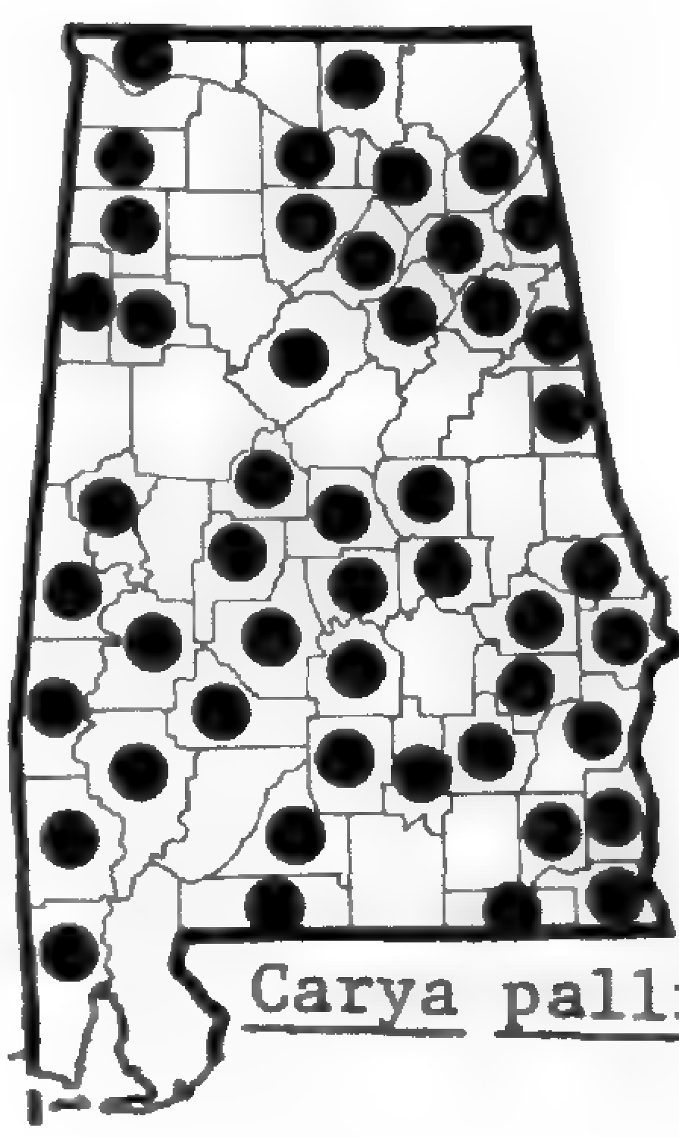
Carya myristicaeformis



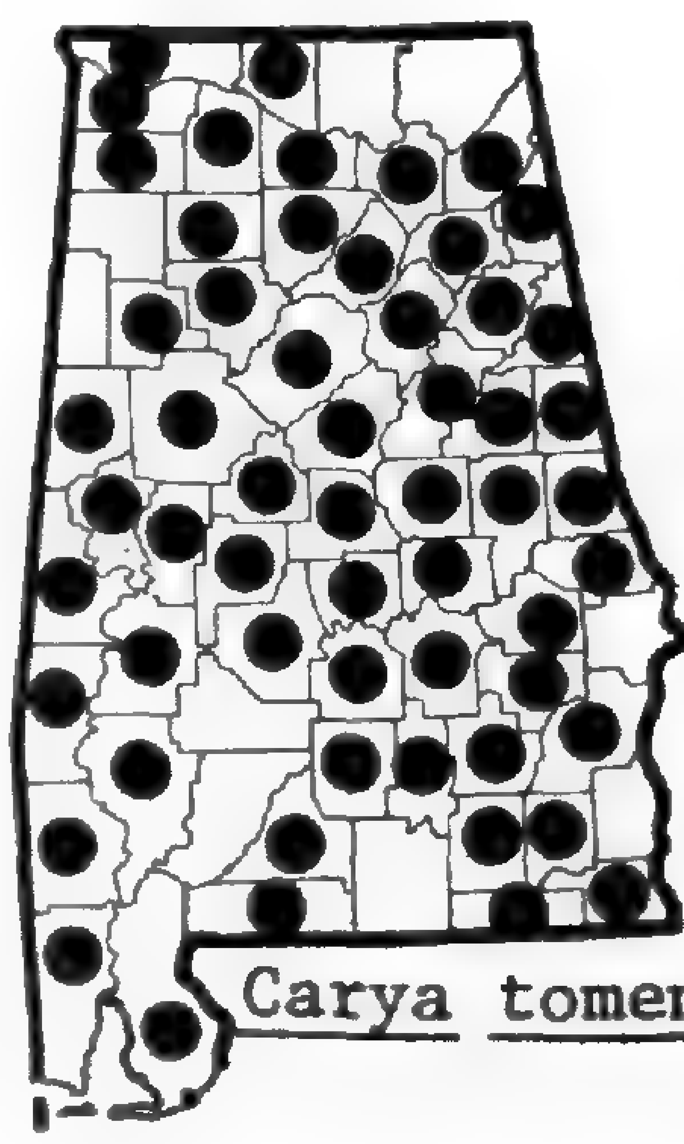
Carya ovalis



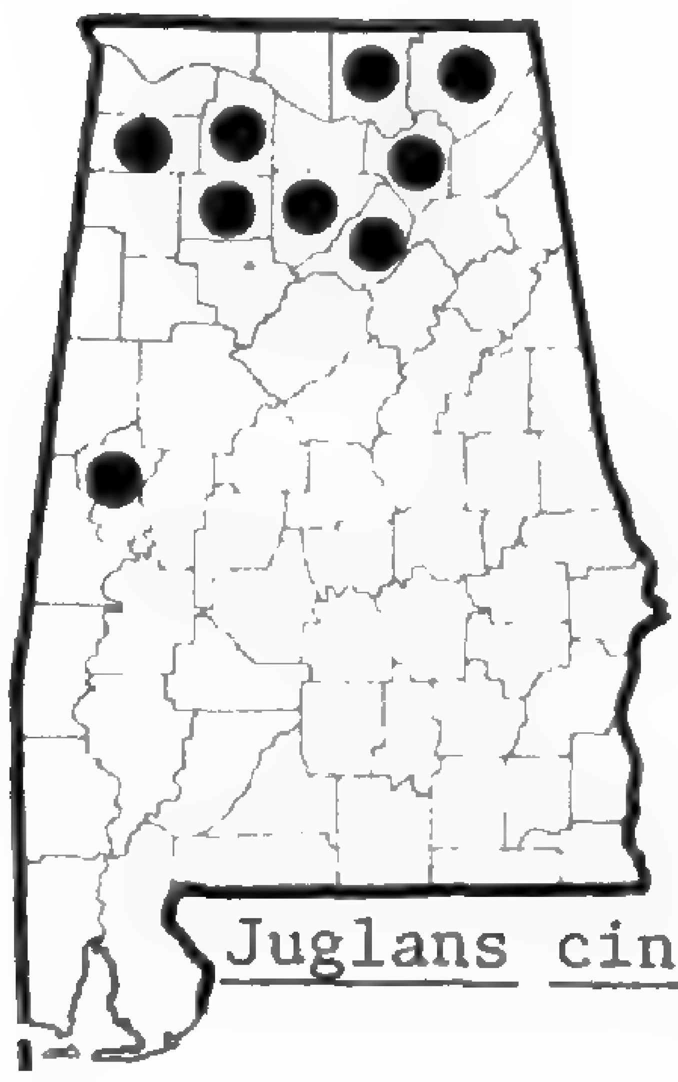
Carya ovata



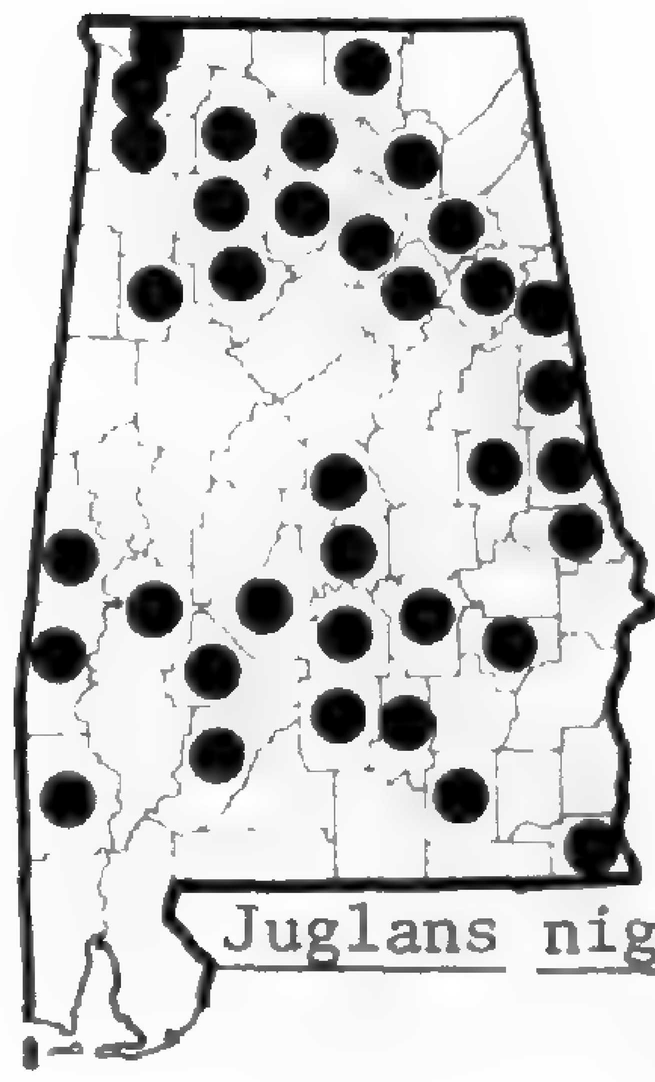
Carya pallida



Carya tomentosa

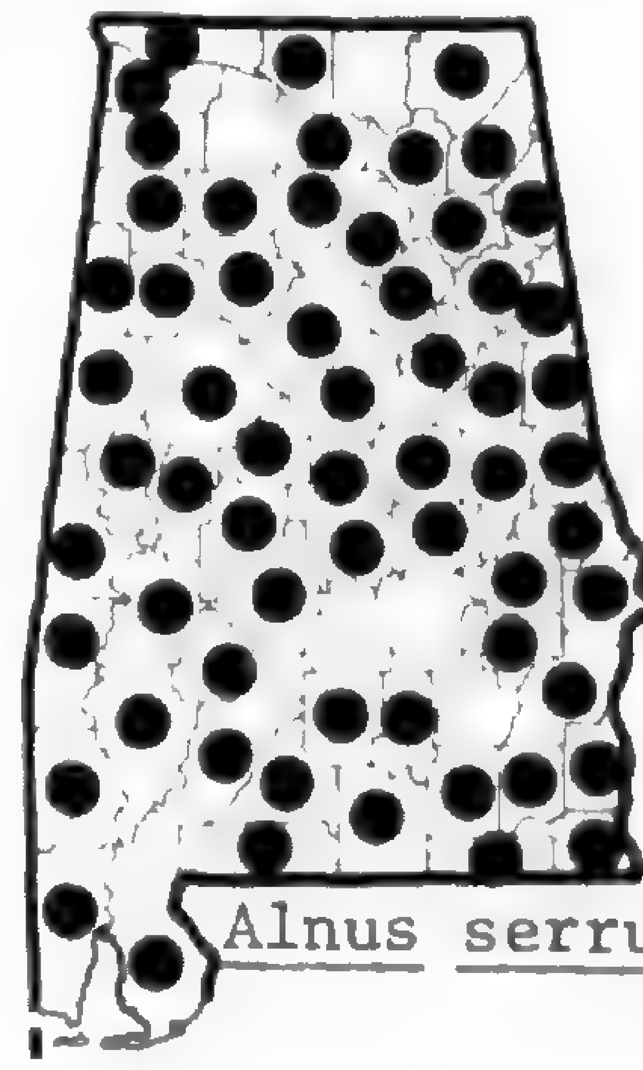


Juglans cinerea

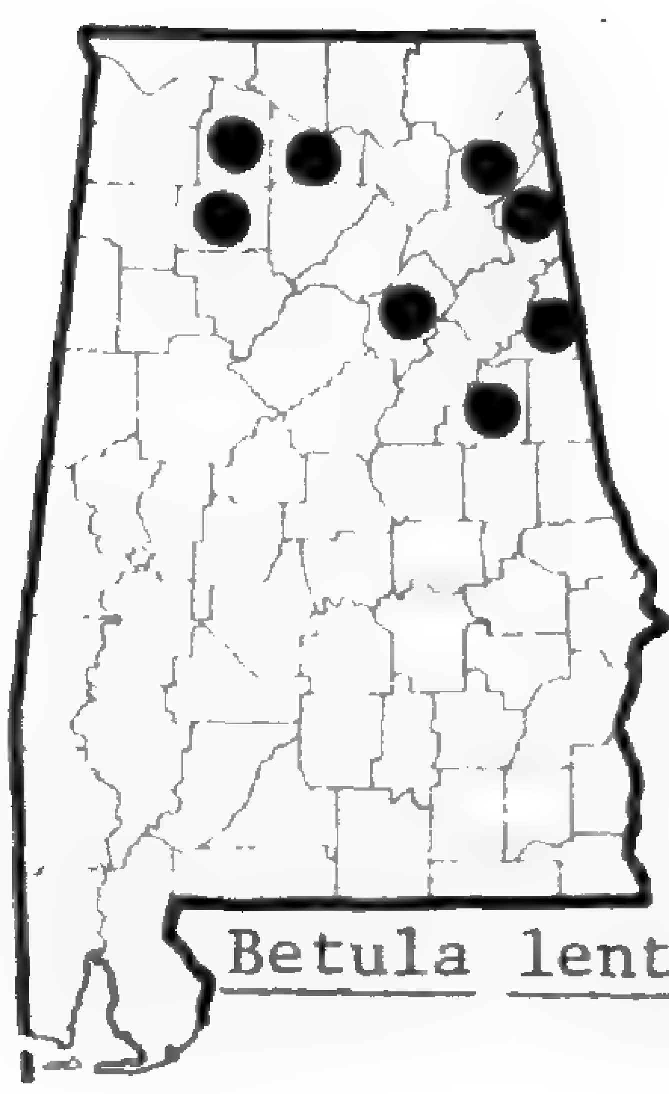


Juglans nigra

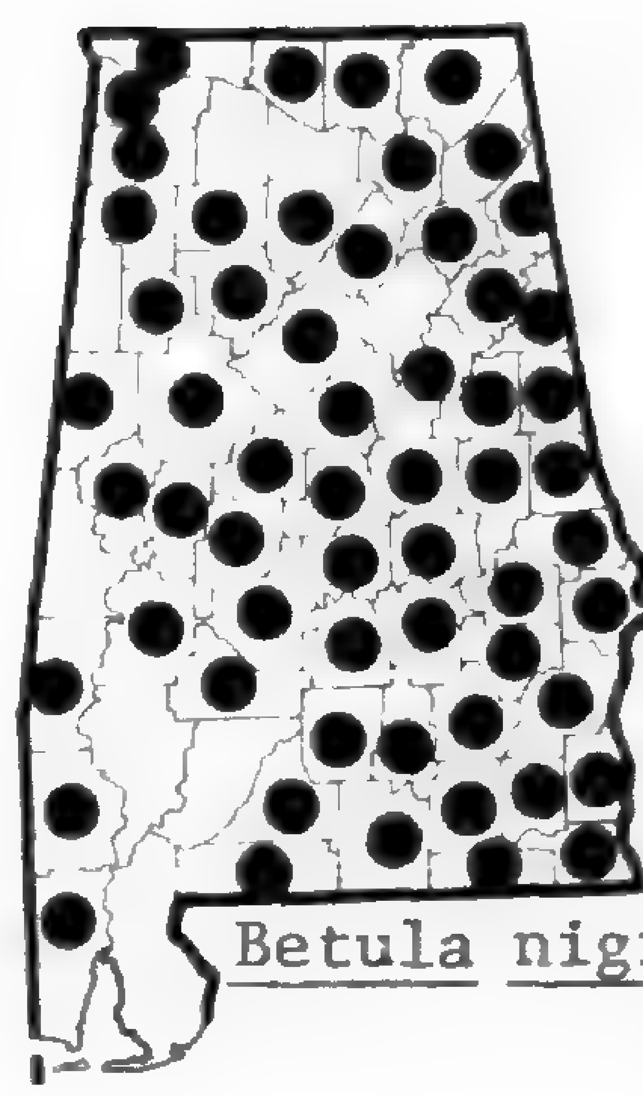
10. BETULACEAE



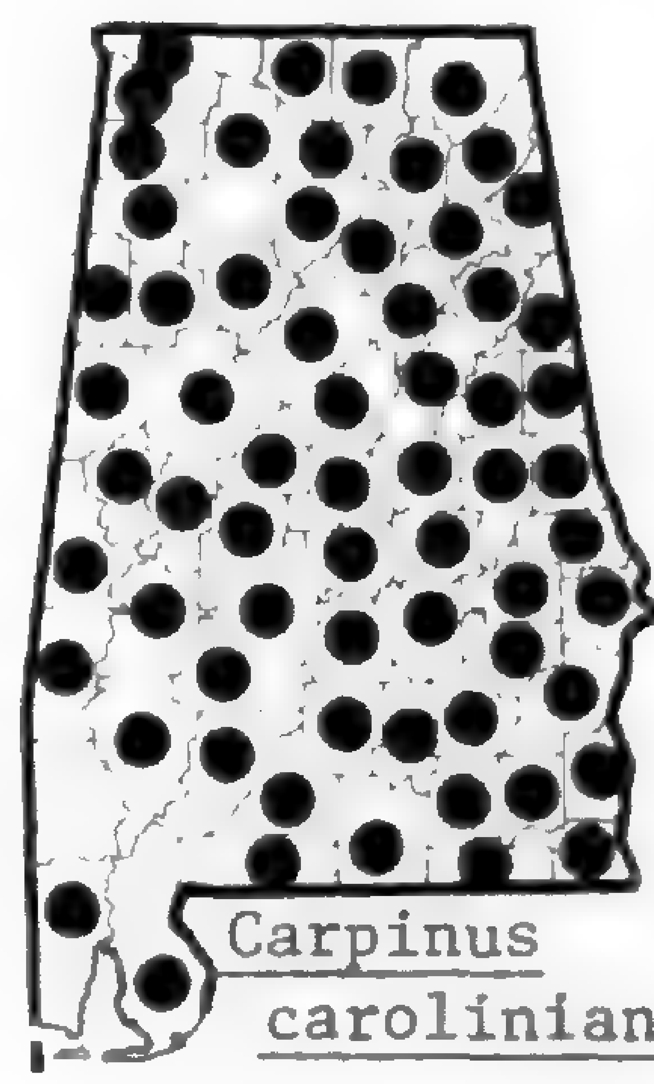
Alnus serrulata



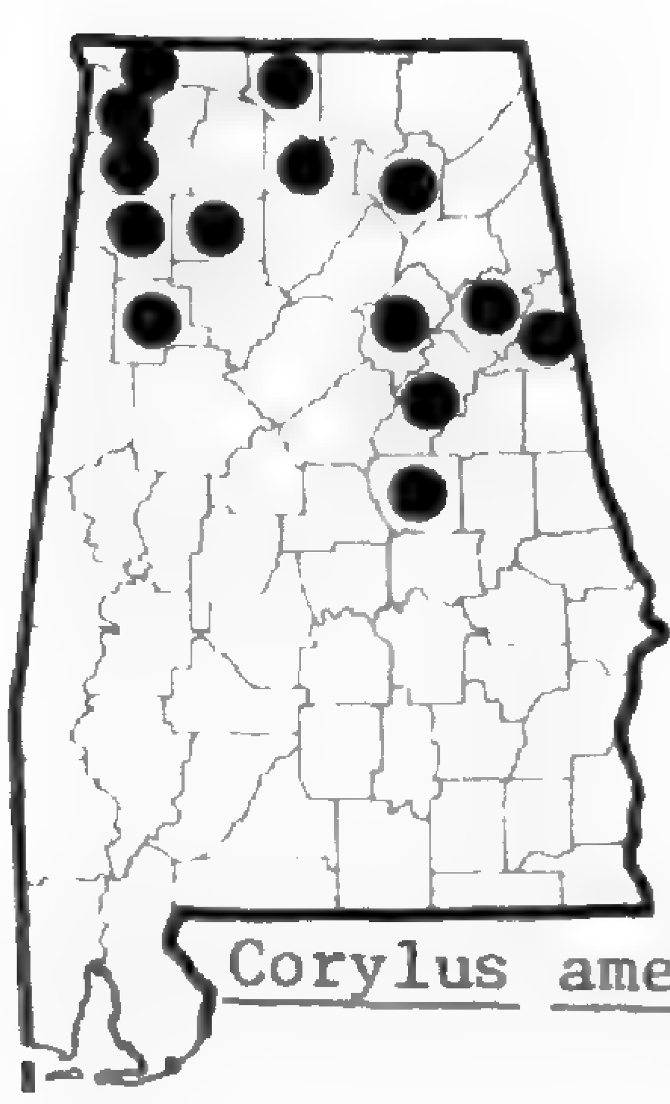
Betula lenta



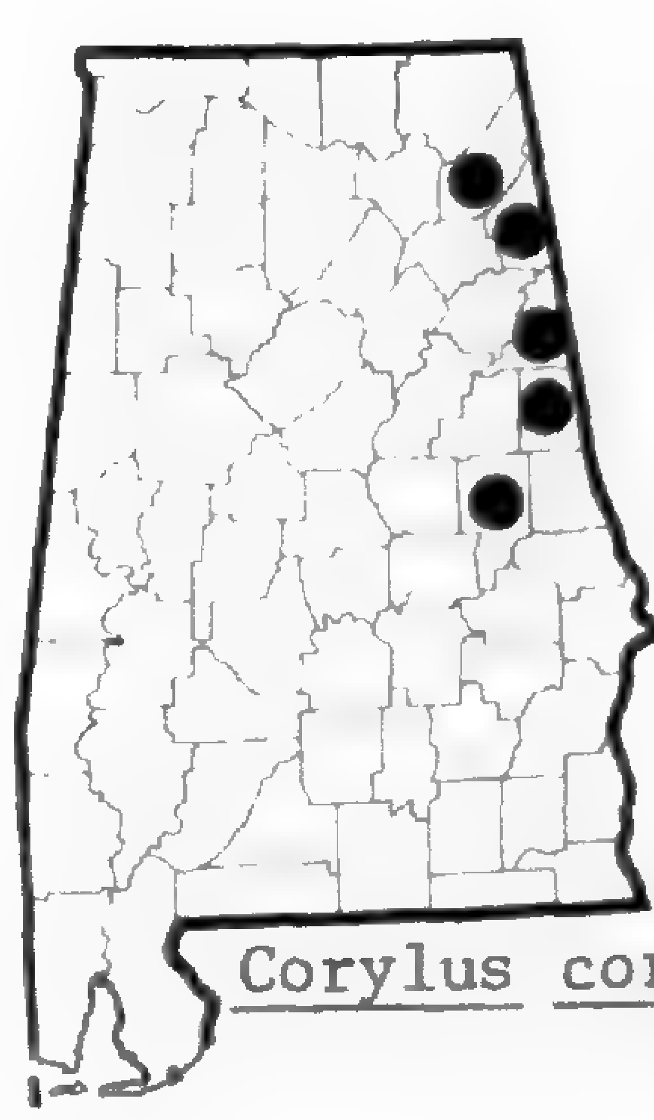
Betula nigra



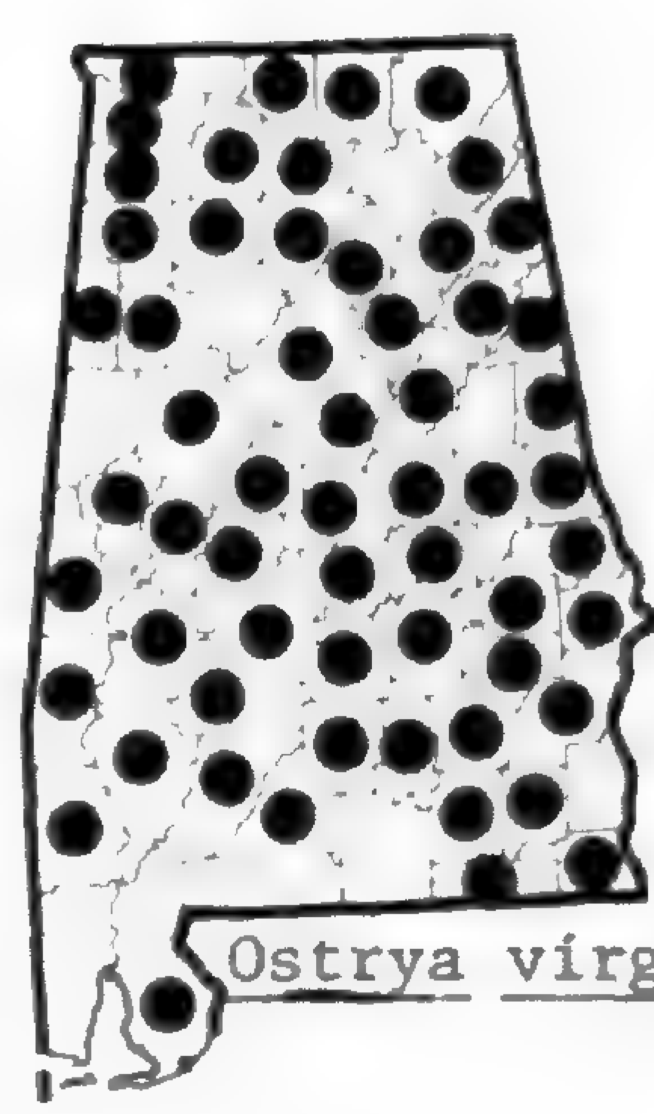
Carpinus caroliniana



Corylus americana



Corylus cornuta



Ostrya virginiana

3. Shrubs; fruit 1 cm or more long; pistillate flowers in heads .... 4. *Corylus*
3. Trees; fruit less than 1 cm long; pistillate flowers in catkins 4
    4. Fruit enclosed by bladder-like bract; apex of staminate bract awned .... 5. *Ostrya*
    4. Fruit subtended by 3-lobed, leaf-like bract; apex of staminate bract acute .... 3. *Carpinus*

1. *Alnus* Ehrhart, Alder

1. *A. serrulata* (Aiton) Willd. Late winter–spring; fall. Low thickets, streambanks, ditches, seepages; throughout. *A. rugosa* (DuRoi) Koch—M, H; *A. rugosa* (DuRoi) Spreng.—S.

2. *Betula* L., Birch

1. Leaf bases, at least some, subcordate to cordate .... 1. *B. lenta*
1. Leaf bases widely cuneate to truncate, not subcordate or cordate .... 2. *B. nigra*

1. *B. lenta* L., Cherry B. Spring; summer. Rocky woods, infrequent; AM, CuP.

2. *B. nigra* L., River B. Spring; summer. Seepages, low thickets, alluvial woods, streambanks; throughout.

3. *Carpinus* L., Ironwood, Blue Beech

1. *C. caroliniana* Walter. Spring; fall. Streambanks, low woods; throughout.

4. *Corylus* L., Hazelnut

1. Petioles stipitate-glandular .... 1. *C. americana*
1. Petioles not stipitate-glandular .... 2. *C. cornuta*

1. *C. americana* Walter. Late winter; fall. Deciduous woods, more frequent in circumneutral soils; AM, VR, CuP, HR.

2. *C. cornuta* Marshall. Late winter; fall. Dry woods, infrequent; AM, CuP. *C. rostrata* Ait.—M, H.

5. *Ostrya* Scop., Hop-Hornbeam

1. *O. virginiana* (Miller) K. Koch. Spring; summer–fall. Mesic or alluvial woods; throughout.

11. Fagaceae

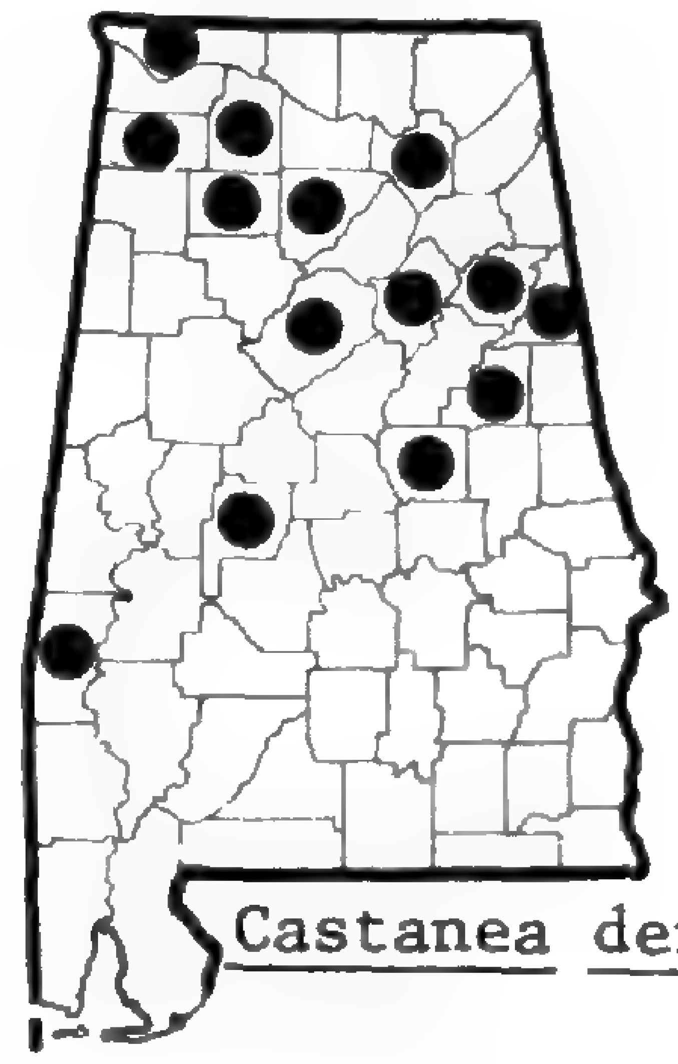
1. Involucre dehiscent, spiny 2
    2. Fruit solitary in involucre, trigonous .... 2. *Fagus*
    2. Fruit 2 or more per involucre, or solitary and terete .... 1. *Castanea*
1. Involucre indehiscent, scaly .... 3. *Quercus*

1. *Castanea* Miller

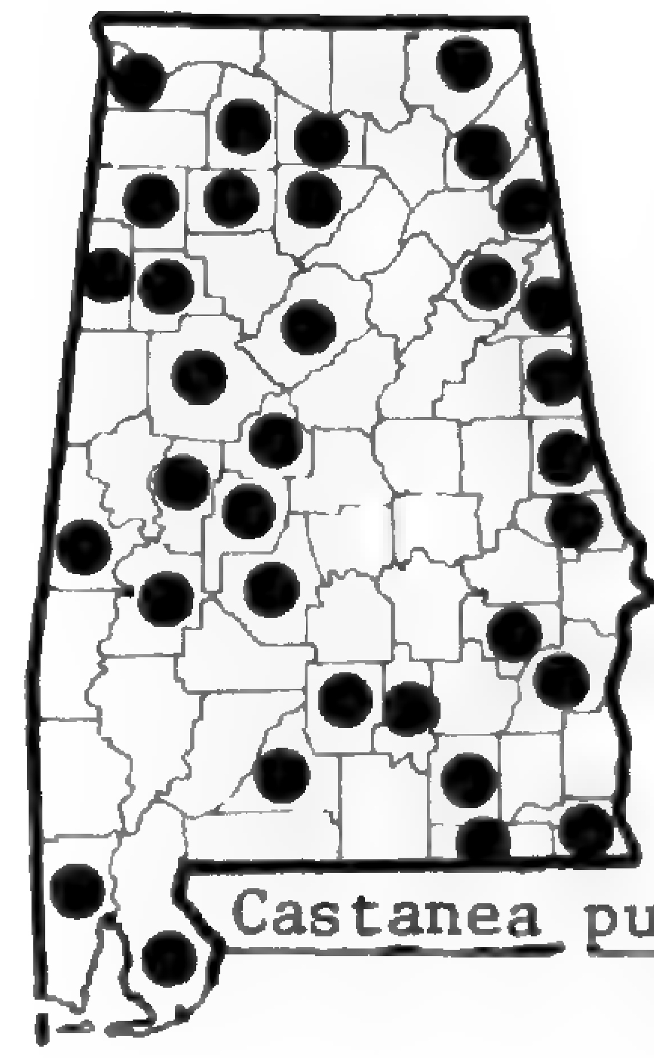
1. Leaves glabrous beneath, or sparsely pubescent on the midvein .... 1. *C. dentata*
1. Leaves pubescent beneath, often densely so 2
    2. Involucres 2 or more at base of inflorescence, later appearing spicate; fruit solitary in involucre .... 2. *C. pumila* complex
    2. Involucre solitary at base of inflorescence, later appearing axillary-solitary; fruit 2 or more in an involucre .... 3. *C. sativa*

1. *C. dentata* (Marshall) Borkh., Chestnut. Late spring–summer; fall. Dry

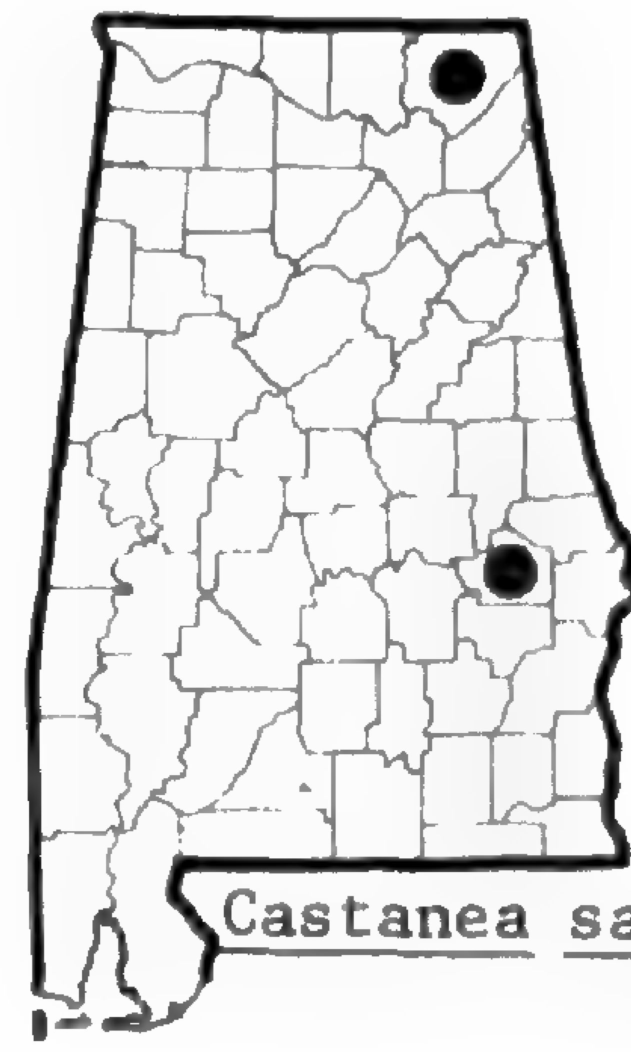
11. FAGACEAE



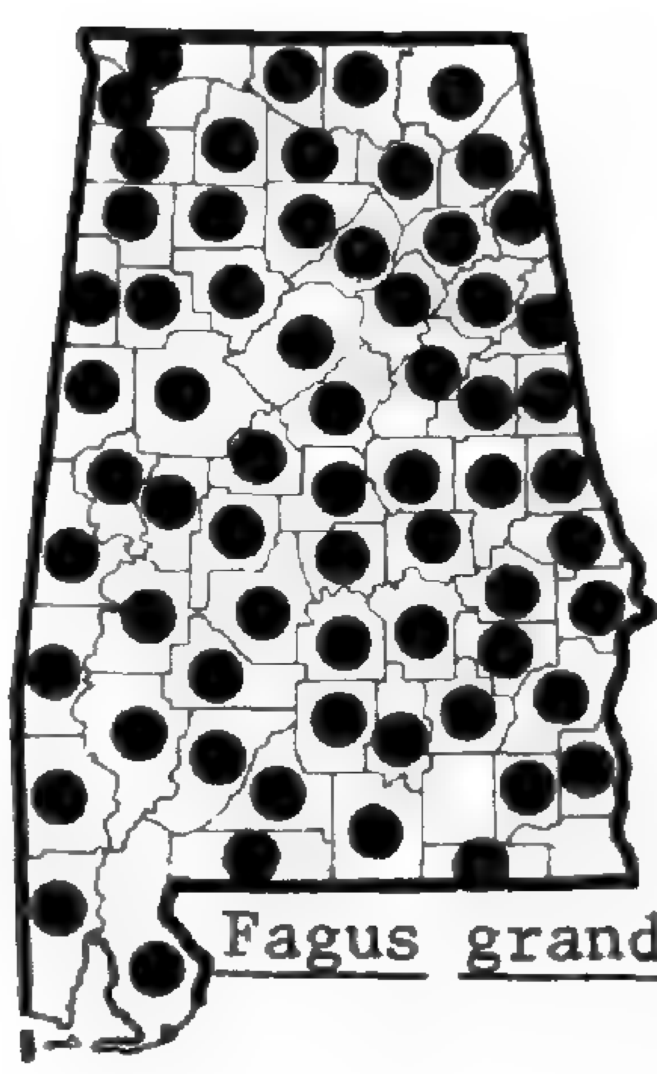
Castanea dentata



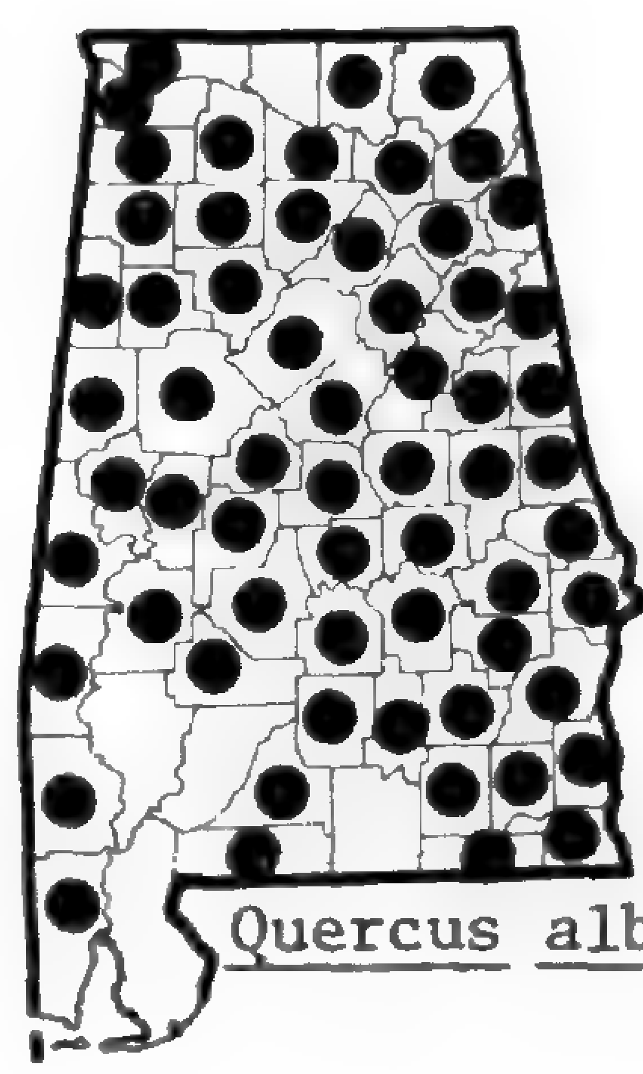
Castanea pumila s. l.



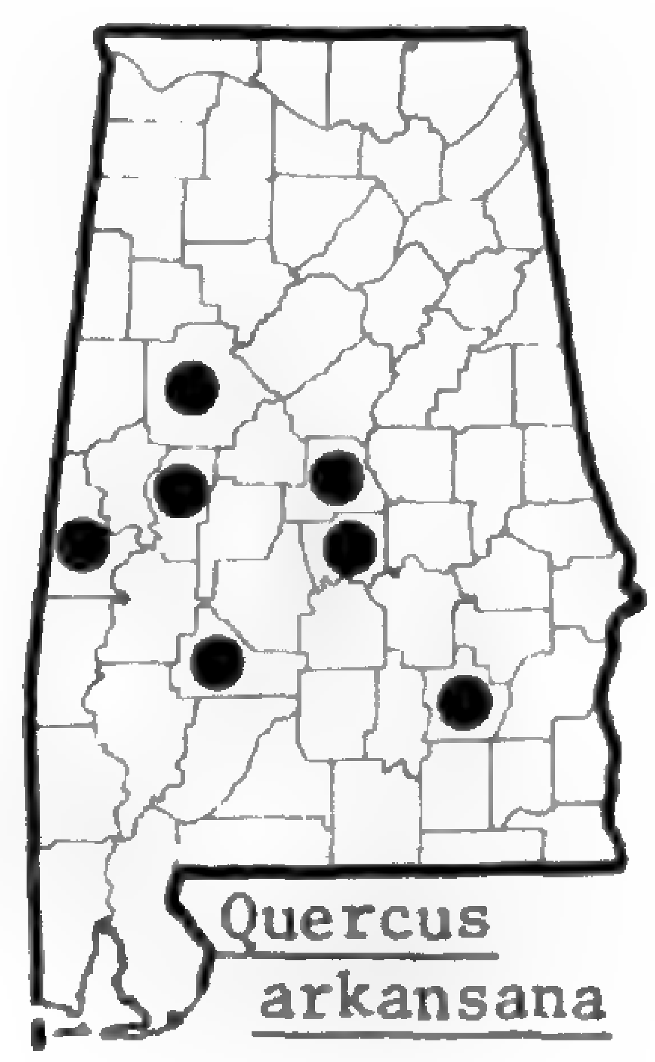
Castanea sativa



Fagus grandifolia



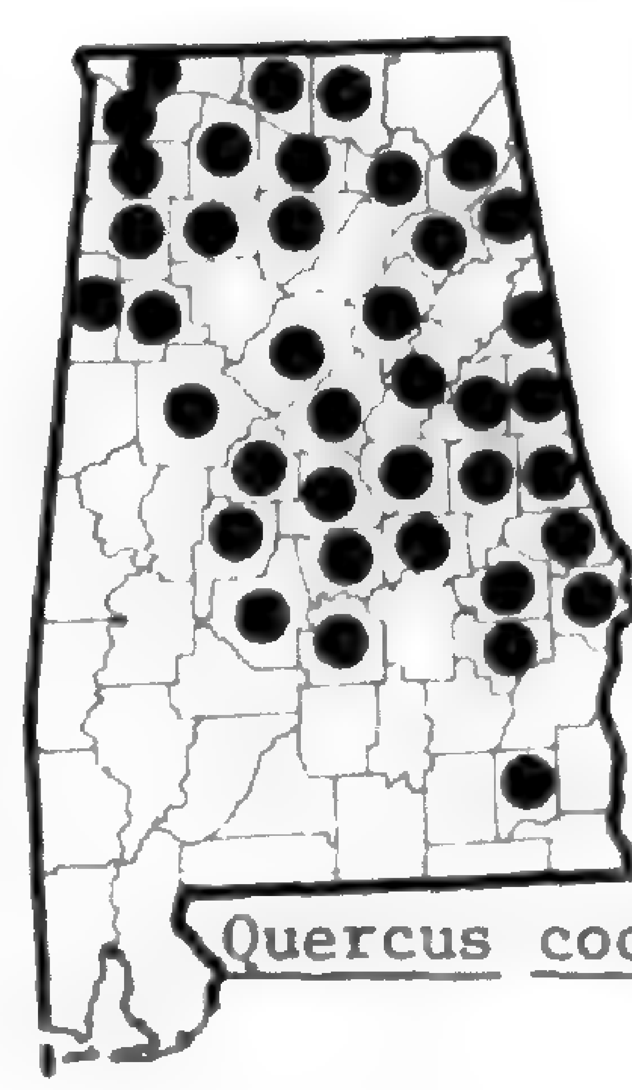
Quercus alba



Quercus arkansana

Quercus bicolor

Quercus chapmanii



Quercus coccinea

deciduous woods, infrequent to rare, formerly more common; CP (rare), AM, VR, CuP, HR.

2. *C. pumila* (L.) Miller, complex, CHINQUAPIN, CHINKAPIN. Late spring–summer; fall. Thickets, various habitats; throughout. *C. ashei* Sudw., *C. floridana* (Sarg.) Ashe—S; *C. alnifolia* Nutt.—S, RAB; *C. alnifolia* var. *floridana* Sarg., *C. pumila* var. *ashei* Sudw.—RAB.

3. *C. sativa* Miller, CHINESE CHESTNUT. Late spring–summer; fall. Rights-of-way, waste places, escaped or persistent, rare; CP, CuP.

Castanea alabamensis Ashe, from several localities in Alabama, has been regarded as a probable hybrid (Logue, 1967) involving *C. dentata* (Marsh.) Borkh. and a member of the Pumilae complex. This writer is inclined to agree, until substantial evidence to the contrary is produced.

2. *Fagus* L., BEECH

1. *F. grandifolia* Ehrhart. Spring; fall. Mesic or low woods; throughout. *F. americana* (Muenchh.) Sw.—M.

3. *Quercus* L., OAK

1. Leaves unlobed 2
  2. Leaves pubescent or scurfy beneath 3
    3. Leaves marginally or apically tipped with bristles more than 1 mm long 4
      4. Leaves spatulate, widest near the distal end 5
        5. Twigs densely stellate-pubescent .... 17. *Q. myrtifolia*
        5. Twigs not densely stellate-pubescent .... 15. *Q. marilandica*
      4. Leaves lanceolate, elliptic or narrowly ovate, widest near the middle or proximal end 6
        6. Fruit maturing on growth of present season; plants strongly soboliferous, shrubby .... 23. *Q. pumila*
        6. Fruit maturing on growth of last year; plant arborescent, not soboliferous 7
          7. Stellate trichomes on lower surfaces of leaves spreading .... 9. *Q. imbricaria*
          7. Stellate trichomes on lower surfaces of leaves tightly appressed .... 10. *Q. incana*
    3. Leaves lacking marginal bristles, sometimes with mucronate marginal teeth 8
      8. Distal bracts of involucral cup caudate; peduncles more than 2 cm long .... 3. *Q. bicolor*
      8. Distal bracts of involucral cup obtuse, acute or acuminate; or peduncles less than 2 cm long 9
        9. Upper ⅓ of fruit glabrous, lustrous; pubescence on fruit (if any) confined to vicinity of style base 10
          10. Involucral cup 2 cm or more broad from rim to rim; leaf margin regularly sinuate-dentate .... 16. *Q. montana*
          10. Involucral cup less than 1 cm broad from rim to rim; leaf margin entire, asymmetrical or weakly lobed .... 6. *Q. durandii*
        9. Upper ⅓ (or more) of fruit scurfy, dull 11
          11. Leaves regularly sinuate-dentate 12
            12. Leaves pubescent beneath with tightly appressed, whitish, sessile, stellate trichomes .... 21. *Q. prinoides*
            12. Leaves tomentose beneath with ascending simple or stellate tawny trichomes .... 22. *Q. prinus*
          11. Leaves entire or asymmetrical 13

13. Fruit 2 or more times longer than broad; interior of involucral cup funnelform, enclosing less than ½ of fruit ..... 28. *Q. virginiana*
13. Fruit less than 2 times as long as broad; interior of involucral cup saucer-shaped, enclosing more than ½ of fruit ..... 4. *Q. chapmanii*
2. Leaves glabrous beneath, or pubescent only near the principal veins 14
14. Leaves spatulate to obovate with an obtuse apex, widest near the distal end 15
15. Twigs glabrate ..... 18. *Q. nigra*
15. Twigs densely stellate-pubescent 16
16. Leaves coriaceous, semi-evergreen, often involute ..... 17. *Q. myrtifolia*
16. Leaves thin, deciduous, flattened to the margin ..... 2. *Q. arkansana*
14. Leaves lanceolate to obovate with an acute apex, usually widest near the middle 17
17. Twigs densely stellate-pubescent ..... 17. *Q. myrtifolia*
17. Twigs glabrate 18
18. Leaves narrowly elliptic or lanceolate to oblanceolate, deciduous ..... 20. *Q. phellos*
18. Leaves elliptic to obovate, semi-evergreen ..... 12. *Q. laurifolia*
1. Leaves lobed 19
19. Leaves marginally or apically tipped with bristles; fruit maturing on growth of last year 20
20. Leaves pubescent or scurfy beneath 21
21. Distal bracts of involucral cup inrolled under fruit ..... 11. *Q. laevis*
21. Distal bracts of involucral cup free of fruit 22
22. Leaves pubescent beneath with densely matted trichomes; involucral cup enclosing less than ½ of fruit ..... 7. *Q. falcata*
22. Leaves pubescent beneath with non-matted trichomes; involucral cup enclosing more than ½ of fruit ..... 27. *Q. velutina*
20. Leaves glabrous beneath, or pubescent only near the principal veins 23
23. Lateral lobes (on entire leaf) 2 or less 24
24. Twigs glabrate ..... 18. *Q. nigra*
24. Twigs densely stellate-pubescent ..... 2. *Q. arkansana*
23. Lateral lobes more than 3 25
25. Involucral cup cup-shaped, enclosing ⅓ or more of fruit 26
26. Fruit apex surrounded by one or more circular grooves ..... 5. *Q. coccinea*
26. Fruit apex not surrounded by a circular groove or grooves 27
27. Leaves pubescent beneath with discrete, axillary tufts of trichomes, often obscuring portions of the veins . 19. *Q. nuttallii*
27. Leaves lacking well-defined, axillary tufts of trichomes beneath, pubescence not obscuring portions of the veins ..... 5. *Q. coccinea*
25. Involucral cup saucer-shaped, enclosing less than ⅓ of fruit 28
28. Leaf blades less than 10 cm long ..... 8. *Q. georgiana*
28. Leaf blades, at least some, more than 10 cm long 29
29. Leaves pubescent beneath with discrete, axillary tufts of trichomes, often obscuring portions of the veins ..... 25. *Q. shumardii*
29. Leaves lacking well-defined, axillary tufts of trichomes beneath, pubescence not obscuring portions of the veins ..... 24. *Q. rubra*
19. Leaves lacking marginal bristles, sometimes with mucronate marginal teeth; fruit maturing on growth of present season 30
30. Distal bracts of involucral cup caudate 31
31. Peduncles more than 2 cm long ..... 3. *Q. bicolor*
31. Peduncles less than 2 cm long ..... 14. *Q. macrocarpa*
30. Distal bracts of involucral cup obtuse, acute or acuminate 32
32. Involucral cup enclosing ¾ or more of fruit ..... 13. *Q. lyrata*
32. Involucral cup enclosing less than ¾ of fruit 33

33. Leaves glabrous beneath, or pubescent only near the principal veins 34
 34. Fruit more than 2 cm long .... 1. *Q. alba*
 34. Fruit less than 2 cm long .... 6. *Q. durandii*
33. Leaves pubescent beneath 35
 35. Upper ⅓ of fruit glabrous, lustrous; pubescence on fruit (if any) confined to vicinity of style base .... 6. *Q. durandii*
 35. Upper ⅓ (or more) of fruit pubescent, dull 36
  36. Cup enclosing ½ or less of fruit .... 26. *Q. stellata*
  36. Cup enclosing more than ½ of fruit .... 4. *Q. chapmanii*

1. *Q. alba* L., WHITE O. Spring; fall. Mesic deciduous woods; throughout.

2. *Q. arkansana* Sargent. Spring; fall. Dry, rocky, or sandy slopes, rare; CP.

3. *Q. bicolor* Willd., SWAMP WHITE O. Spring; fall. Low woods, very rare; CuP.

4. *Q. chapmanii* Sargent. Spring; fall. Sandy woods; OCP.

5. *Q. coccinea* Muenchh., SCARLET O., SPANISH O. Spring; fall. Dry woods; throughout, but rare in southern CP.

6. *Q. durandii* Buckley.

1. Leaves pubescent over the lower surfaces .... *Q. durandii* var. *durandii*
1. Leaves glabrous over the lower surfaces .... *Q. durandii* var. *austrina*

Q. durandii Buckley var. *durandii*, PIN O. Spring; fall. Deciduous upland woods, thickets, usually on circumneutral soil; CP, CuP. *Q. brevilobata* (Torr.) Sarg.—M.

Q. durandii var. *austrina* (Small) Palmer. Spring; fall. River bluffs, alluvial woods; CP, CuP. *Q. austrina* Sm.—S, RAB.

7. *Q. falcata* Michaux. Spring; fall.

1. Leaves rusty-tomentose beneath; old bark quickly cracking and becoming roughened .... *Q. falcata* var. *falcata*
1. Leaves white-tomentose beneath; old bark cracking tardily, not conspicuously roughened .... *Q. falcata* var. *pagodaefolia*

Q. falcata Michaux var. *falcata*, SOUTHERN RED O. Upland and low woods; throughout. *Q. digitata* (Marsh.) Sudw.—M; *Q. rubra* L.—S.

Q. falcata var. *pagodaefolia* Elliott, CHERRY-BARK O. Rich woods, often alluvial, more common in circumneutral habitats; CP, P, VR, CuP, HR. *Q. pagoda* Raf.—H, S; *Q. pagodaefolia* (Ell.) Ashe—M.

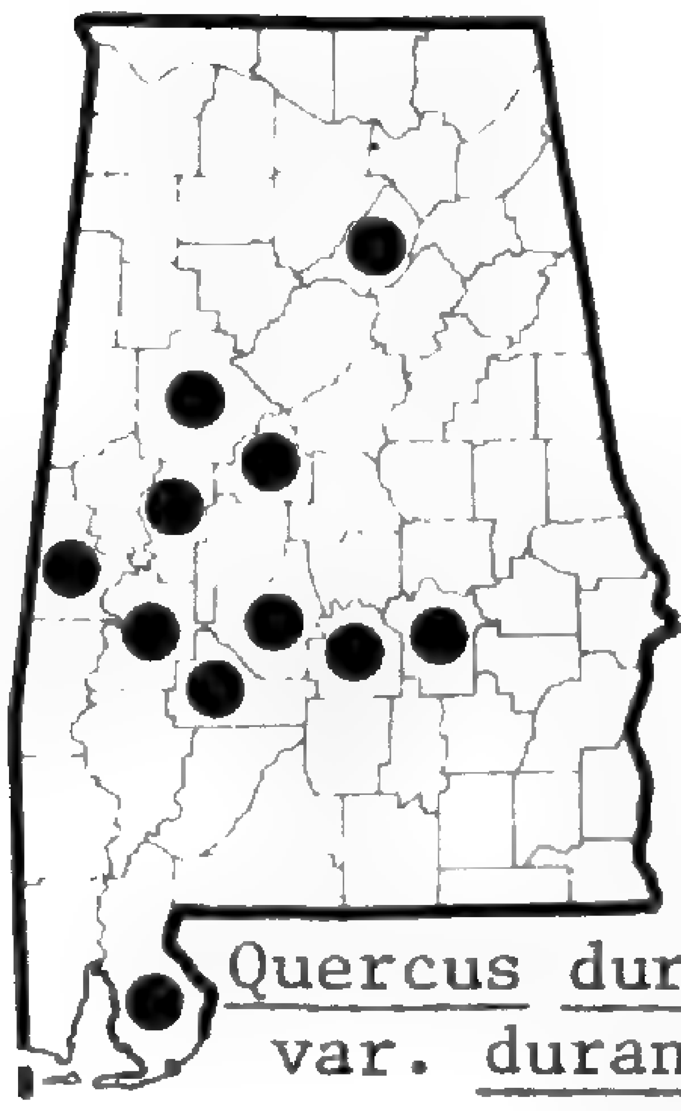
8. *Q. georgiana* Curtis, GEORGIA O. Spring; fall. Dry woods, very rare; southern CuP.

9. *Q. imbricaria* Michaux, SHINGLE O. Spring; fall. Mesic woods, very rare; OCP, VR.

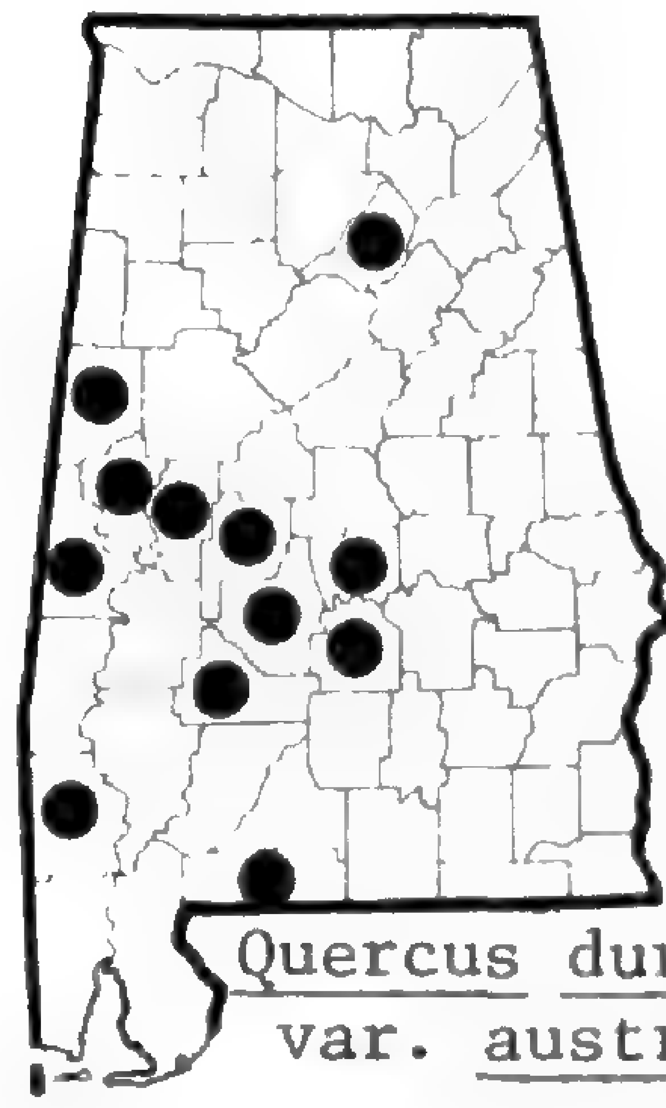
10. *Q. incana* Bartram, BLUEJACK O., UPLAND WILLOW O. Spring; fall. Dry woods, thickets; CP, VR, CuP. *Q. brevifolia* (Lam.) Sarg.—M; *Q. cinerea* Michx.—H, S.

11. *Q. laevis* Walter, TURKEY O., FORKED-LEAF BLACKJACK O. Spring; fall. Upland woods; CP. *Q. catesbaei* Michx.—M, H.

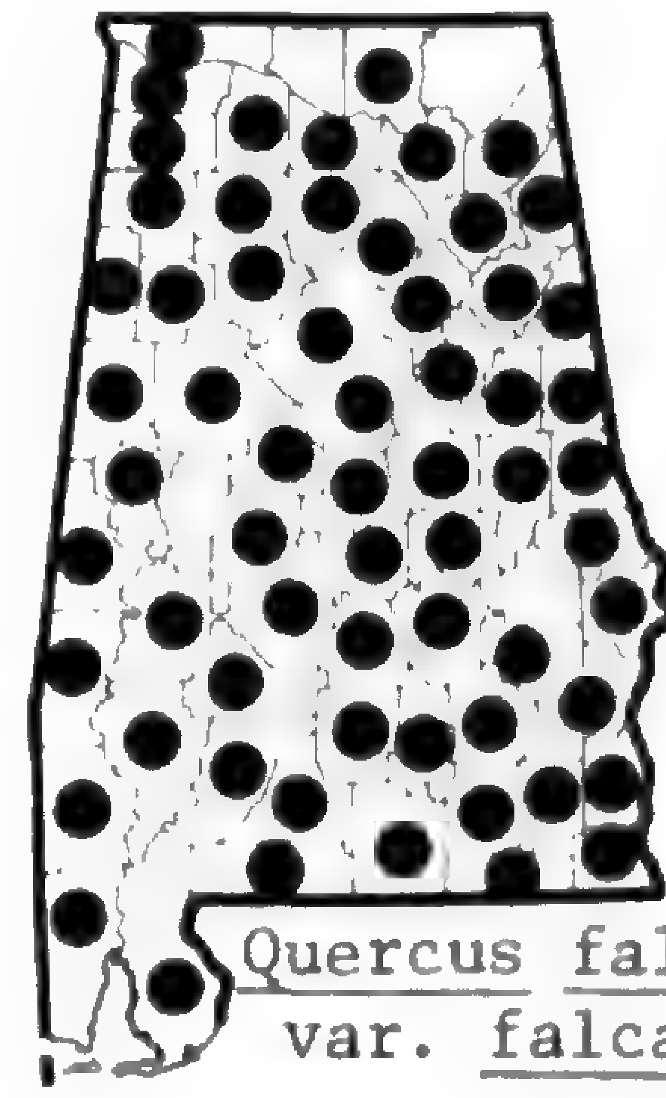
12. *Q. laurifolia* Michaux, LAUREL O. Spring; fall. Mesic woods; CP, P (rare), CuP. *Q. obtusa* (Willd.) Ashe—H, S.—The conjunctive status of this species and of *Q. nigra* L. and *Q. phellos* L. is worthy of further study.



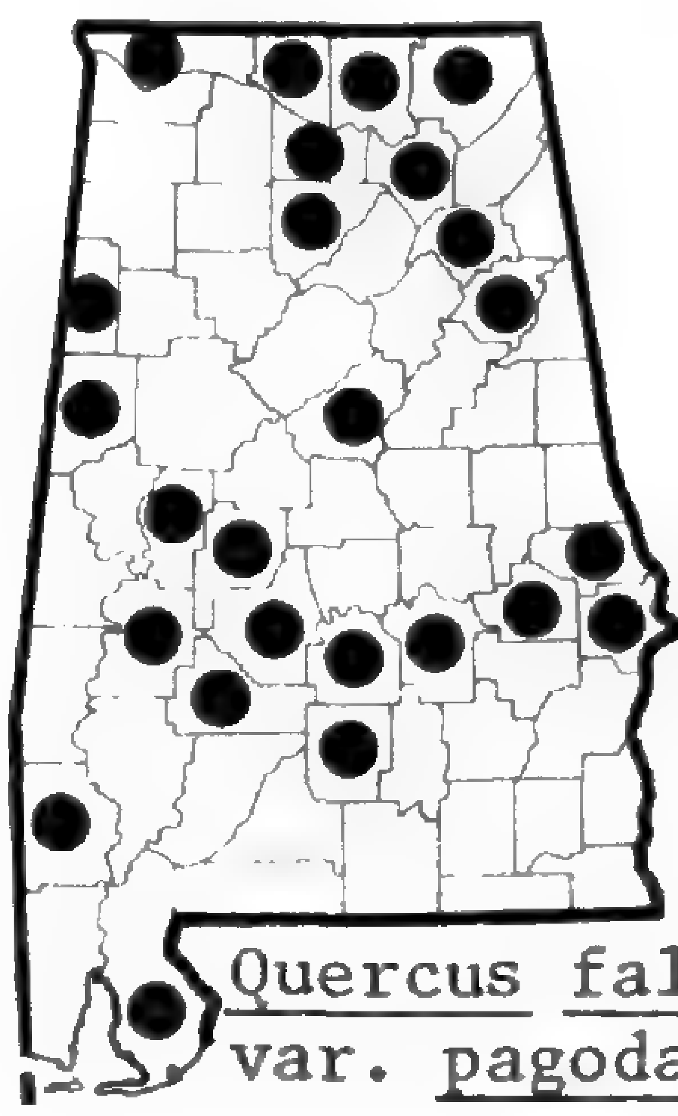
Quercus durandii var. durandii



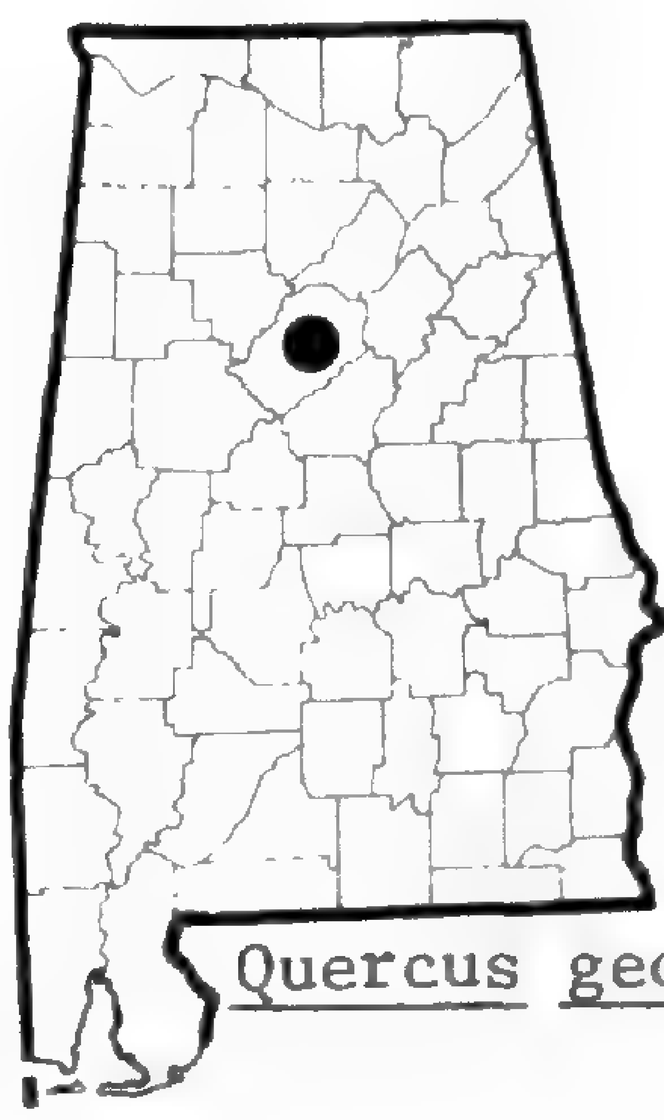
Quercus durandii var. austrina



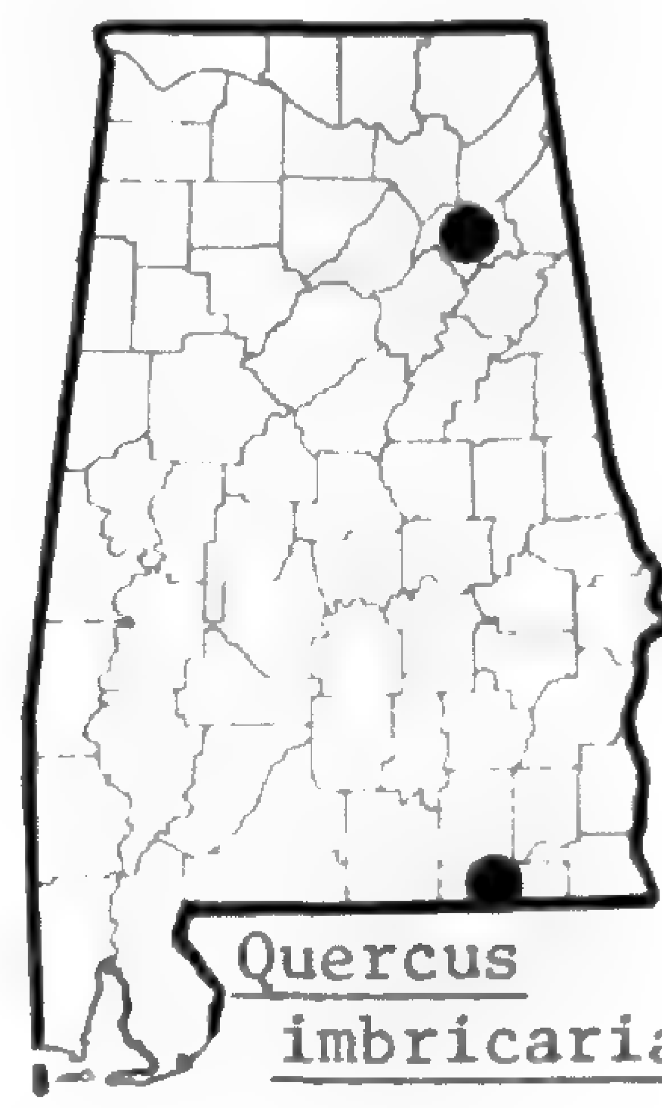
Quercus falcata var. falcata



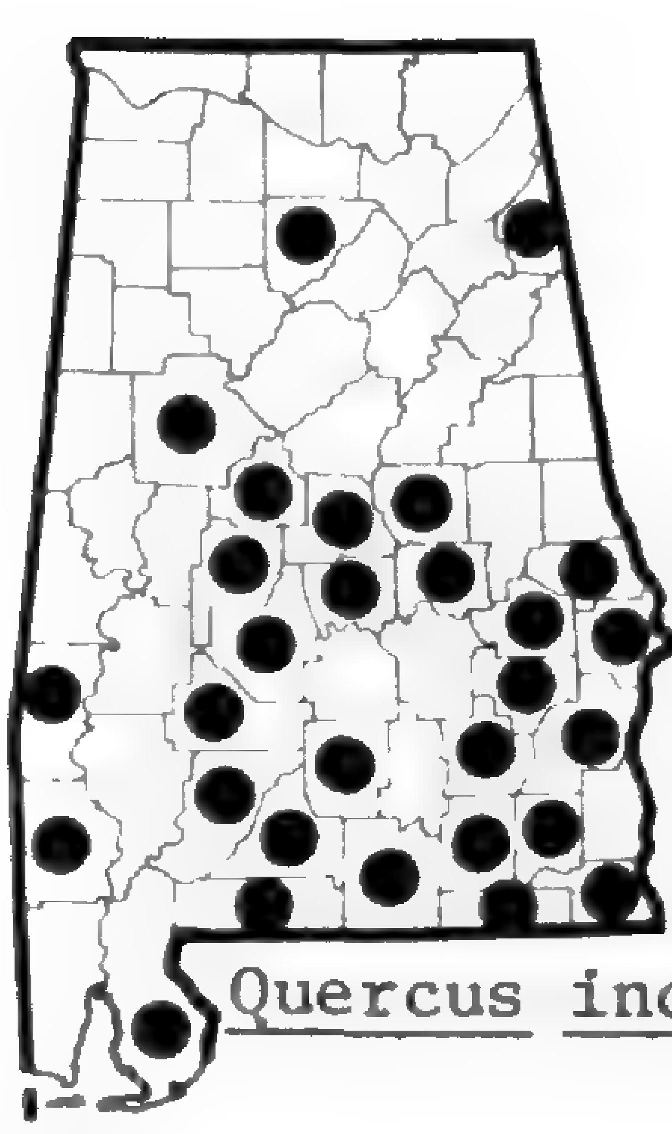
Quercus falcata var. pagodaefolia



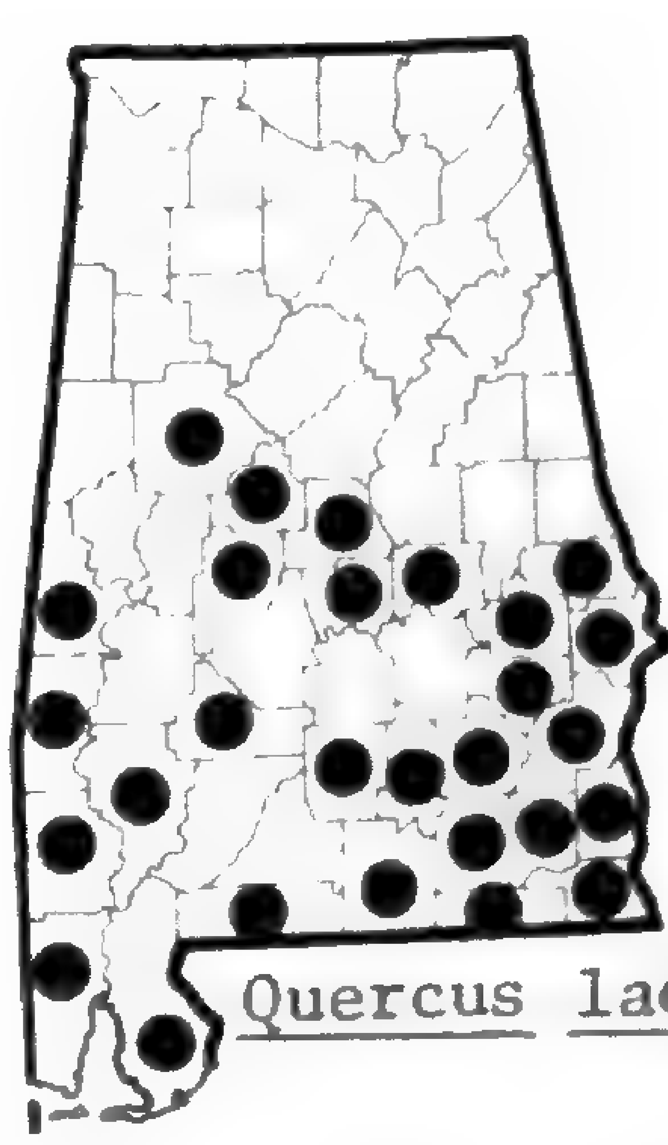
Quercus georgiana



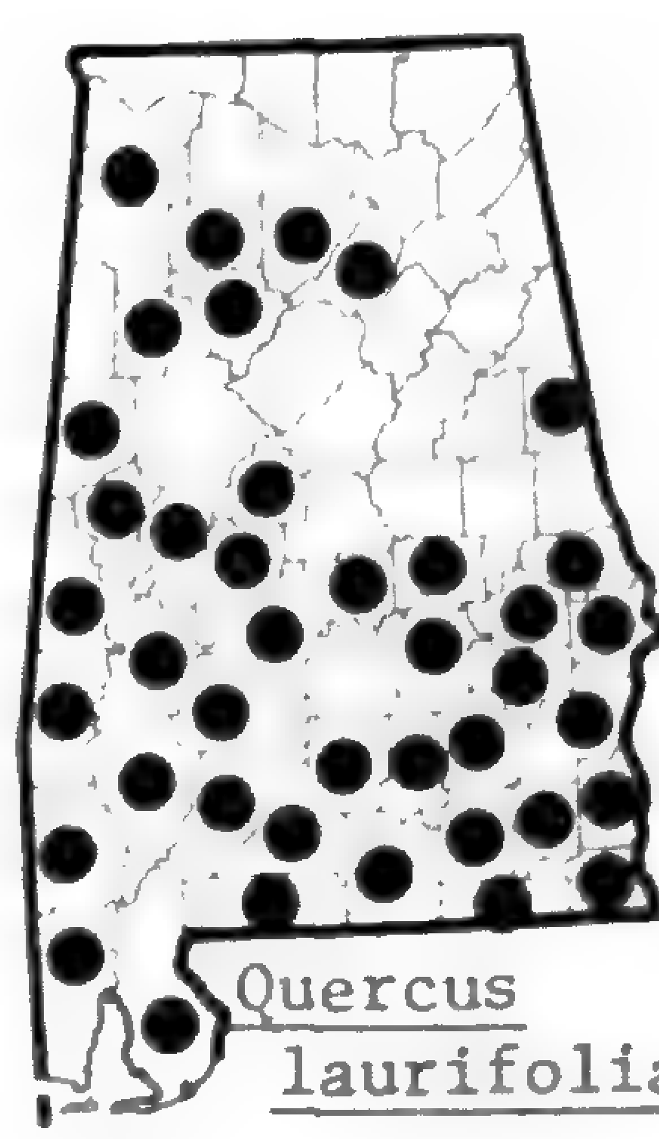
Quercus imbricaria



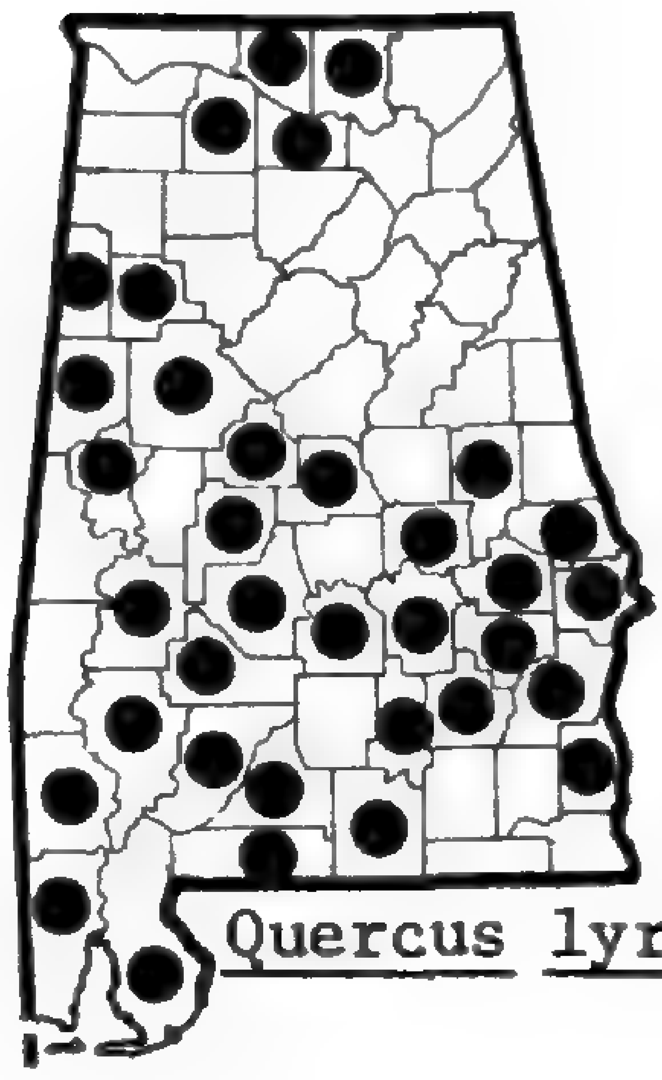
Quercus incana



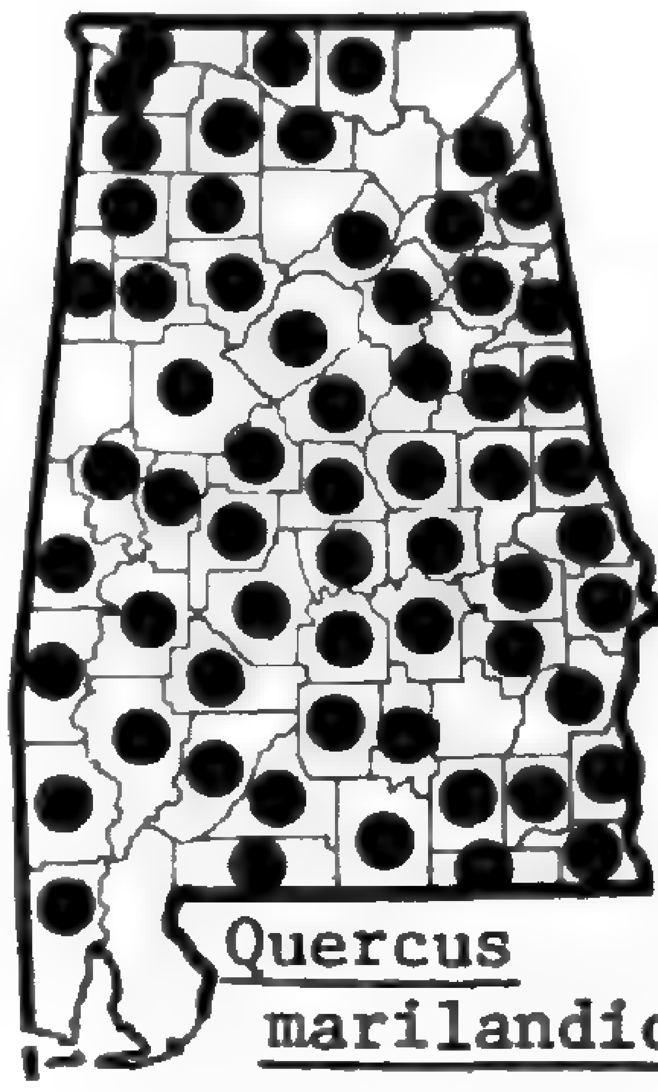
Quercus laevis

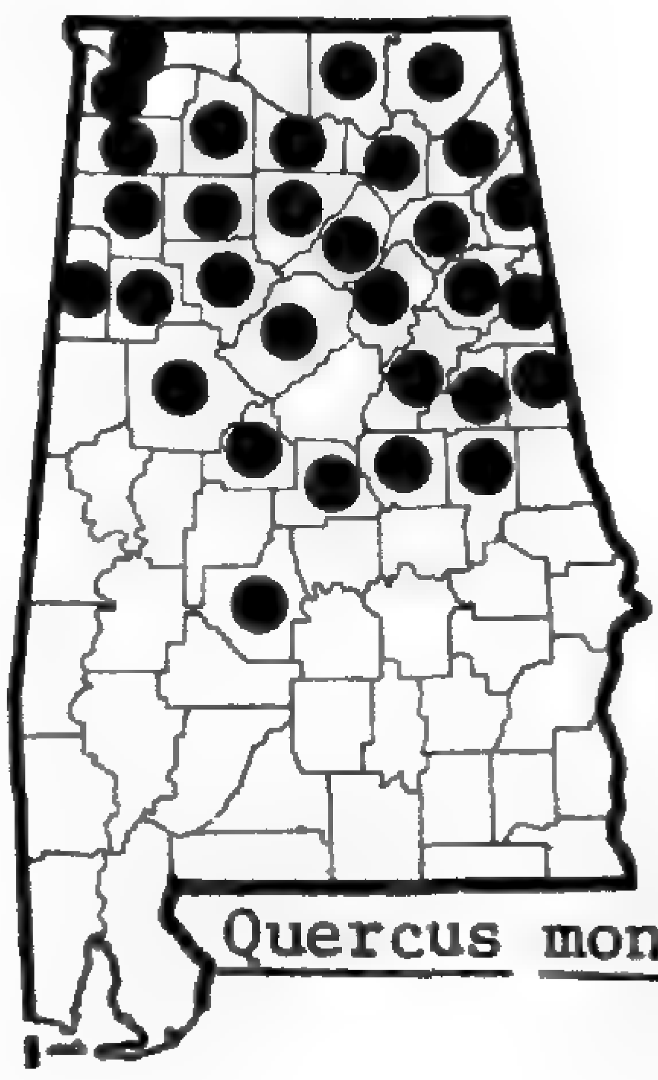


Quercus laurifolia

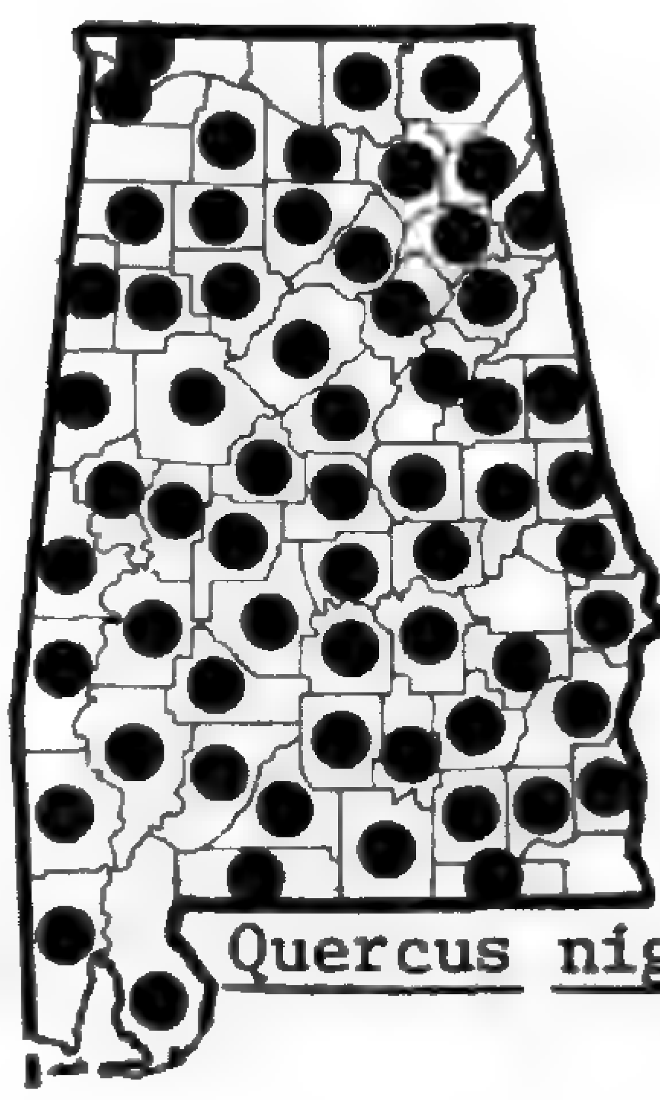

Quercus lyrata

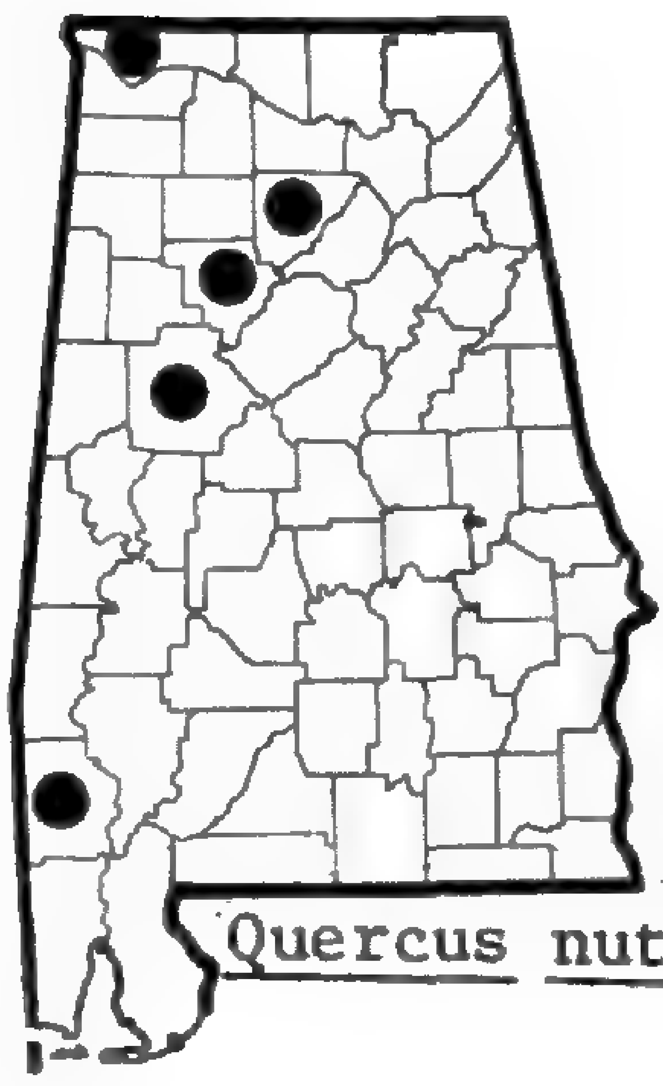

Quercus macrocarpa

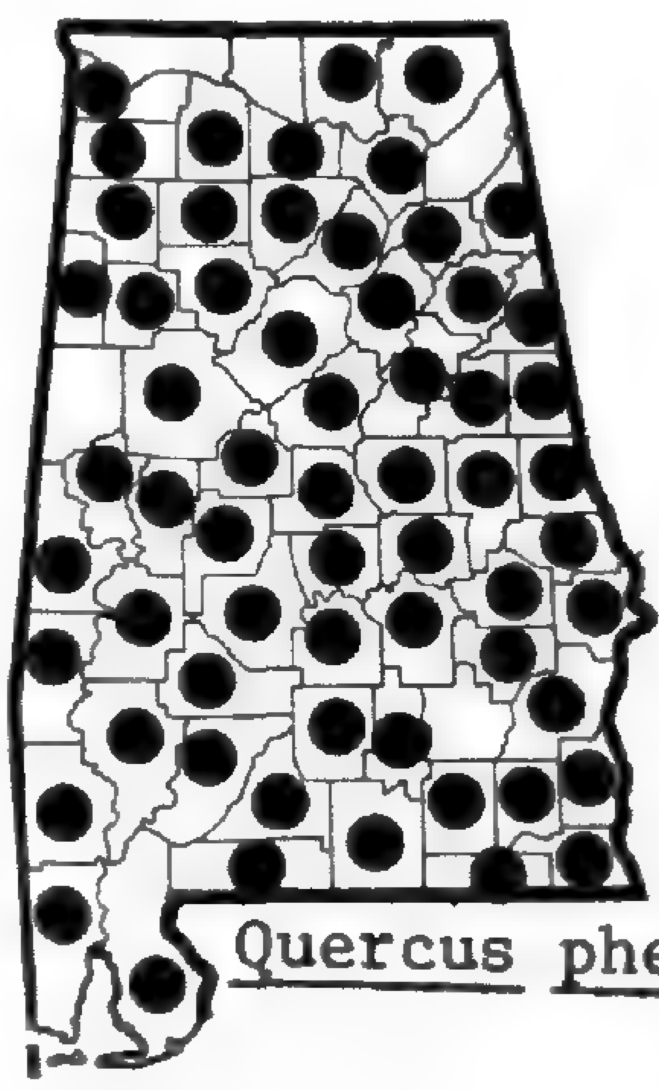

Quercus marilandica

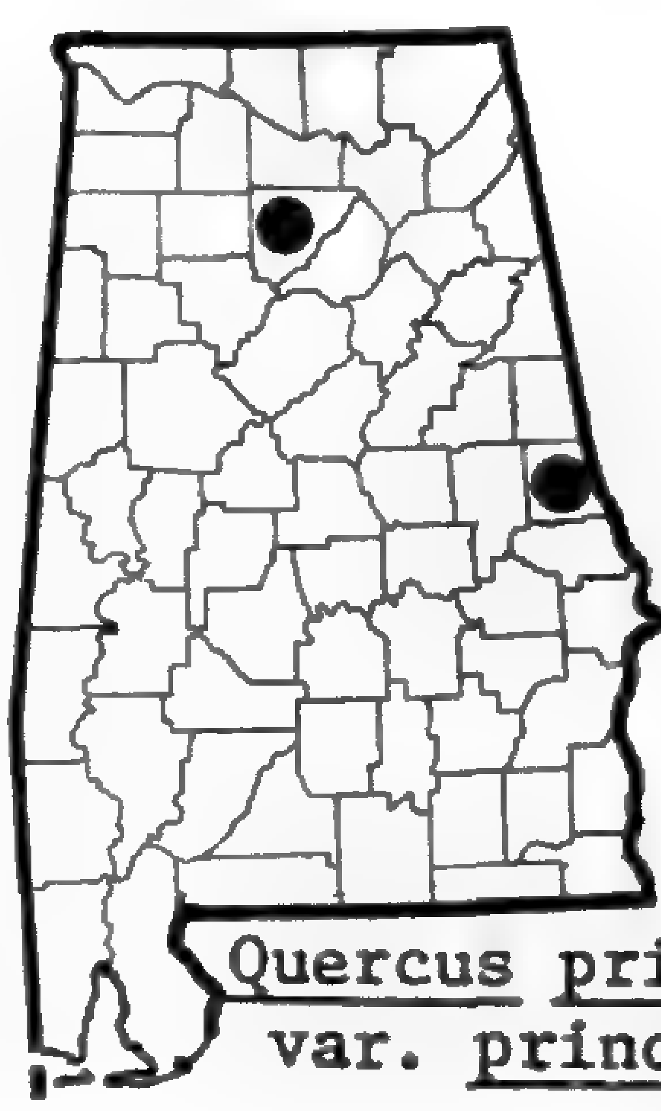

Quercus montana


Quercus myrtifolia


Quercus nigra


Quercus nuttallii


Quercus phellos


Quercus prinoides var. prinoides

13. *Q. lyrata* Walter, OVERCUP O. Spring; fall. Alluvial woods and swamps; CP, HR.

14. *Q. macrocarpa* Michaux, BUR O. Spring; fall. Pasture, very rare; Black Belt of CP.

15. *Q. marilandica* Muenchh., BLACKJACK O. Spring; fall. Upland woods; throughout.—*Q. marylandica* is a spelling employed by some authors.

16. *Q. montana* Willd., CHESTNUT O. Spring; fall. Upland woods; throughout, except for southern CP. *Q. prinus* L.—RAB.

17. *Q. myrtifolia* Willd., MYRTLE O. Late winter–early spring; fall. Dunes, sandy woods and thickets; OCP.

18. *Q. nigra* L., WATER O. Spring; fall. Mesic and low woods; throughout. See comment under *Q. laurifolia.*

19. *Q. nuttallii* Palmer. Spring; fall. River swamps, alluvial woods, infrequent; CP, southern CuP. *Q. texana* Buckl.—M, in part.—This species appears to be confined to the western half of Alabama. Occasionally planted.

20. *Q. phellos* L., WILLOW O. Spring; fall. Alluvial and mesic woods; throughout. See comment under *Q. laurifolia.*

21. *Q. prinoides* Willd. Spring; fall.

1. Plant shrubby, soboliferous .... *Q. prinoides* var. *prinoides*
1. Plant arborescent .... *Q. prinoides* var. *acuminata*

Q. prinoides Willd. var. *prinoides*, DWARF CHINKAPIN O. Upland thickets, very rare; P, CuP.

Q. prinoides var. *acuminata* (Michaux) Gleason, CHINKAPIN O. Mesic or dry woods, usually over calcareous substrata; throughout, except rare or absent in southern CP. Much more common than the typical variety. *Q. acuminata* (Michx.) Sarg.—M; *Q. muehlenbergii* Engelm.—H, S, RAB.

22. *Q. prinus* L., SWAMP CHESTNUT O., BASKET O. Spring; fall. River swamps, alluvial woods; CP, VR (rare), CuP (rare), HR. *Q. michauxii* Nutt.—M, H, RAB.

23. *Q. pumila* Walter. Spring; fall. Thickets, low pinelands; OCP.

24. *Q. rubra* L., RED O., NORTHERN RED O. Spring; fall. Mesic woods; throughout, but infrequent southward. *Q. borealis maxima* (Marsh.) Sarg. or Ashe[3]—H; *Q. maxima* (Marsh.) Ashe, *Q. borealis* Michx. f.—S; *Q. rubra* var. *borealis* (Michx. f.) Farw.—RAB.

25. *Q. shumardii* Buckley, SHUMARD'S O. Spring; fall. Mesic and alluvial woods; throughout, except rare in southern CP. *Q. texana* Buckl.—M, in part; *Q. schneckii* Britt.—H, S.

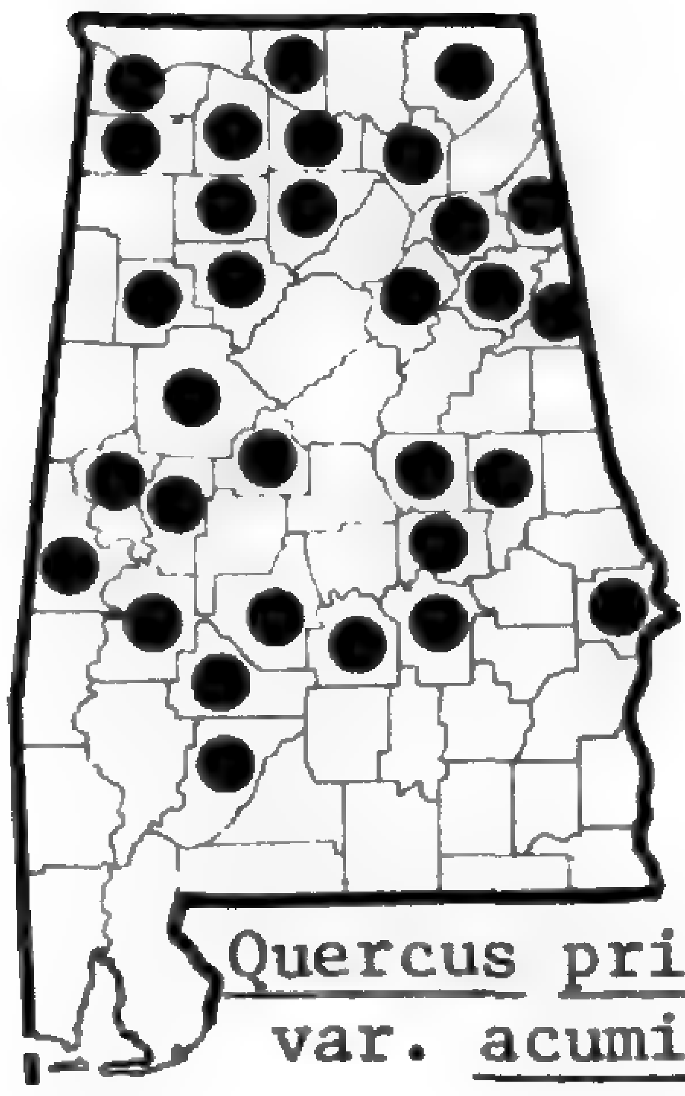
26. *Quercus stellata* Wang. Spring; fall.

1. Twigs tomentose; petioles usually more than 1 cm long .... *Q. stellata* var. *stellata*
1. Twigs glabrous; petioles usually less than 1 cm long .... *Q. stellata* var. *margaretta*

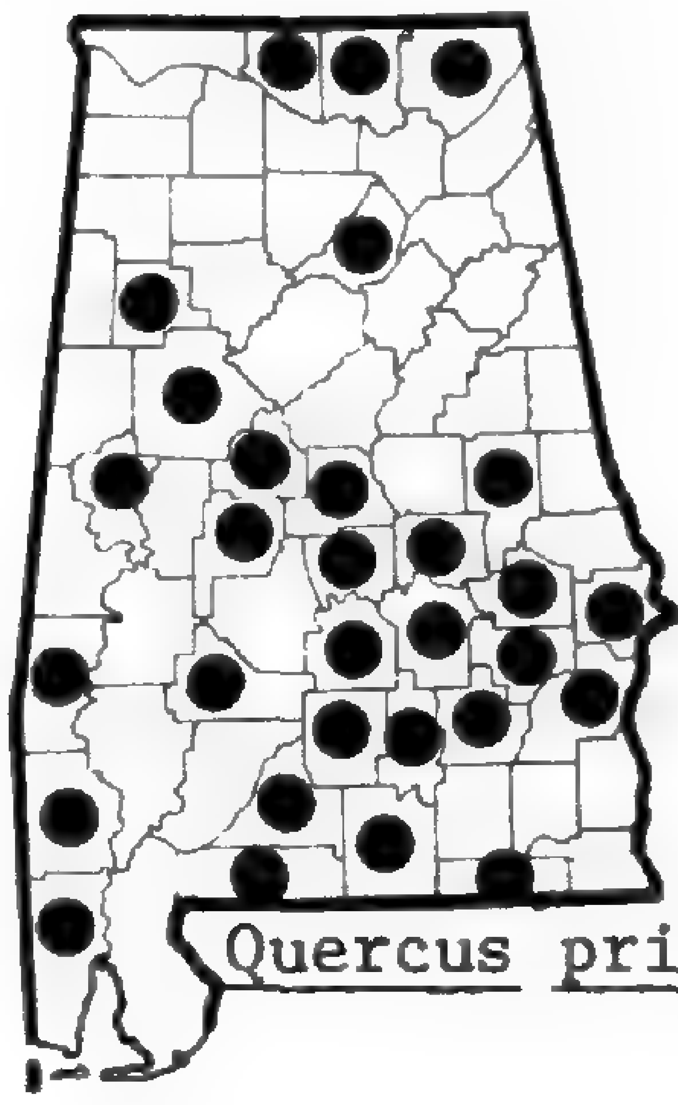
Q. stellata var. *stellata*, POST O. Upland and mesic woods; throughout. *Q. minor* (Marsh.) Sarg.—M.

Q. stellata var. *margaretta* (Ashe) Sargent, DWARF POST O. Upland woods, dry thickets; CP, southern CuP, VR. *Q. margaretta* Ashe—S, RAB.—Although

[3] See citation and footnote of Harper (1928:124.).

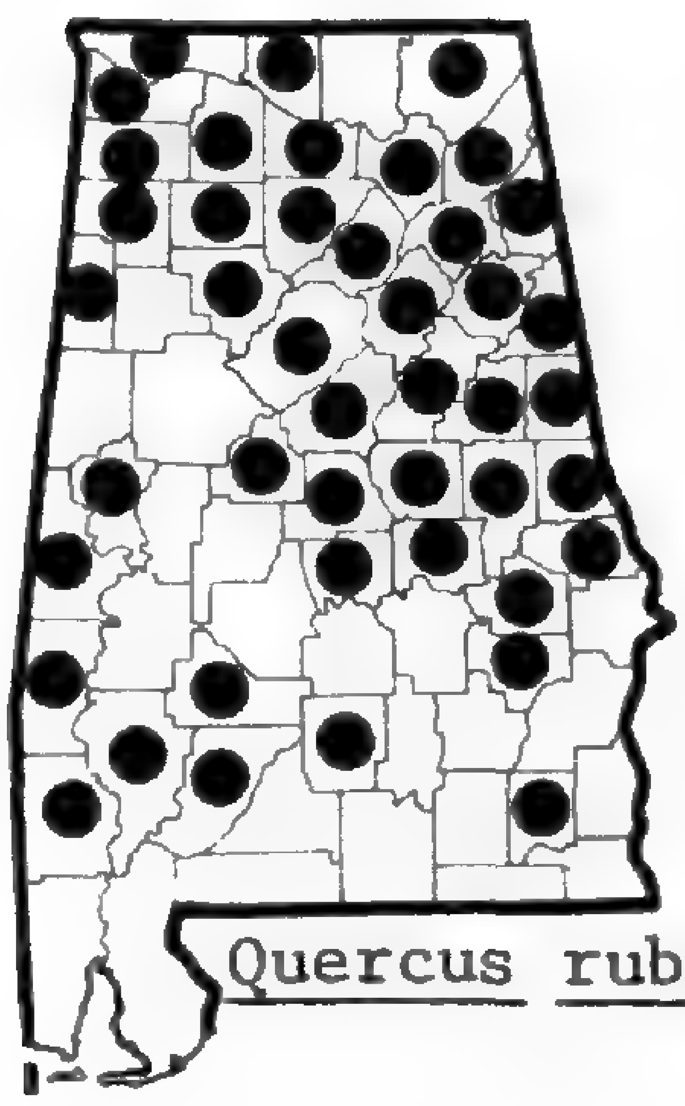


Quercus prinoides var. acuminata

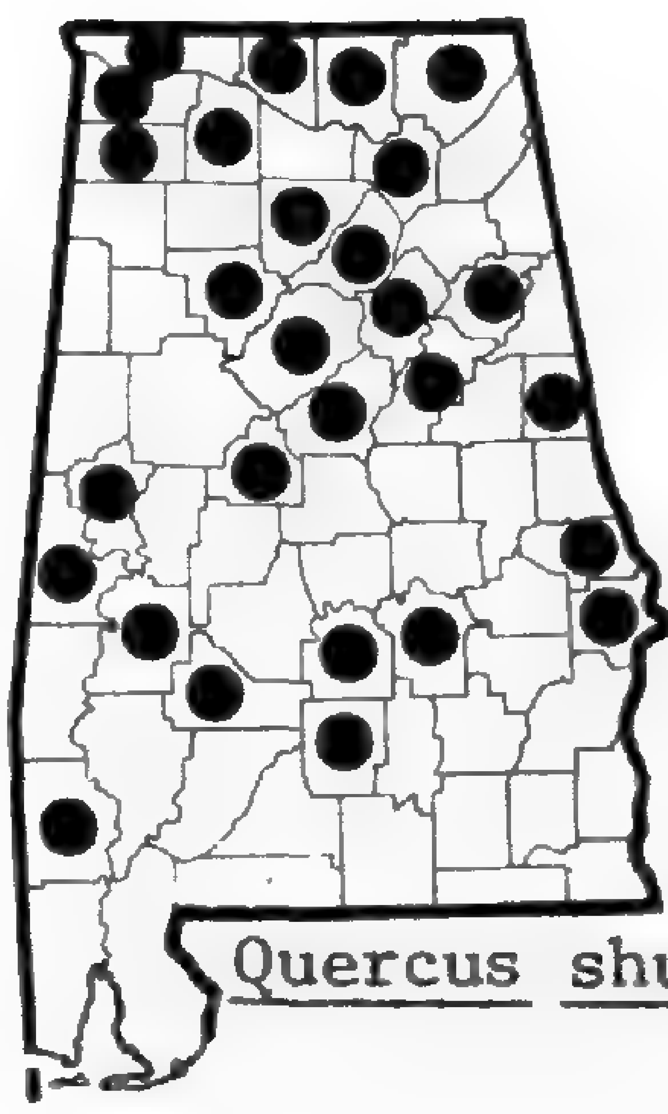


Quercus prinus

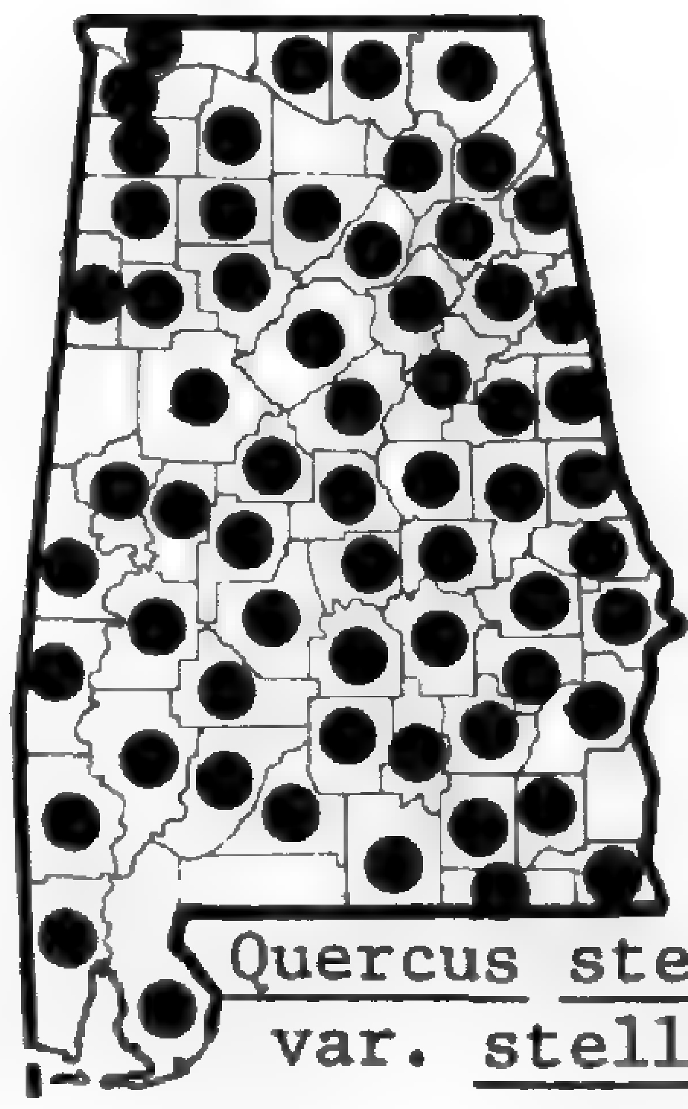
Quercus pumila



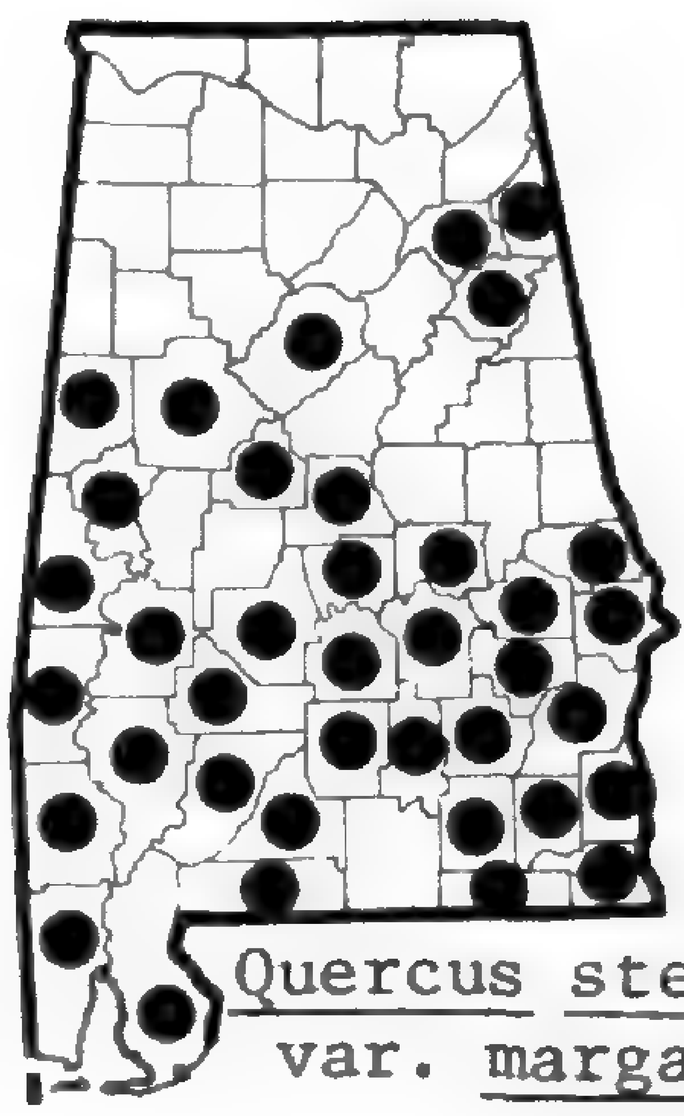
Quercus rubra



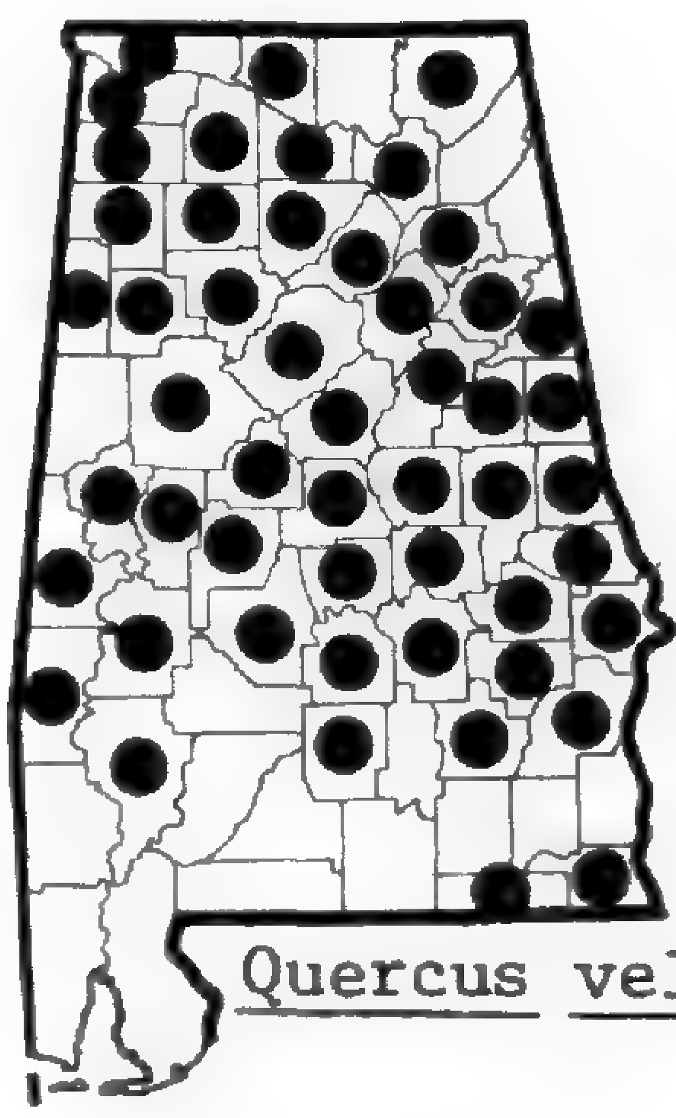
Quercus shumardii



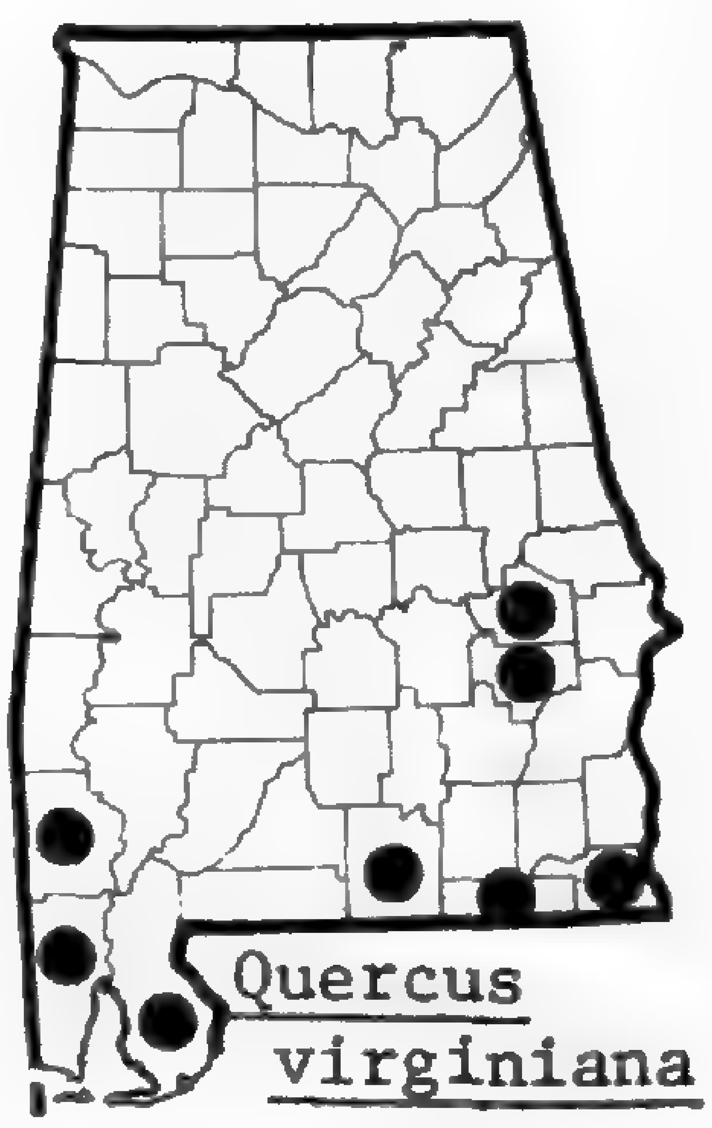
Quercus stellata var. stellata



Quercus stellata var. margaretta



Quercus velutina



Quercus virginiana

this variety is usually of smaller size than the typical variety, the writer has seen trees more than 2 feet in diameter (DBH) in southern Alabama. This variety appears more distinct than it actually is because of a consistently smaller average leaf size than the typical variety displays. This rather subjective difference is the usual method of differentiating the two taxa. Populations of *Q. stellata* var. *margaretta* in the Valley and Ridge Province have been called *Q. boyntonii* Bead., but they differ in no consistent or significant way from the main series of populations in the Coastal Plain. Other "coastal plain oaks" (*Q. incana* Bartr., *Q. prinus* L., *etc.*) also occur in the Valley and Ridge Province, and also appear little-diverged from their main genetic stocks.

27. *Q. velutina* Lam., Black O. Spring; fall. Dry and mesic woods; throughout, but rare in southern CP.

28. *Q. virginiana* Miller, Live O. Spring; fall. Sandy woods; OCP. Occasionally planted and rarely escaped further inland. *Q. virginiana maritima* (Michx.) Sarg.—M; *Q. geminata* Sm.—H, S; *Q. minima* Sm.—H, S.

12. Ulmaceae

1. Fruit drupaceous; leaves with 3 principal veins .... 1. *Celtis*
1. Fruit samaroid or bur-like; leaves with a single principal vein 2
   2. Fruit a bur-like nut or nutlet .... 2. *Planera*
   2. Fruit a samara .... 3. *Ulmus*

1. *Celtis* L., Hackberry, Sugarberry

1. Leaves of fertile branches lanceolate, 2 times or more as long as wide, uniformly green on both surfaces, serrate to entire .... 1. *C. laevigata*
1. Leaves of fertile branches ovate to ovate-lanceolate, usually less than 2 times as long as wide, clearly darker in color above than beneath, serrate-dentate to entire .... 2. *C. occidentalis* complex

1. *C. laevigata* Willd. Spring; summer–fall. Low, alluvial, or mesic woods; throughout. *C. mississippiensis* Bosc—M, S; *C. smallii* Bead.—S.

2. *C. occidentalis* L., complex. Spring; summer–fall. Deciduous woods, thickets, throughout. *C. occidentalis pumila* (Pursh) Gray—M; *C. pumila* Pursh—H; *C. georgiana* Sm.—S; *C. occidentalis* var. *georgiana* (Sm.) Ahles—RAB.

2. *Planera* Gmelin, Water Elm

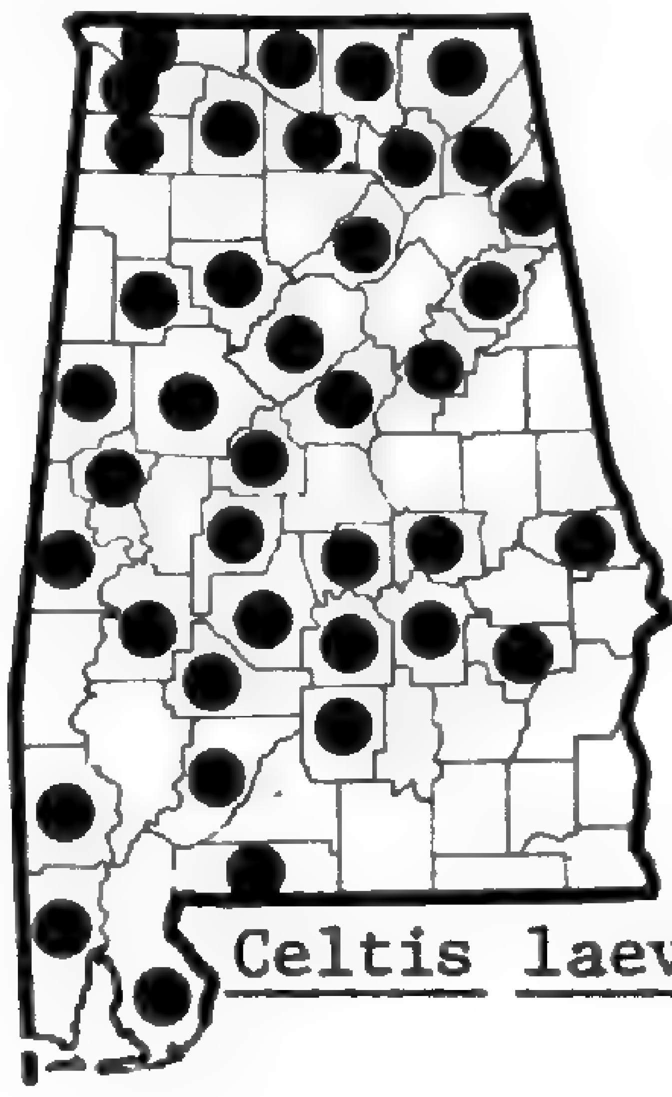
1. *P. aquatica* Gmelin. Spring. Riverbanks, swamps, infrequent; principally CP.

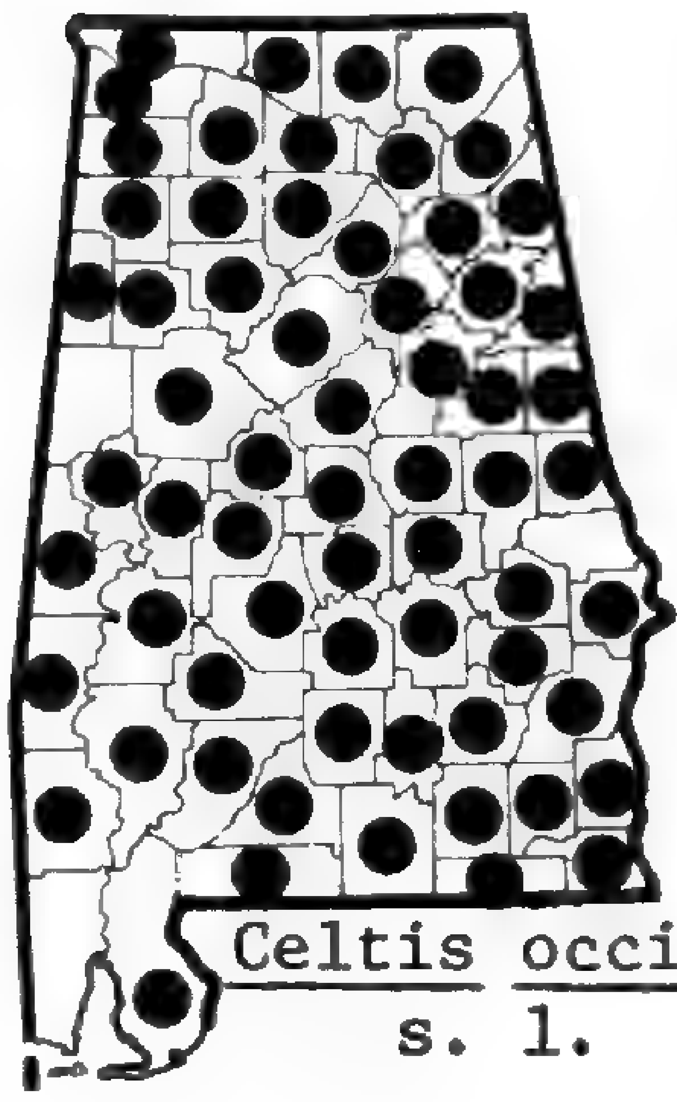
3. *Ulmus* L., Elm

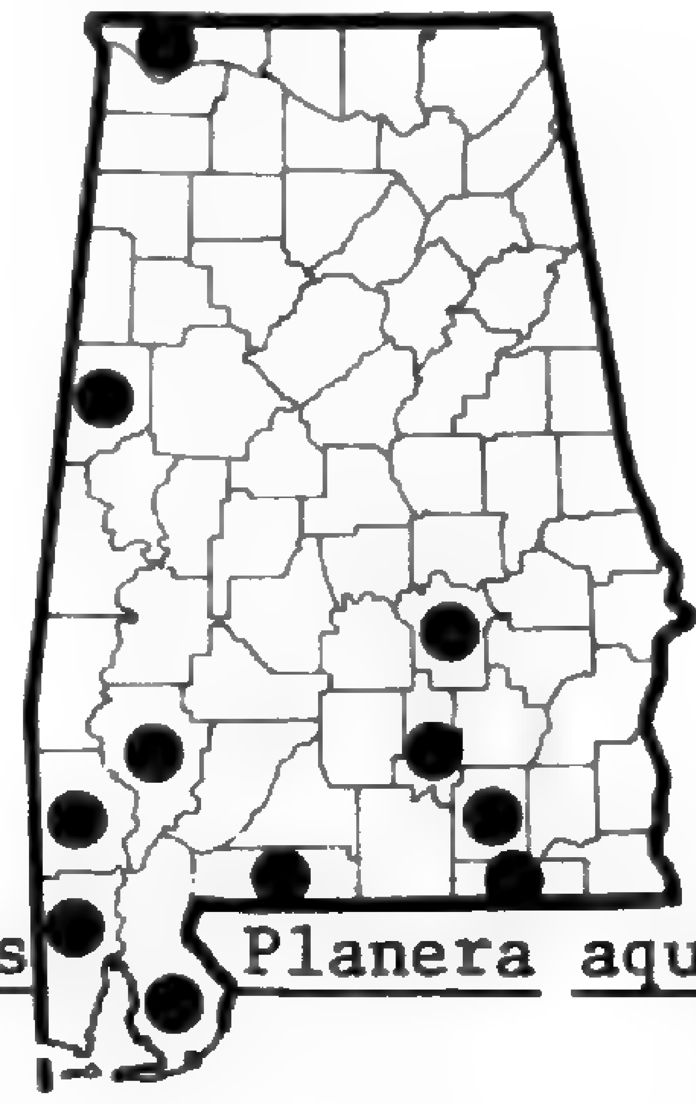
1. Flowers and fruits vernal 2
   2. Inflorescence racemose; samara prominently ciliate 3
      3. Faces of ovary and fruit pubescent .... 1. *U. alata*
      3. Faces of ovary and fruit glabrous .... 2. *U. americana*
   2. Inflorescence fasciculate; samara eciliate, or remotely ciliate .... 3. *U. rubra*
1. Flowers and fruits autumnal .... 4. *U. serotina*

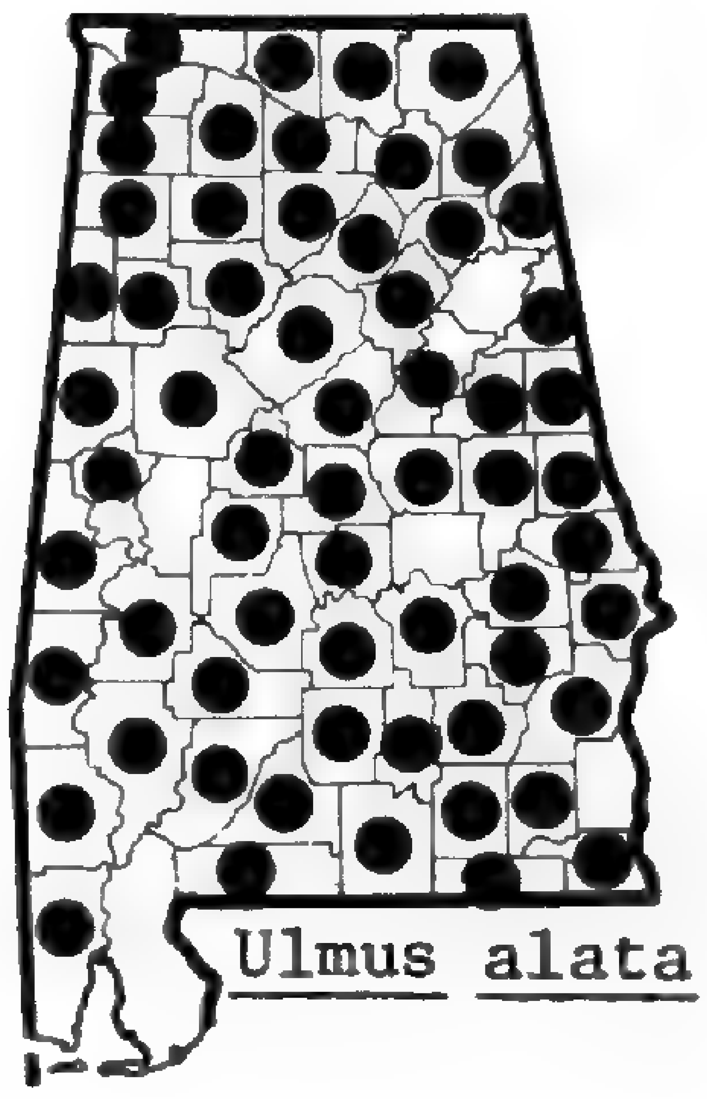
1. *U. alata* Michaux, Winged E., Piss E. Late winter–spring; spring. Upland or low woods; throughout.

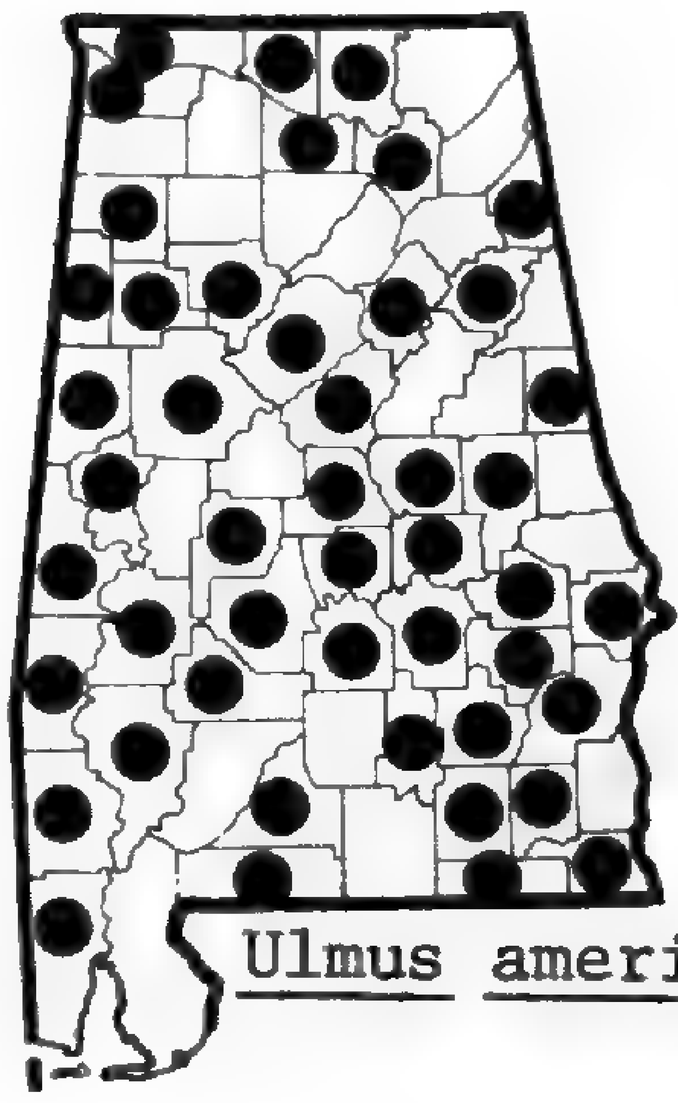
12. ULMACEAE

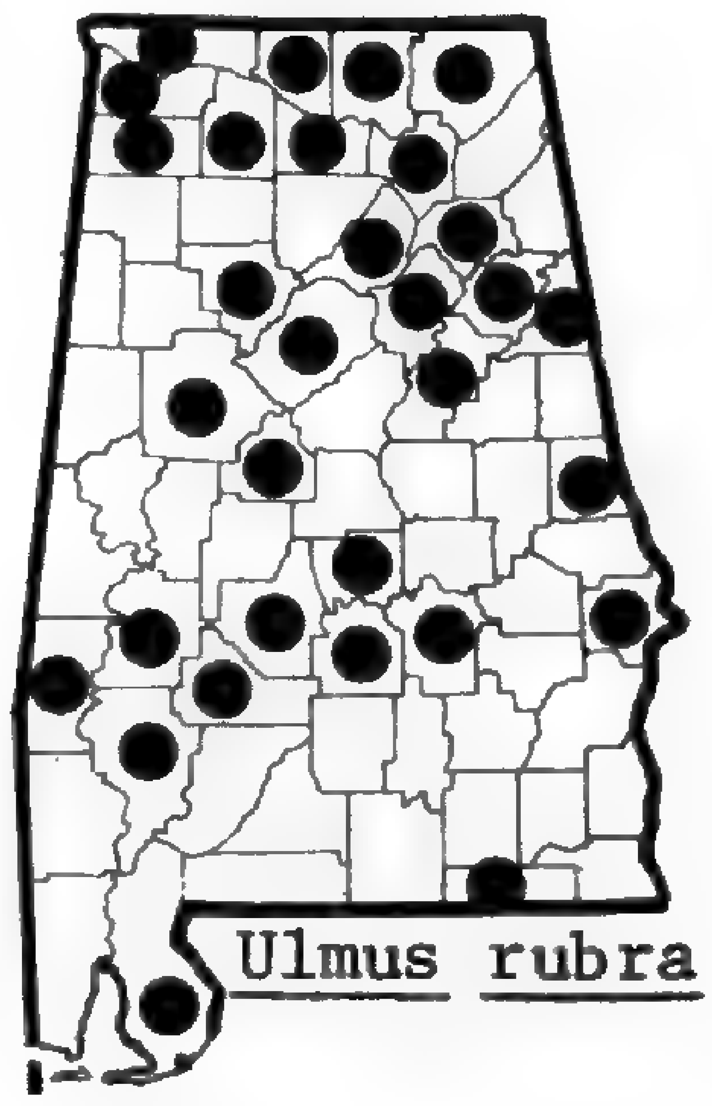

Celtis laevigata


Celtis occidentalis s. l.


Planera aquatica

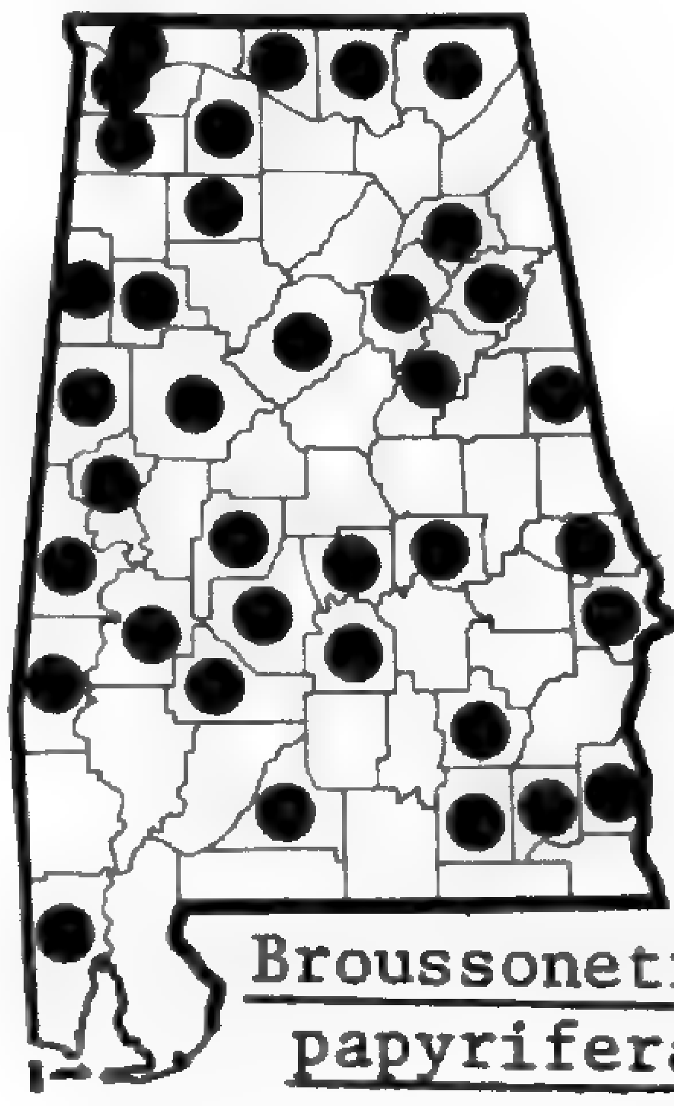

Ulmus alata

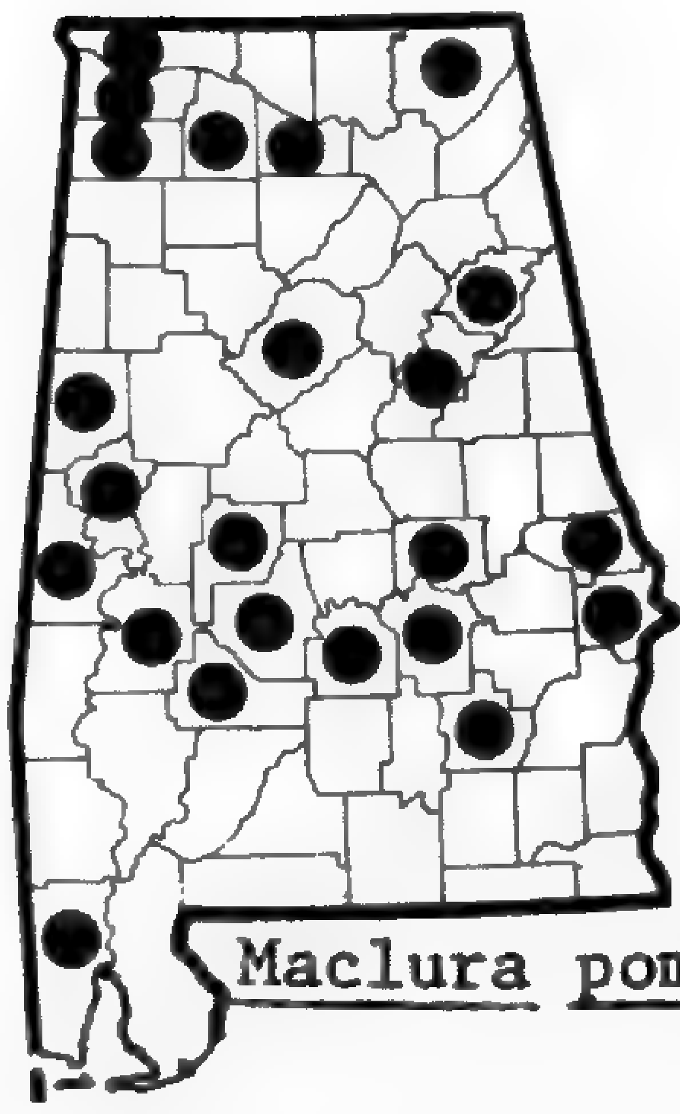

Ulmus americana


Ulmus rubra


Ulmus serotina

13. MORACEAE


Broussonetia papyrifera


Maclura pomifera

2. *U. americana* L., WHITE E., AMERICAN E. Late winter–spring; spring. Alluvial, low or mesic woods; throughout.

3. *U. rubra* Muhl., SLIPPERY E., RED E. Late winter–spring; spring. Rich woods, usually over calcareous substrata; throughout. *U. fulva* Michx.—M, H, S.

4. *U. serotina* Sargent. Fall. Rich woods, rare; VR, CuP, HR.

13. MORACEAE

1. Leaves entire; stipular thorns often present .... 2. *Maclura*
1. Leaves dentate; stipular thorns absent 2
   2. Twigs and petioles densely hirsute .... 1. *Broussonetia*
   2. Twigs and petioles glabrous or cinereous .... 3. *Morus*

1. *Broussonetia* L'Her, PAPER MULBERRY

1. *B. papyrifera* (L.) Vent. Spring; fruit not seen. Woodlots, fencerows, waste places; throughout. *Papyrius papyrifera* (L.) Kuntze—H, S.

2. *Maclura* Nuttall

1. *M. pomifera* (Rafinesque) Schneider, OSAGE ORANGE, MOCK ORANGE, BOIS D'ARC (commonly pronounced "bo-darc"). Spring; summer–fall. Upland woods, infrequent except in Black Belt; throughout. *Toxylon pomiferum* Raf.—M, H, S.

3. *Morus* L., MULBERRY

1. Leaves glabrous beneath, or pubescent only on the principal veins .... 1. *M. alba*
1. Leaves pubescent beneath throughout .... 2. *M. rubra*

1. *M. alba* L., WHITE M. Spring; late spring–early summer. Infrequent escape; throughout.

2. *M. rubra* L., RED M., (common) M. Spring; late spring–early summer. Alluvial and mesic woods, fencerows; throughout.

Ficus carica L., FIG, is rarely persistent but not established as a member of the flora.

14. SANTALACEAE

1. Leaves opposite or subopposite, entire .... 1. *Nestronia*
1. Leaves alternate, usually irregularly serrate .... 2. *Pyrularia*

1. *Nestronia* Raf.

1. *N. umbellula* Rafinesque. Spring; summer. Sandy woods-margins, rare; CP, P, CuP. *N. umbellulata* Raf.—M, H.

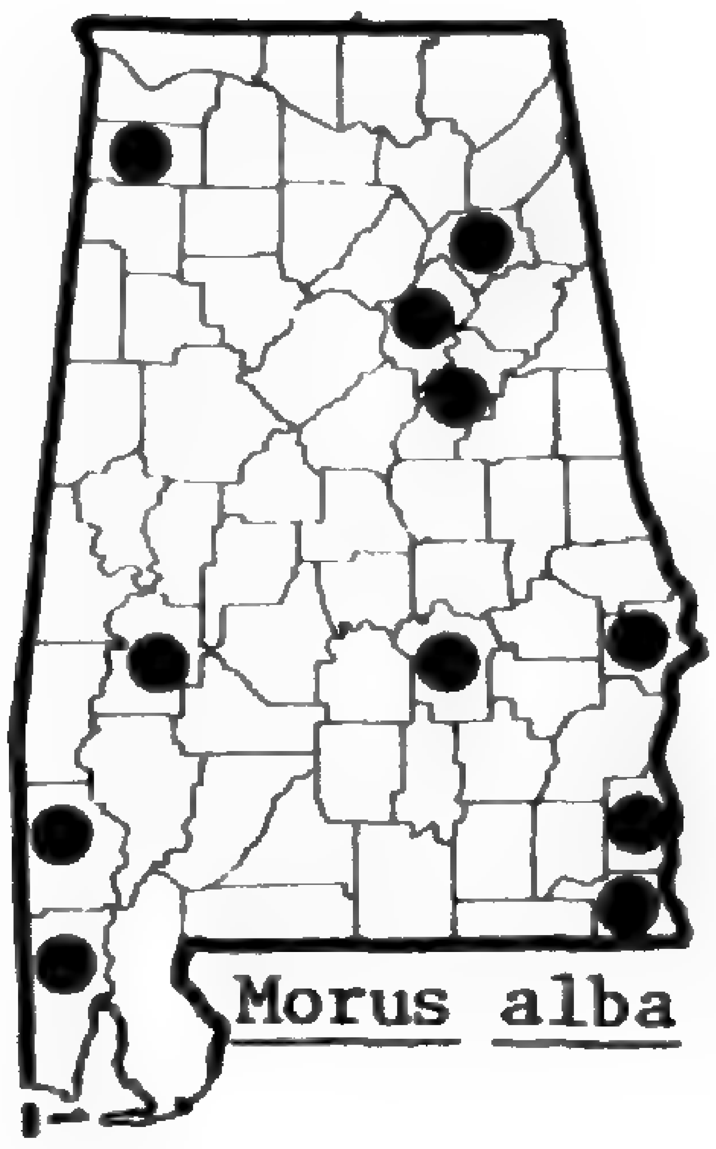
2. *Pyrularia* Michaux

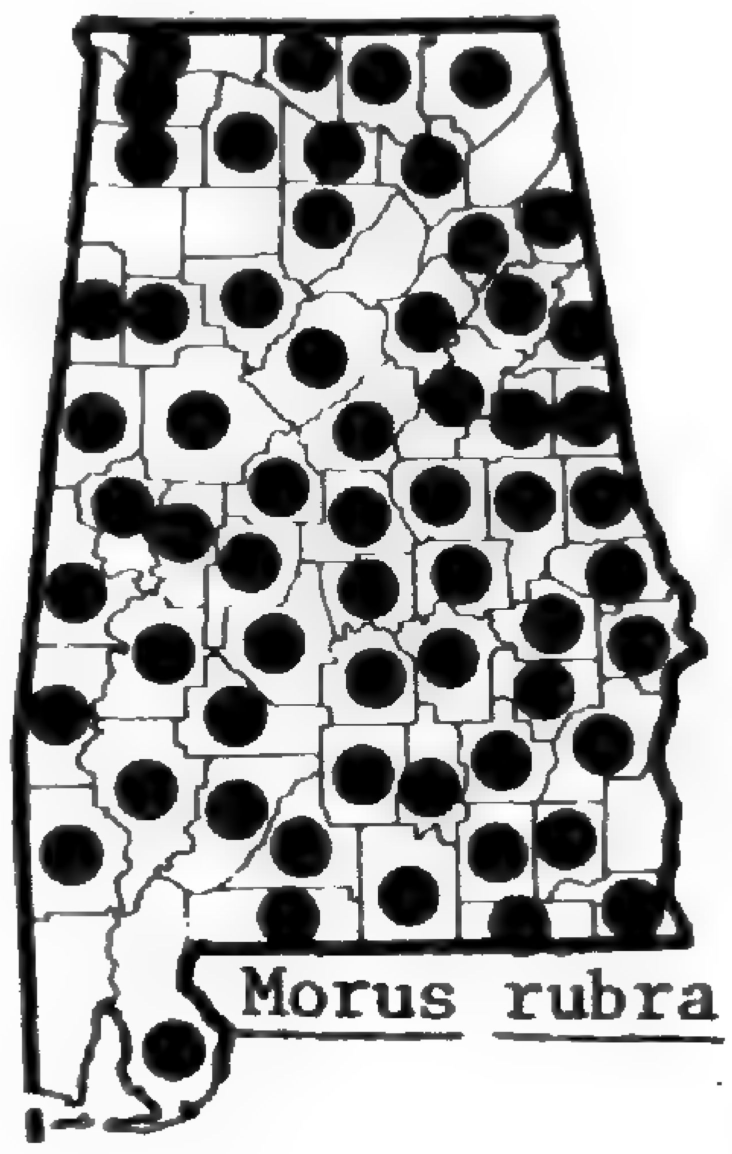
1. *P. pubera* Michaux. Spring; fall. Alluvial woods, rare; AM, CuP.

15. LORANTHACEAE

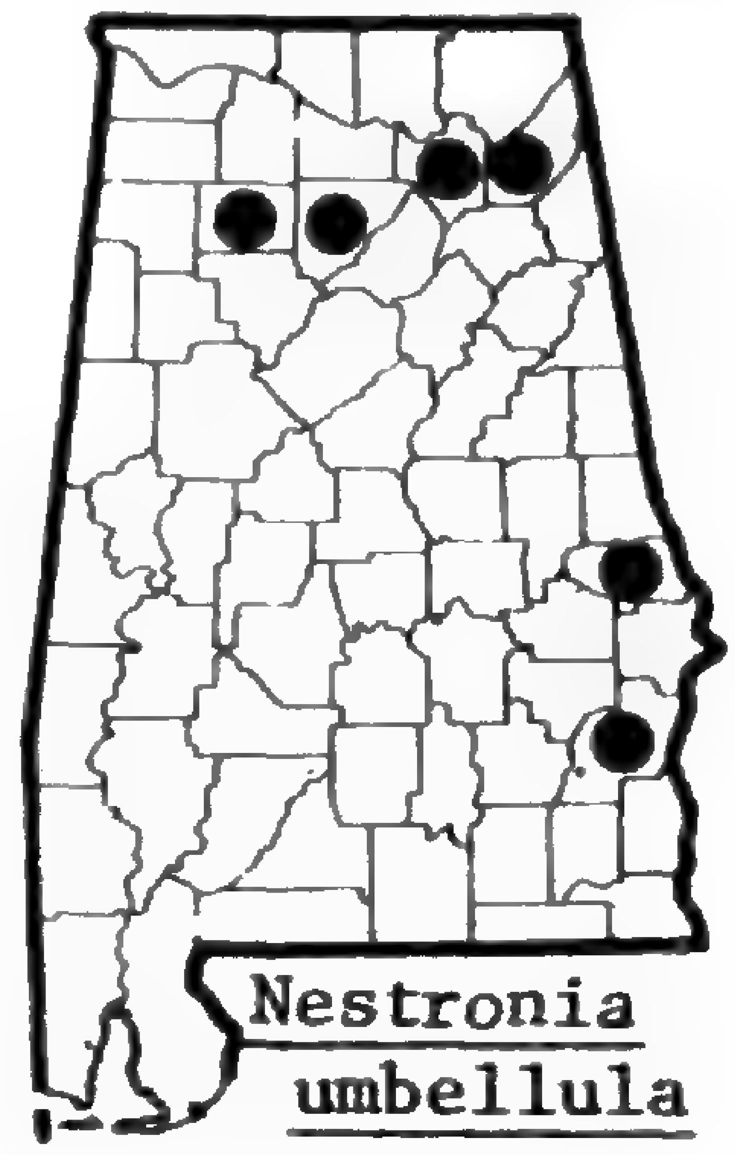
1. *Phoradendron* Nuttall, MISTLETOE

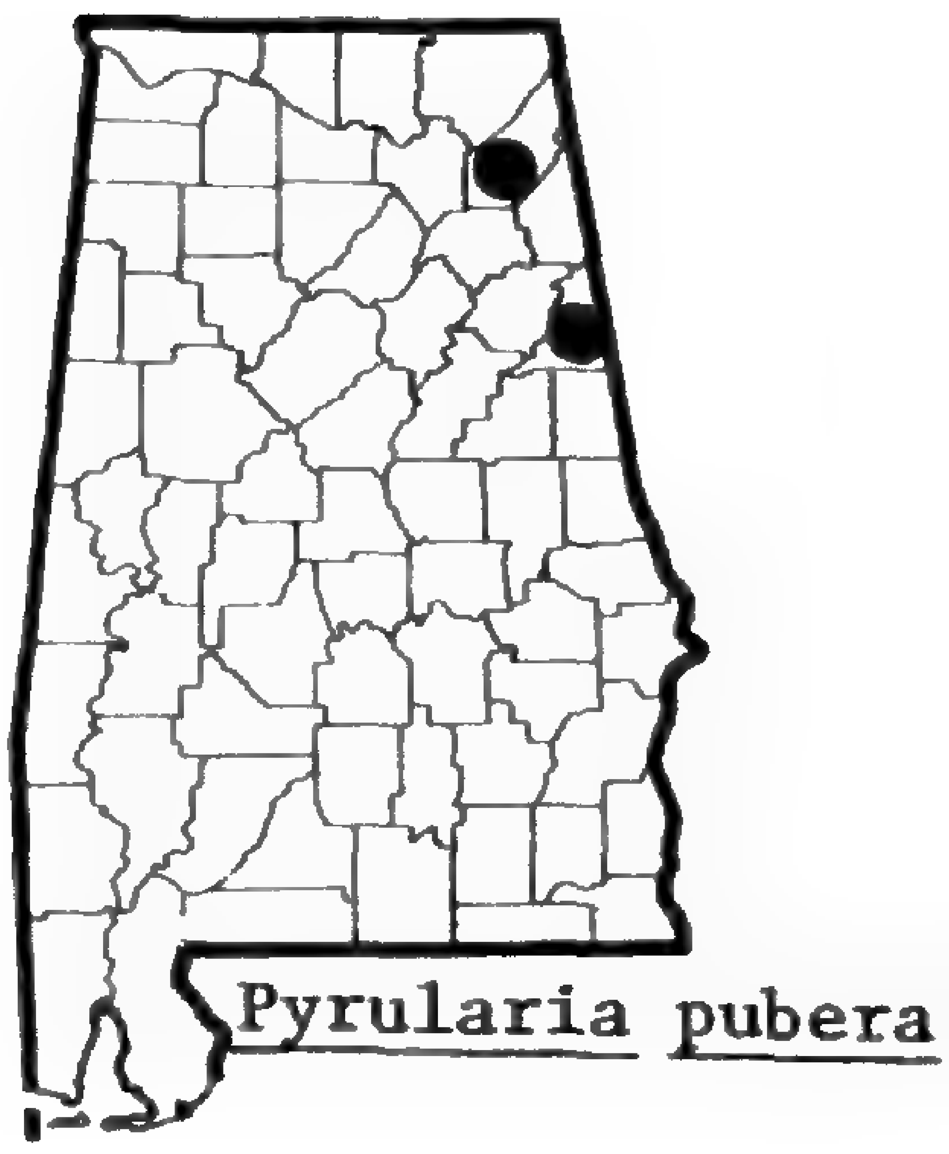
1. *P. serotinum* (Rafinesque) Johnston. Late winter–early spring; winter. On



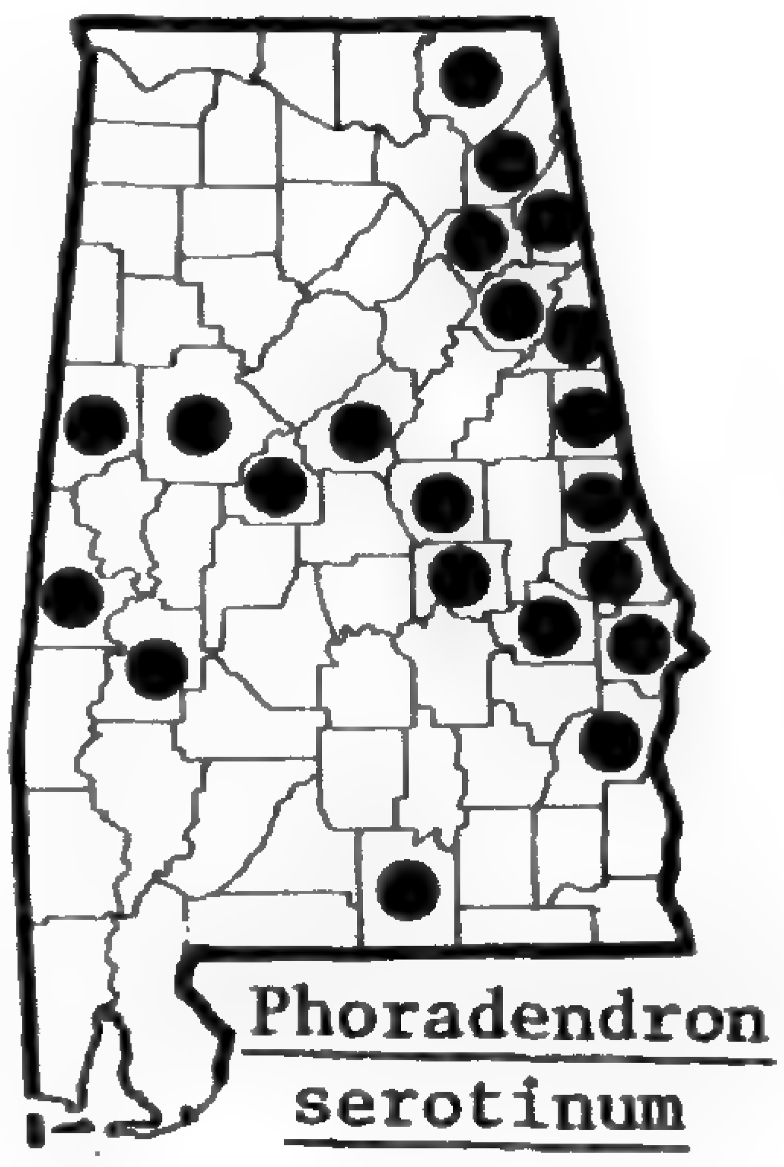


14. SANTALACEAE

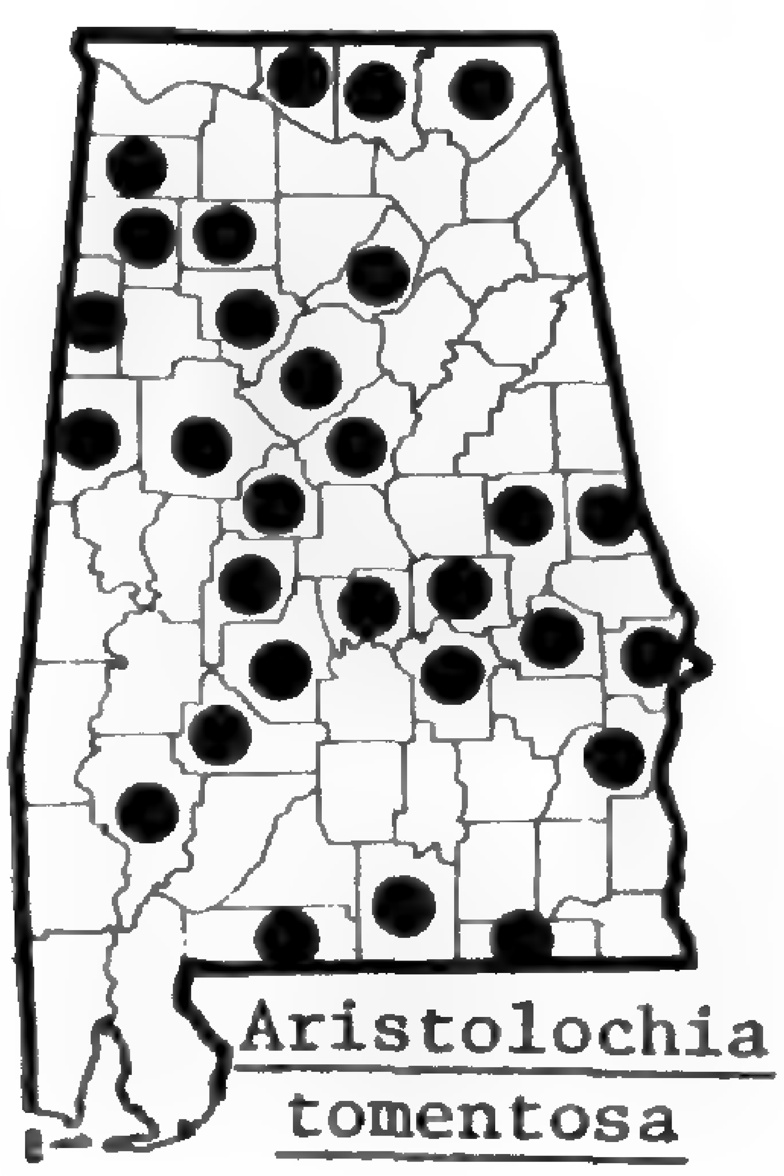




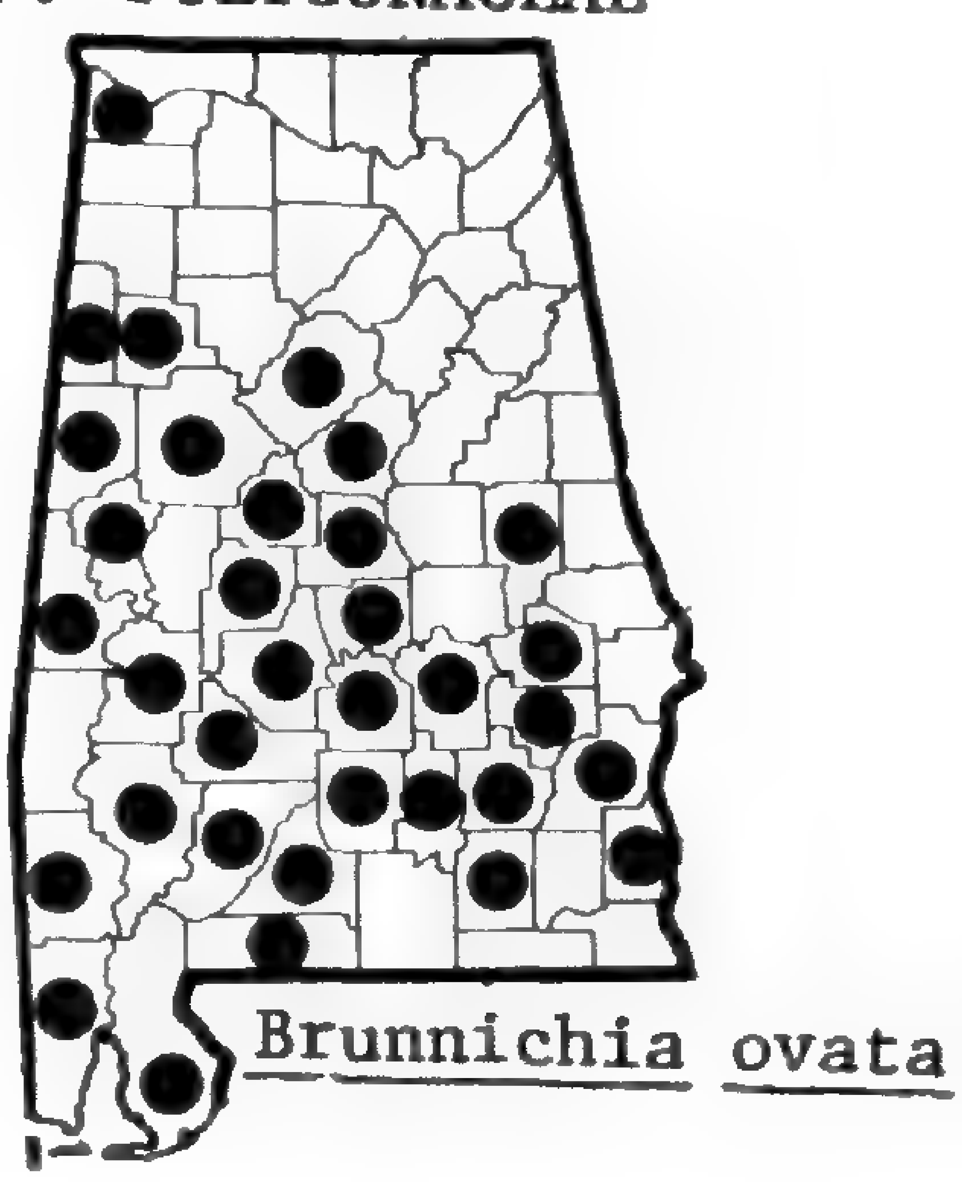
15. LORANTHACEAE



16. ARISTOLOCHIACEAE



17. POLYGONACEAE



deciduous trees; throughout, but poorly collected. *P. flavescens* (Pursh) Nutt.—M, H, S.

16. Aristolochiaceae

1. *Aristolochia* L.

1. *A. tomentosa* Sims. Spring; fall. Alluvial and rich woods, infrequent; throughout.

Aristolochia durior Hill (= *A. macrophylla* Lam.) has been reported.

17. Polygonaceae

1. Plant a high-climbing vine .... 1. *Brunnichia*
1. Plant low-growing, shrubby or suffruticose .... 2. *Polygonella*

1. *Brunnichia* Banks *ex* Gaertn., Ladies' Ear-Drops

1. *B. ovata* (Walter) Shinners. Late spring–summer; summer–fall. Alluvial woods, river swamps; principally CP. *B. cirrhosa* Banks—M, H, RAB.

2. *Polygonella* Michaux

1. Flowers perfect; calyx more than 2 mm long in flower, more than 3 mm long in fruit .... 1. *P. americana*
1. Flowers imperfect; calyx less than 2 mm long in flower, less than 3 mm long in fruit .... 2. *P. polygama*

1. *P. americana* (Fisch. & Mey.) Small. Sandy soil, rare; CuP.
2. *P. polygama* (Vent.) Engelmann & Gray. Dunes; OCP.

Bataceae

Alabama is within the range cited by Small (1933) for *Batis maritima* L. No specimens have been seen by the writer.

18. Ranunculaceae

1. Leaves opposite, 3-foliolate .... 1. *Clematis*
1. Leaves alternate, commonly 5- or more-foliolate .... 2. *Xanthorhiza*

1. *Clematis* L.

1. *C. virginiana* L., Virgin's Bower. Summer; fall. Low thickets, mesic woods; throughout. *C. catesbyana* Pursh—M, S.

2. *Xanthorhiza* Marshall, Yellow-Root

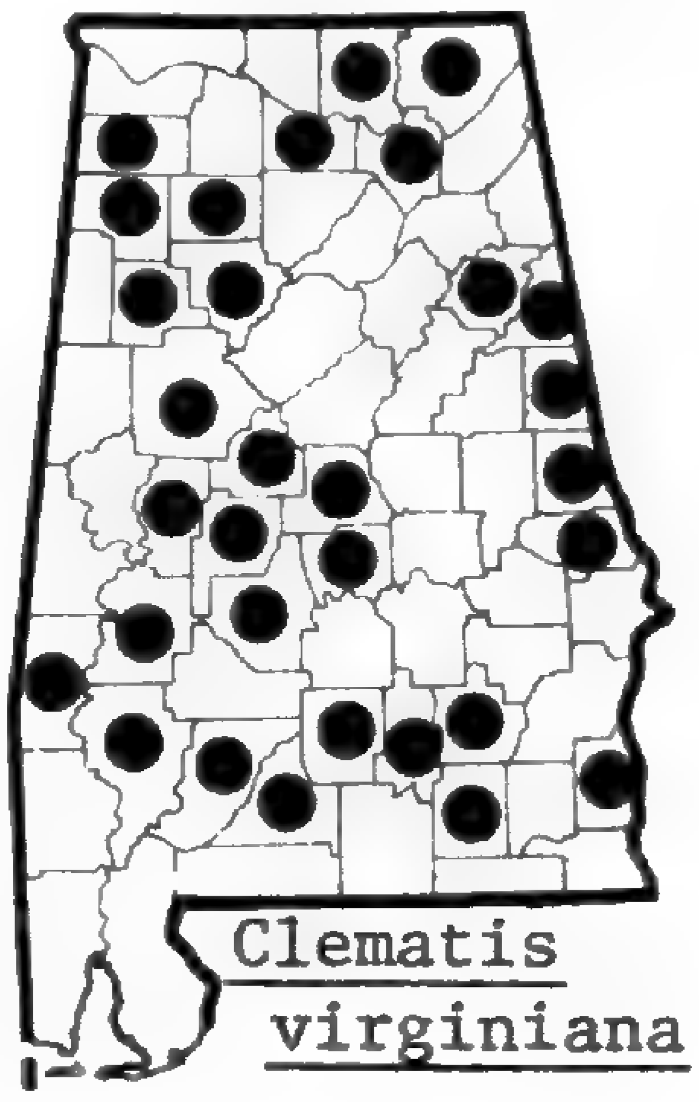
1. *X. simplicissima* Marshall. Spring; spring–early summer. Stream-banks, alluvial woods; CP, P, AM, CuP, VR. Rare southward in CP. *Zanthorhiza apiifolia* L'Her—M.

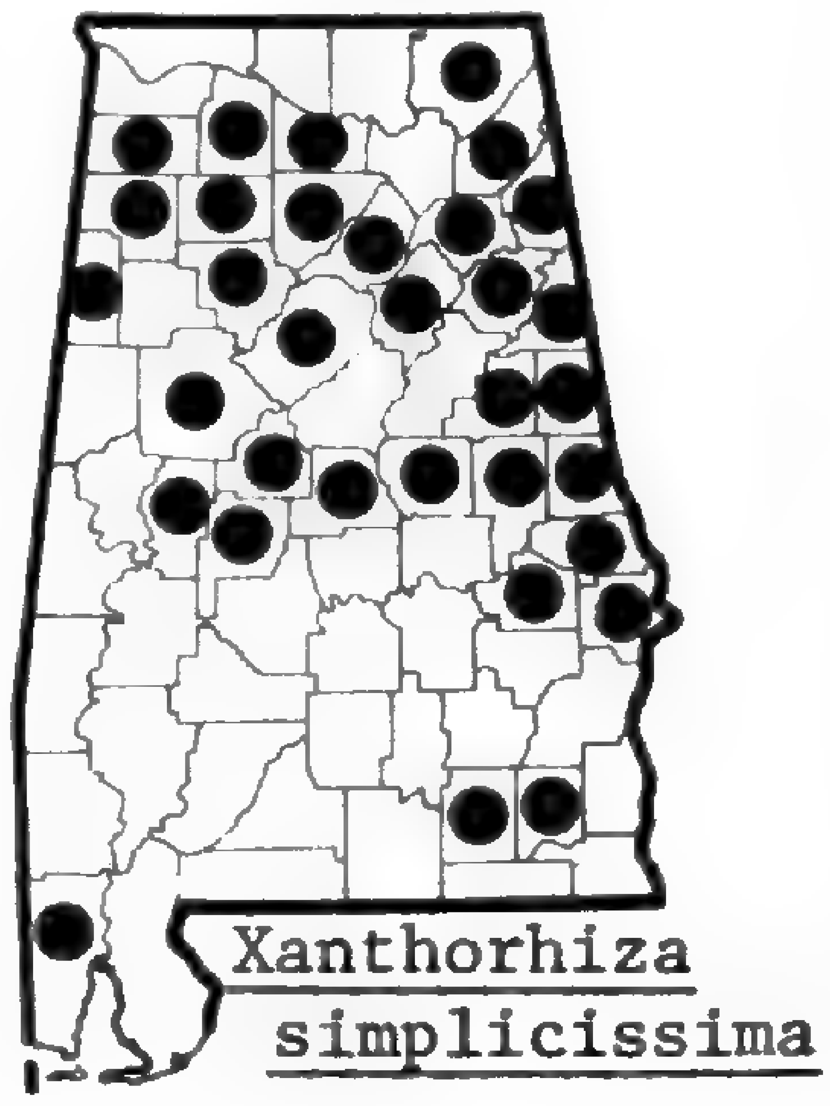
19. Menispermaceae

1. *Cocculus* DC.

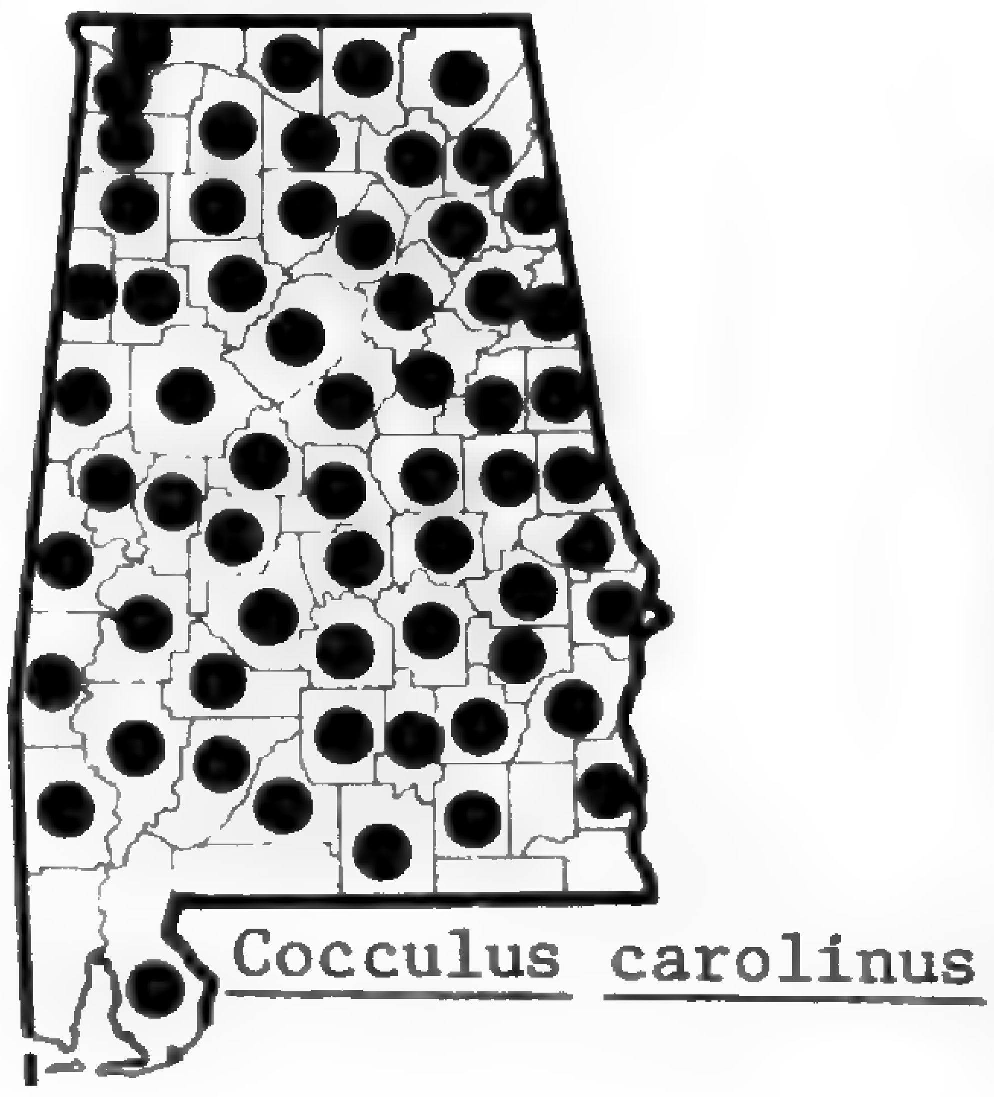
1. *C. carolinus* (L.) DC. Summer; summer–fall. Thickets, fields, fencerows, rights-of-way; throughout. *Cebatha carolina* (L.) Britt.—M; *Epibaterium carolinum* (L.) Britt.—S.

18. RANUNCULACEAE

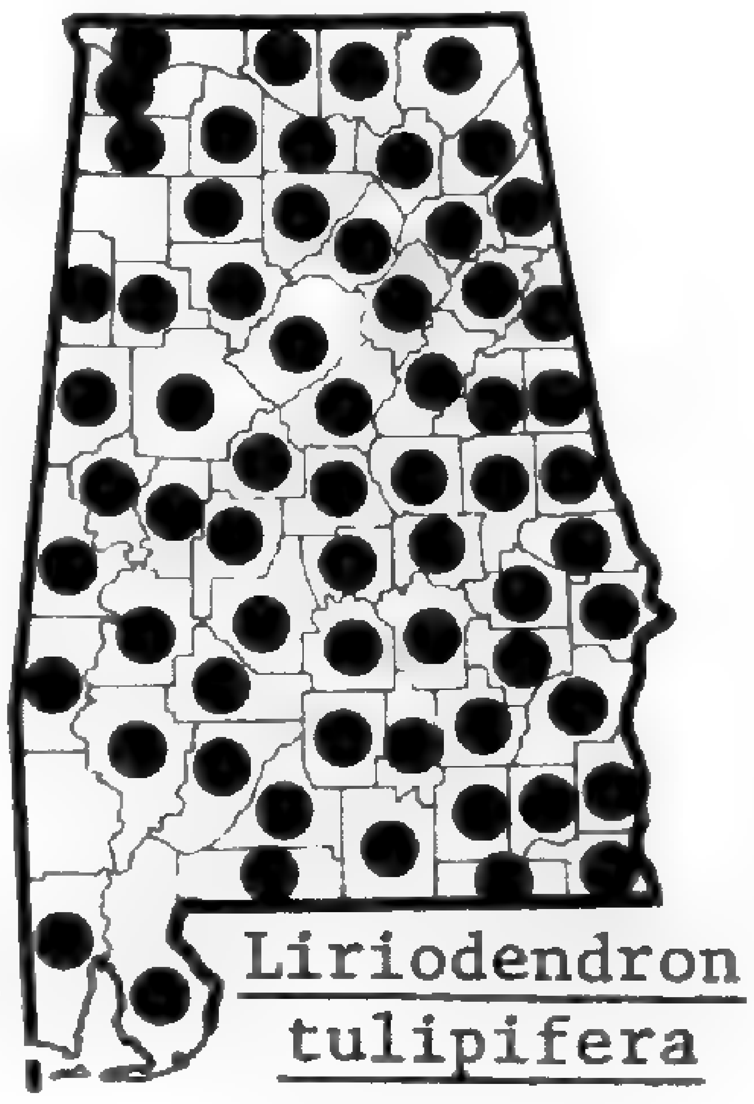


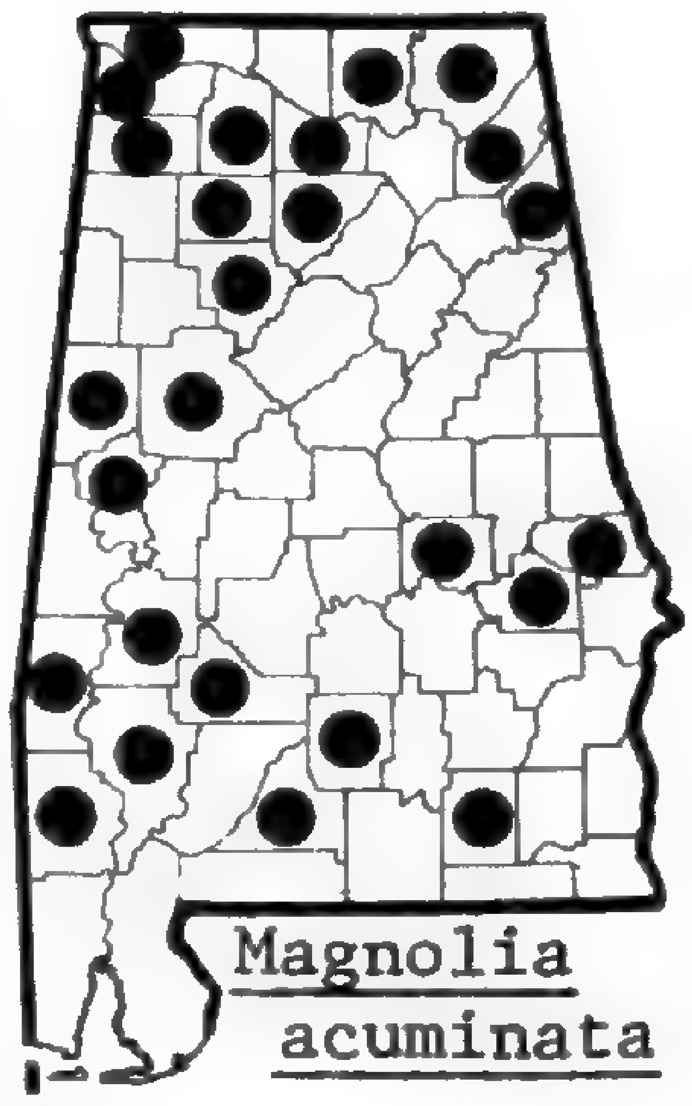


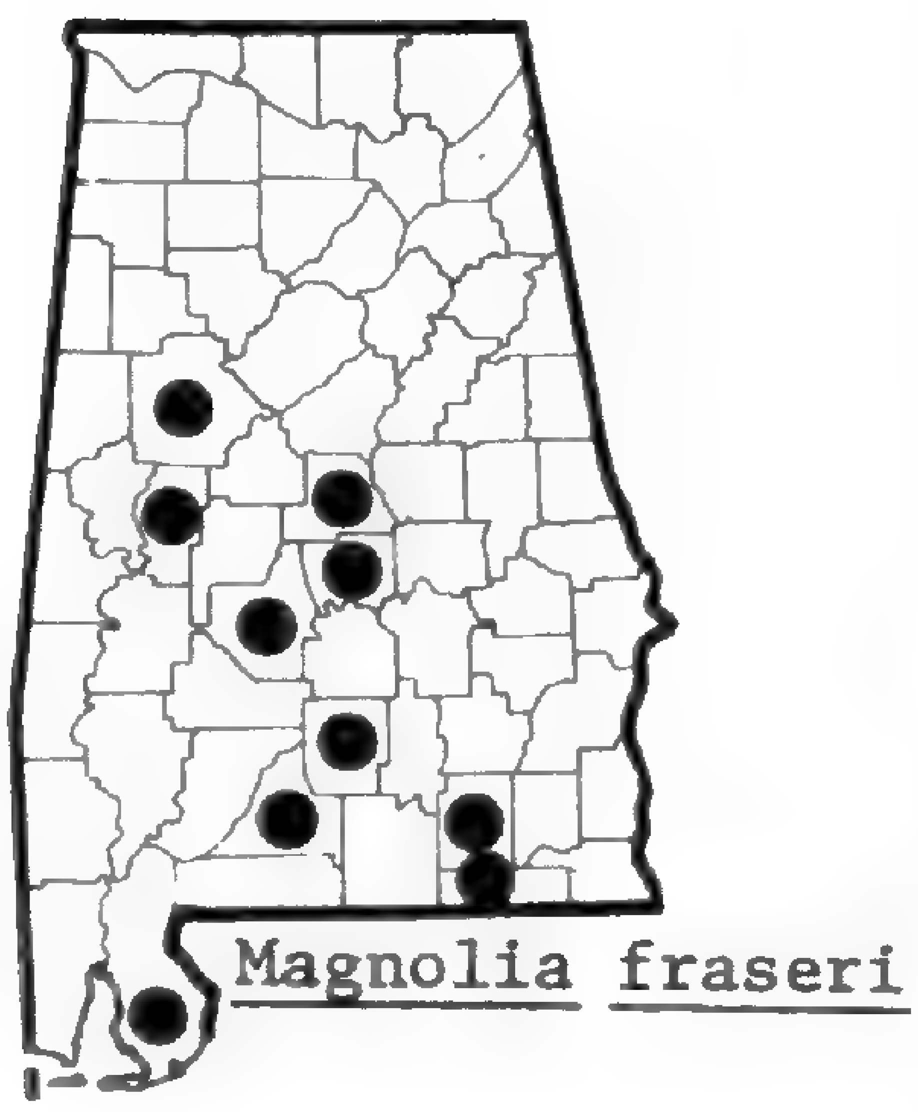
19. MENISPERMACEAE

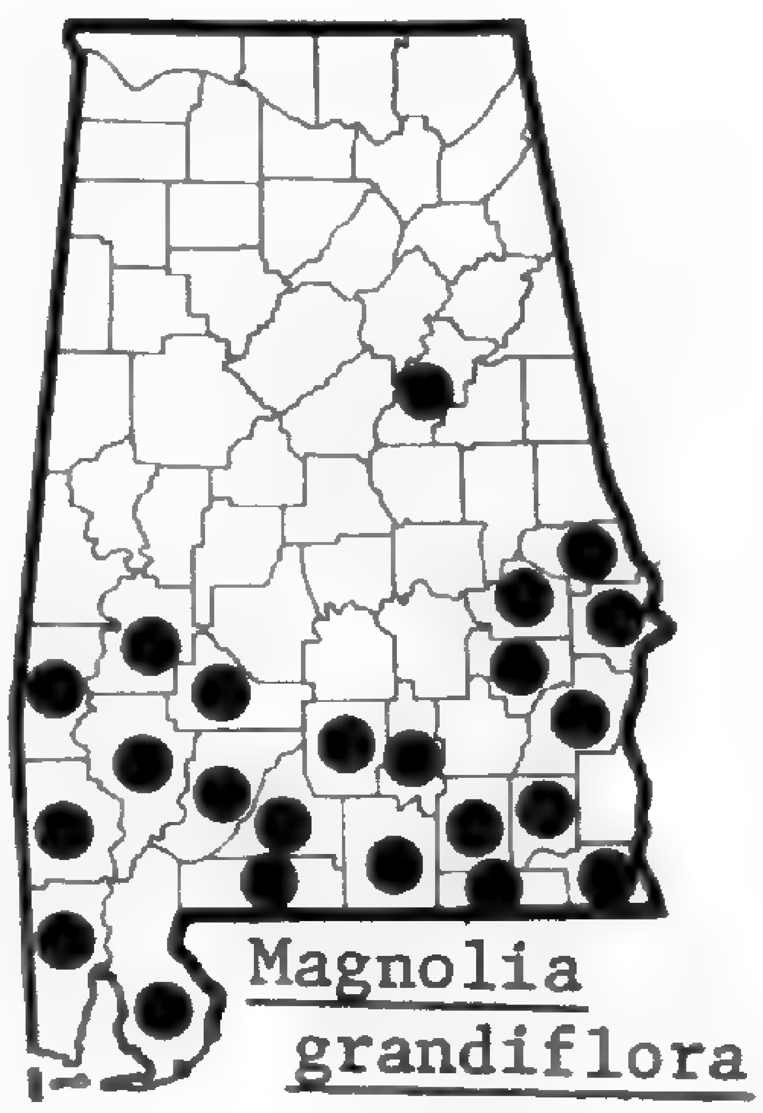


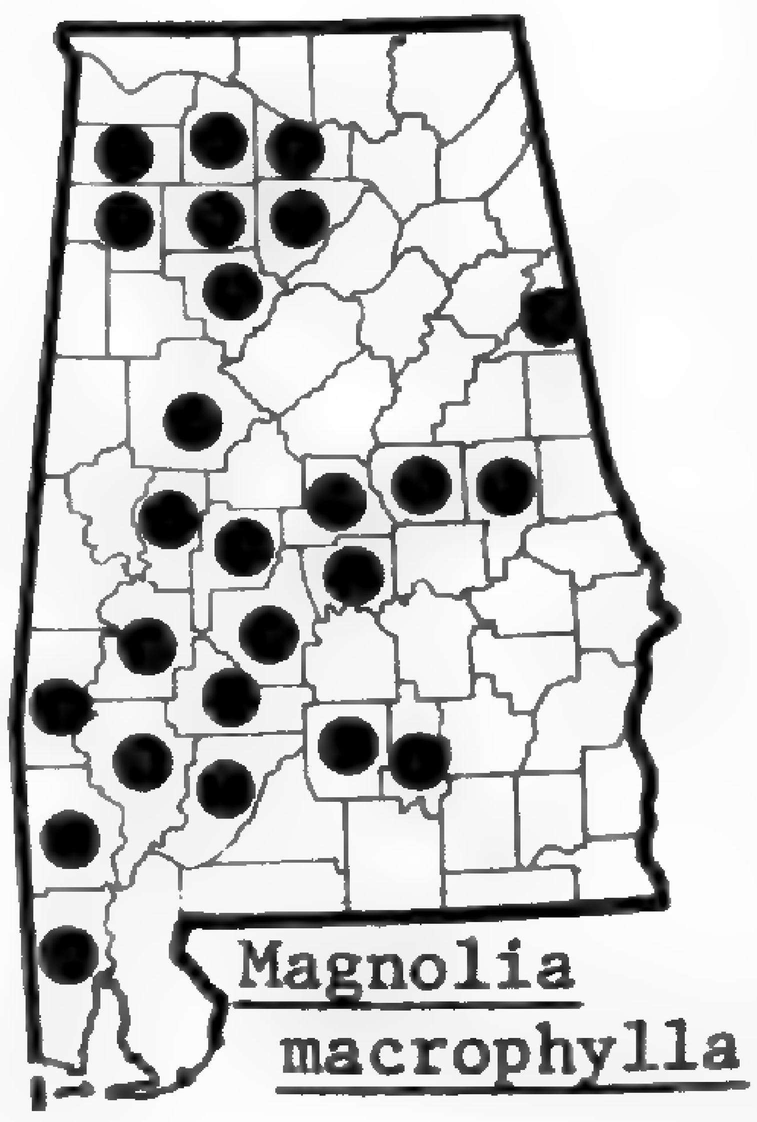
20. MAGNOLIACEAE











20. Magnoliaceae

1. Leaves broadly emarginate, lobed; exauriculate; fruit samaroid .... 1. *Liriodendron*
1. Leaves obtuse to acuminate, unlobed, often auriculate; fruit follicular .... 2. *Magnolia*

1. *Liriodendron* L., Yellow Polar, Tulip Tree

1. *L. tulipifera* L. Spring; fall. Mesic woods, low woods; throughout.

2. *Magnolia* L.

1. Leaf bases auriculate 2
   2. Leaves glaucous beneath .... 4. *M. macrophylla*
   2. Leaves not glaucous beneath .... 2. *M. fraseri*
1. Leaf bases not auriculate 3
   3. Leaves glaucous beneath .... 6. *M. virginiana*
   3. Leaves not glaucous beneath 4
      4. Leaves evergreen, coriaceous .... 3. *M. grandiflora*
      4. Leaves not evergreen, not coriaceous 5
         5. Leaves clustered terminally on twig; follicles beaked .... 5. *M. tripetala*
         5. Leaves not clustered terminally on twig; follicles rounded .... 1. *M. acuminata*

1. *M. acuminata* L., Cucumber Tree. Spring; summer. Rich woods, often in circumneutral soils; CP, P, CuP, HR. *M. acuminata cordata* (Michx.) Sarg.—M; *M. cordata* Michx.—H; *Tulipastrum acuminatum* (L.) Sm., *T. cordatum* Sm.—S.—*Magnolia cordata* Michaux is a yellow-flowered form. The common name of this species and others below is often pronounced "cowcumber."

2. *M. fraseri* Walter. Spring; summer. Rich woods; CP. *M. pyramidata* Pursh—H, S; *M. pyramidata* Bartr. *ex* Pursh—RAB.—*Magnolia pyramidata* Bartr. has been applied to the coastal plain plants of this taxon, which are usually smaller than mature plants from further inland. There is no apparent reason to consider these as distinct entities, even though there is a range discontinuity.

3. *M. grandiflora* L., Magnolia. Spring–early summer; fall. Low or rich woods; CP, occasionally escaped northward. *M. foetida* (L.) Sarg.—M.

4. *M. macrophylla* Michaux, Bigleaf Cucumber Tree. Spring; fall. Low or upland rich woods; CP, AM, CuP.—Mohr (1901) speaks of trees "16 to 30 inches in diameter."

5. *M. tripetala* L., Umbrella Tree, Cucumber Tree. Spring; summer–fall. Rich woods; CP, P, AM, VR, CuP.

6. *M. virginiana* L., Bay. Spring–summer; summer–fall. Ditches, swamps, seepages, bogs, swamp ecotones; CP, P, AM, VR. *M. glauca* L.—H.

21. Illiciaceae

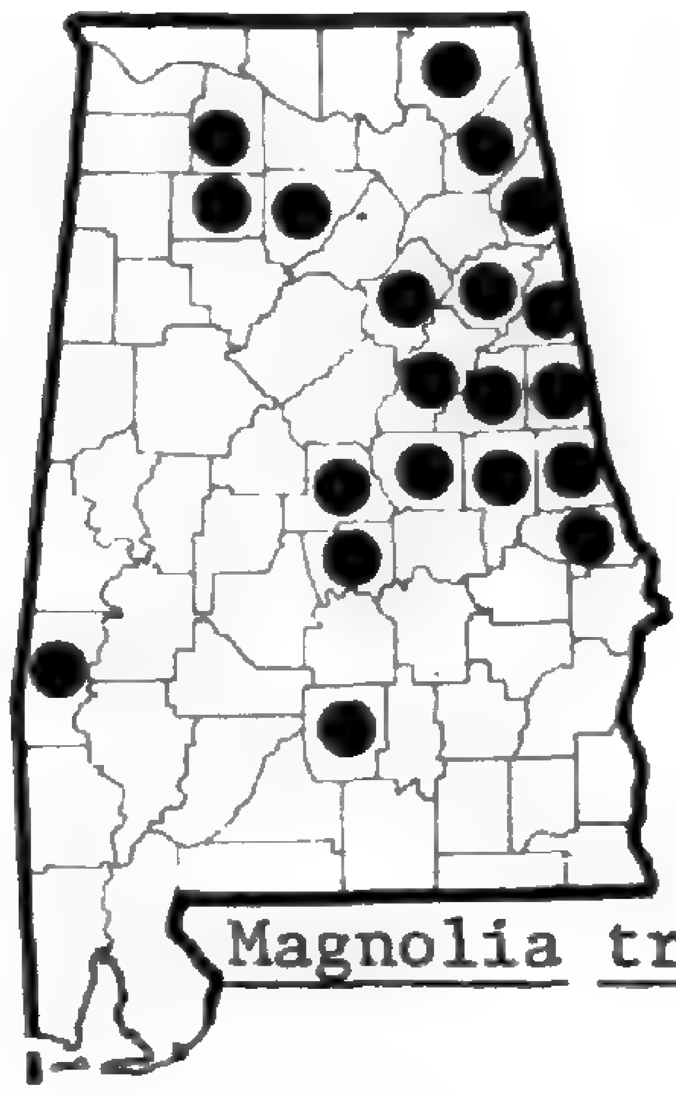
1. *Illicium* L.

1. *I. floridanum* Ellis, Stinking Laurel, Stinkbush. Spring; fall. Low woods; principally CP.

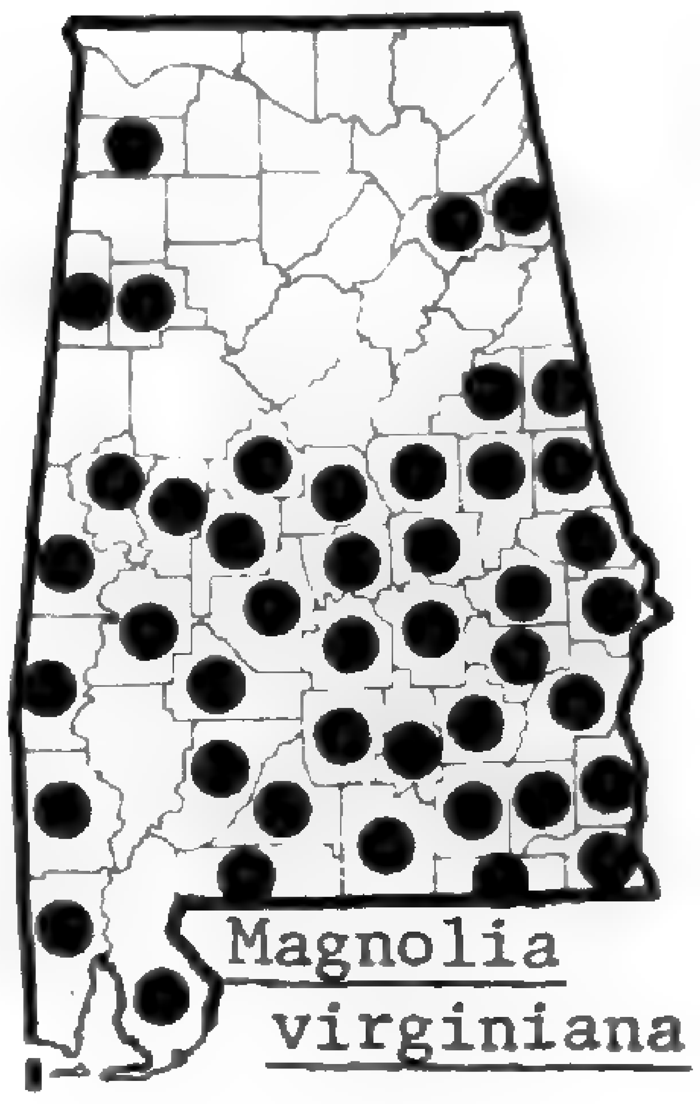
22. Annonaceae

1. *Asimina* Adanson

1. Leaves averaging 6 times or more longer than broad, attenuate, narrowly oblanceolate to linear .... 1. *A. longifolia*

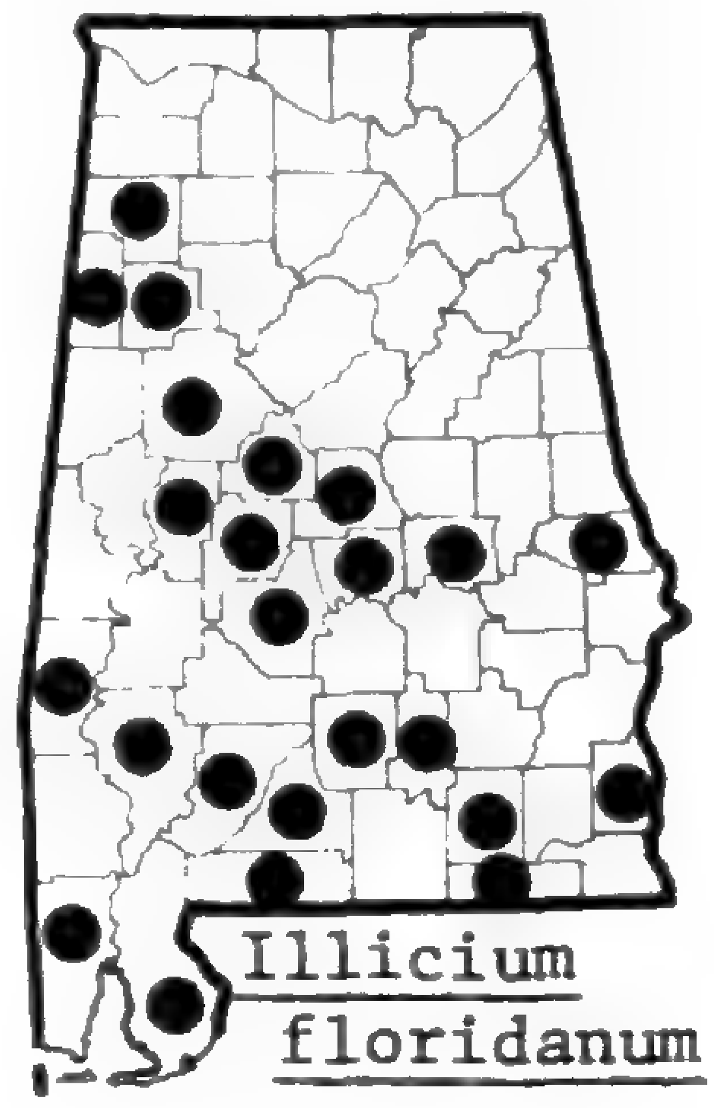


Magnolia tripetala



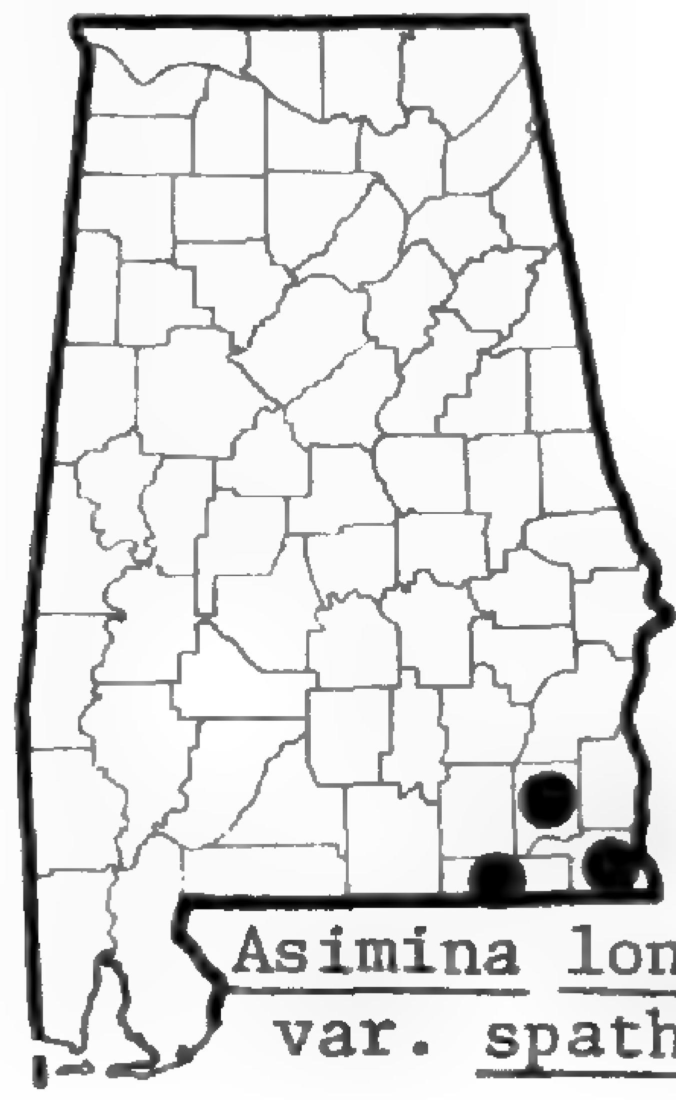
Magnolia virginiana

21. ILLICIACEAE

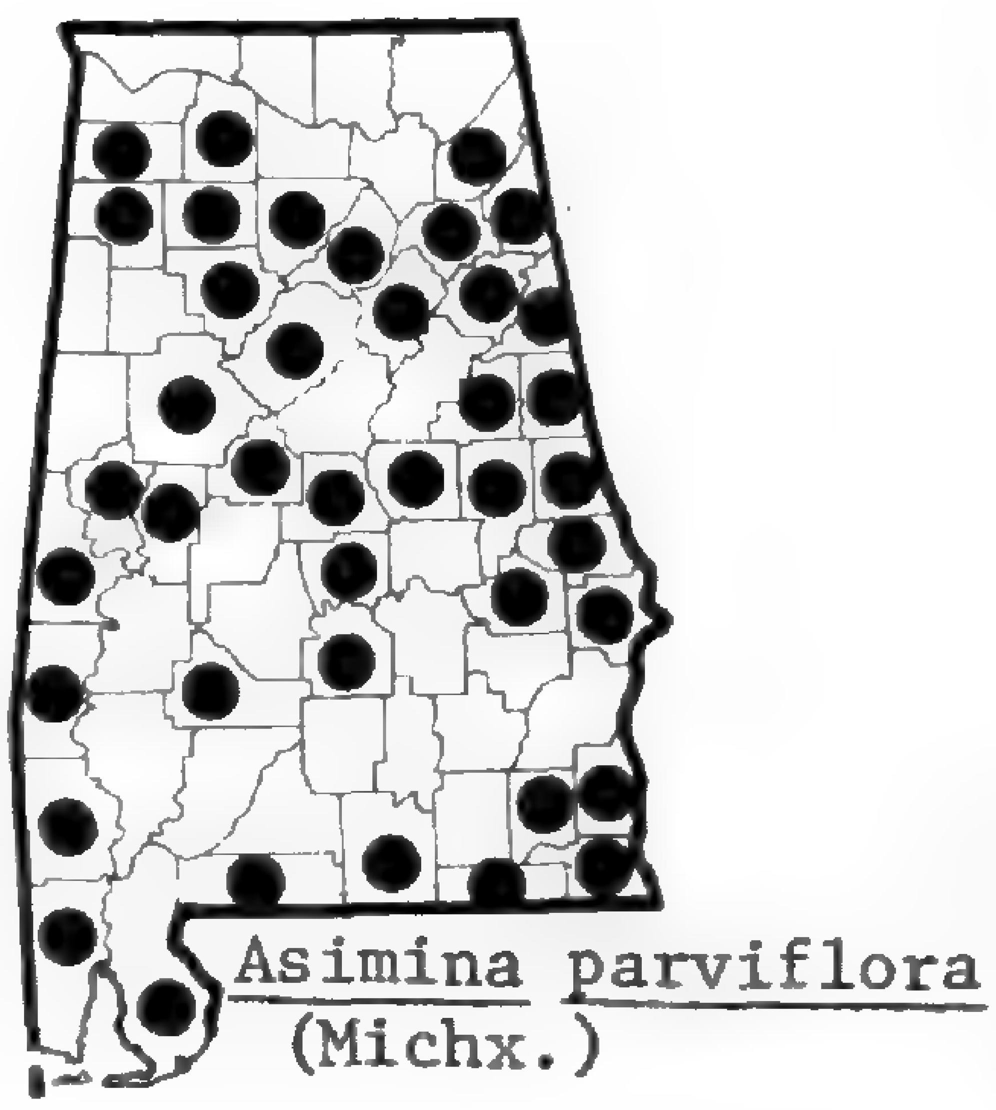


Illicium floridanum

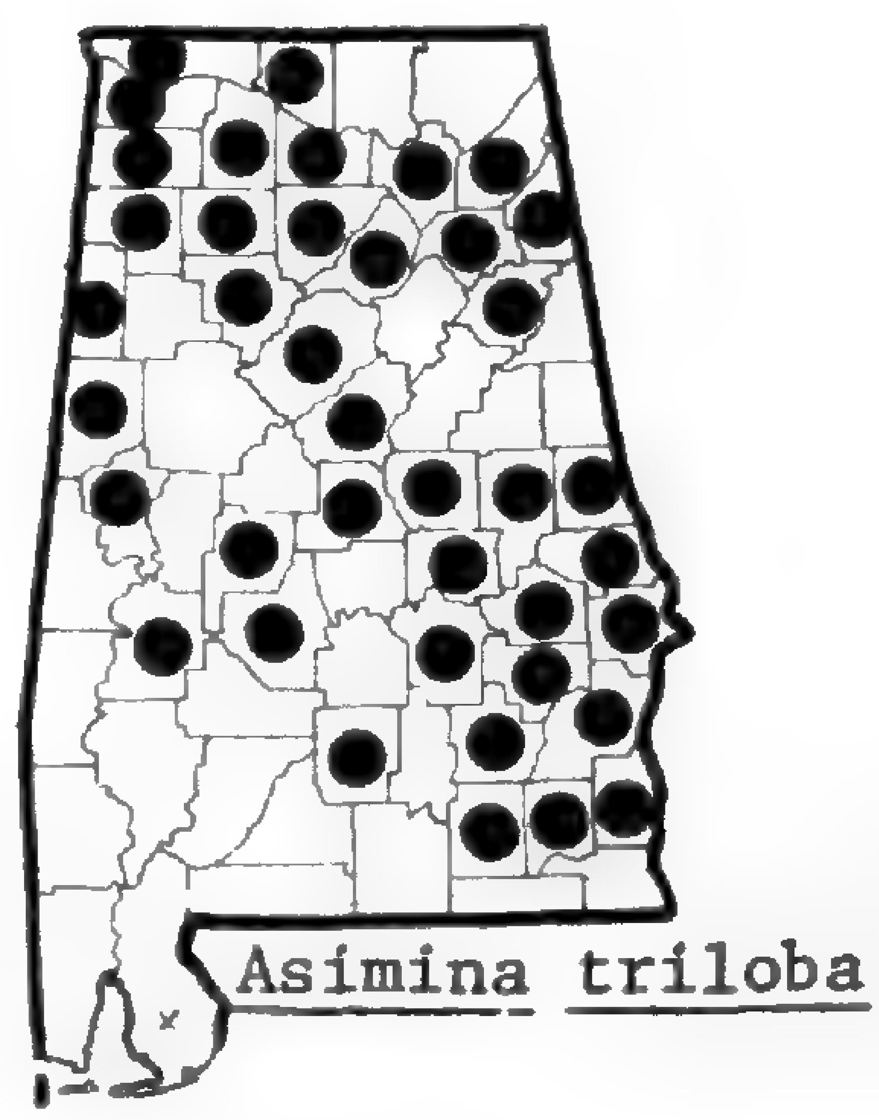
22. ANNONACEAE



Asimina longifolia var. spathulata

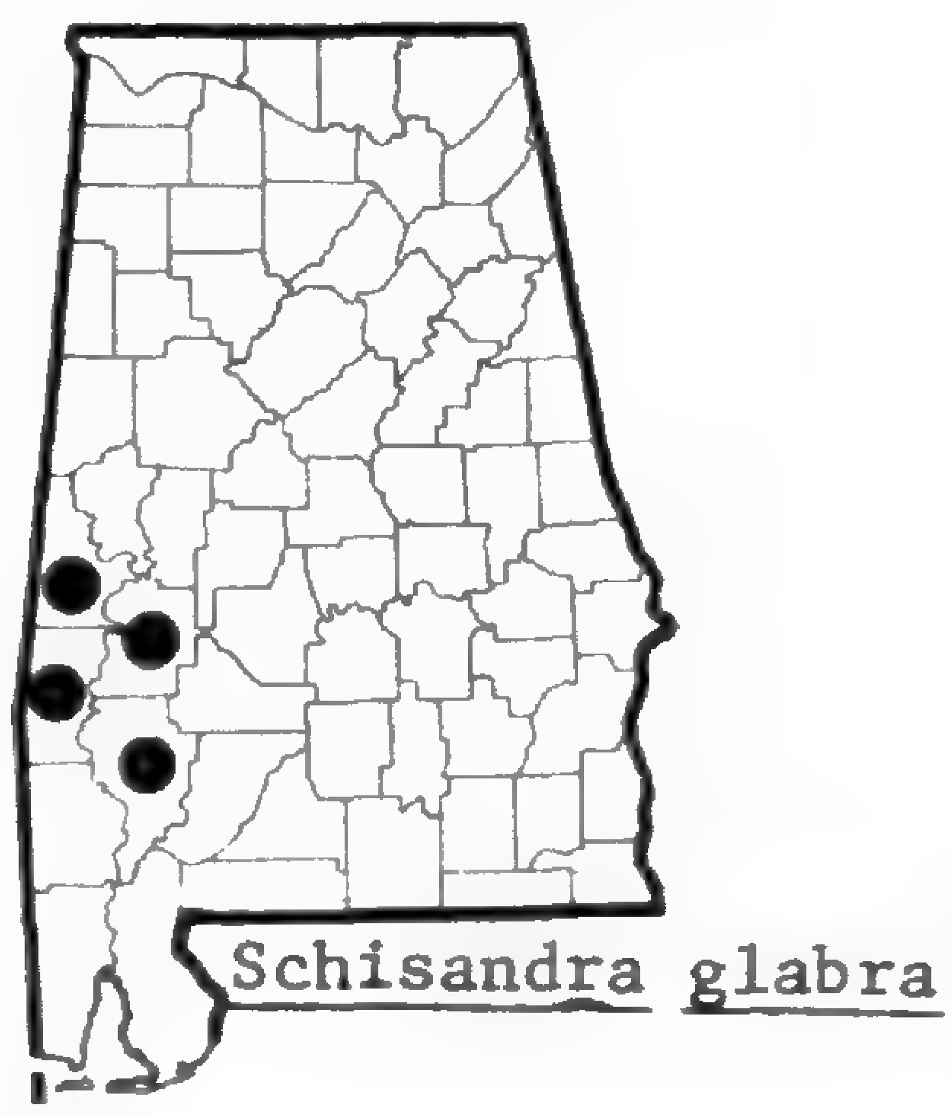


Asimina parviflora (Michx.)



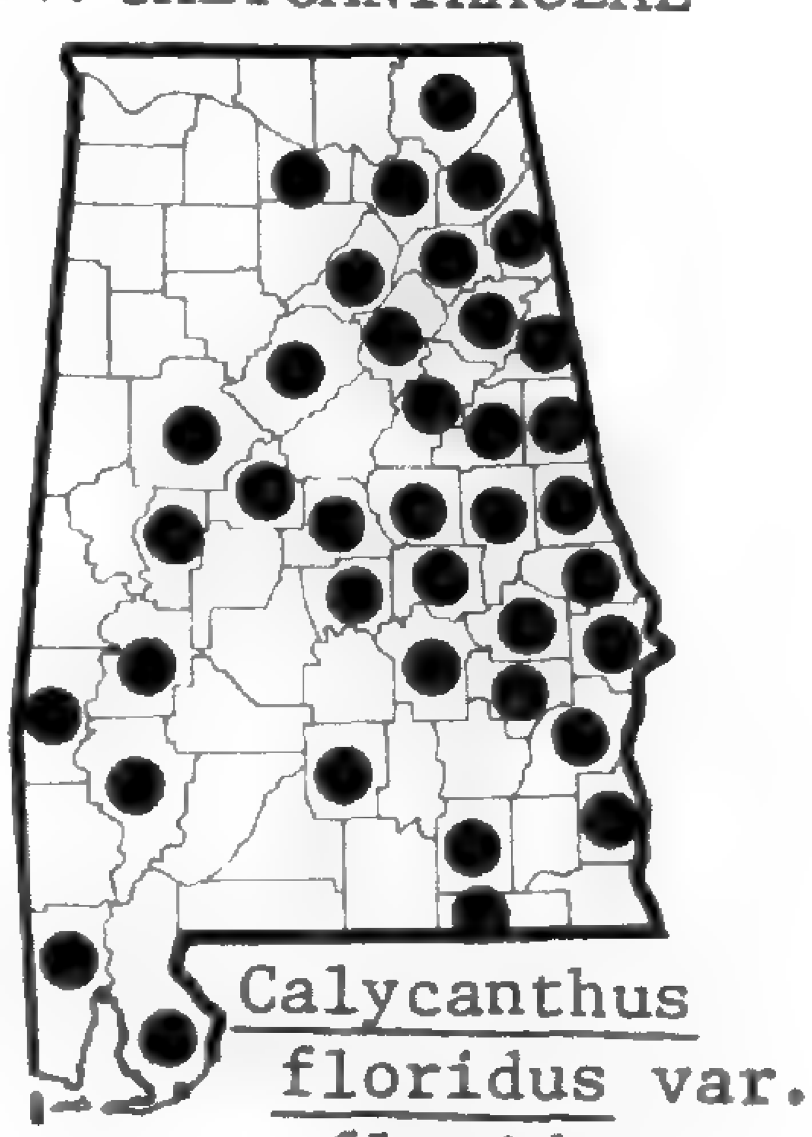
Asimina triloba

23. SCHISANDRACEAE

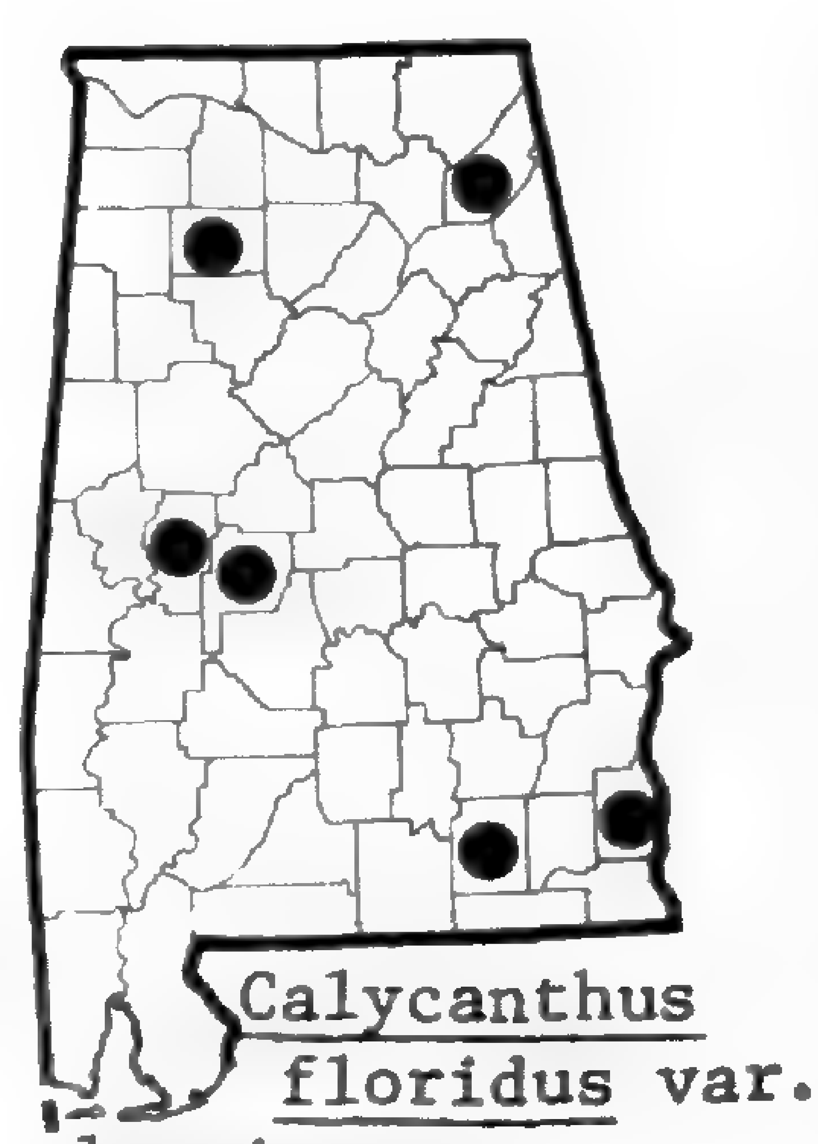


Schisandra glabra

24. CALYCANTHACEAE



Calycanthus floridus var. floridus



Calycanthus floridus var. laevigatus

1. Leaves averaging less than 4 times as long as broad, obtuse to cuneate, obovate to broadly oblanceolate 2
   2. Flowers 2 cm or less broad; peduncles less than 8 mm long; fruit usually less than 3 cm long ..... *A. parviflora*
   2. Flowers more than 2 cm broad; peduncles 10 mm or more long; fruit usually more than 3 cm long ..... *A. triloba*

1. *A. longifolia* Kral var. *spathulata* Kral. Spring; summer. Open, sandy ground; southeastern OCP. *A. pygmaea* (Bartr.) Gray—M; *A. angustifolia* Gray—H; *Pityothamnus angustifolius* (Gray) Sm.—S.

2. *A. parviflora* (Michaux) Dunal, Dwarf Pawpaw. Spring; summer–fall. Dry or mesic woods; throughout.

3. *A. triloba* (L.) Dunal, Pawpaw. Spring; summer–fall. Low or rich woods, infrequent; throughout.

23. Schisandraceae

1. *Schisandra* Michaux

1. *S. glabra* (Brickell) Rehder. Spring; summer. Rich woods, rare; western CP. *Schizandra coccinea* Michx.—M, H, S.

24. Calycanthaceae

1. *Calycanthus* L.

1. *C. floridus* L., Sweet Shrub. Spring; summer.

1. Leaves pubescent beneath ..... *C. floridus* var. *floridus*
1. Leaves glabrous or glabrate beneath ..... *C. floridus* var. *laevigatus*

C. floridus L. var. *floridus*. Low or mesic woods; CP, P, AM, CuP, VR. Much more common in eastern Alabama; rare westward. *Butneria florida* (L.) Kearn.—M; *C. mohrii* Sm.—S.

C. floridus L. var. *laevigatus* (Willd.) Torrey & Gray. Low woods, rare; CP, CuP. *Butneria fertilis* (Walt.) Kearn.—M; *C. nanus* (Loisel.) Sm., *C. fertilis* Walt.—S.

25. Lauraceae

1. Leaves, at least some, lobed ..... 4. *Sassafras*
1. Leaves unlobed 2
   2. Leaves deciduous ..... 2. *Lindera*
   2. Leaves evergreen or semi-evergreen 3
      3. Leaves pinnately veined ..... 3. *Persea*
      3. Leaves palmately veined ..... 1. *Cinnamomum*

1. *Cinnamomum* Blume

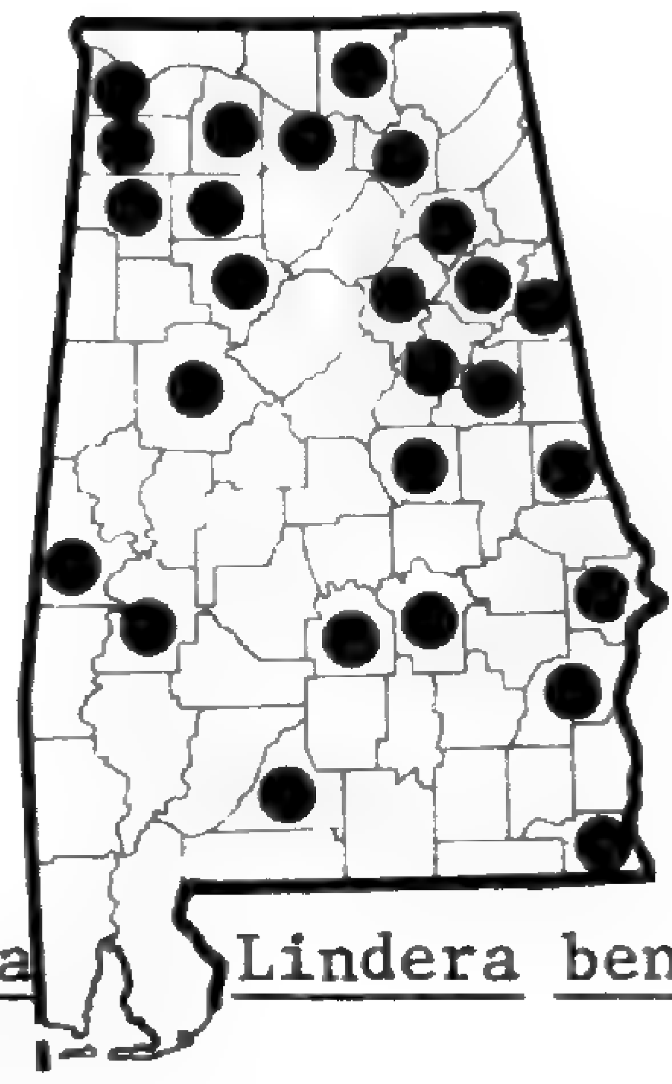
1. *C. camphora* (L.) Nees & Ebermaier, Camphor Tree. Flowers, fruit not seen. Escaped to low pinelands, rare; OCP. *Camphora camphora* (L.) Karst.—S.

2. *Lindera* Thunberg

1. Leaves, at least most, ovate to obovate ..... 1. *L. benzoin*
1. Leaves broadly lanceolate ..... 2. *L. melissaefolium*

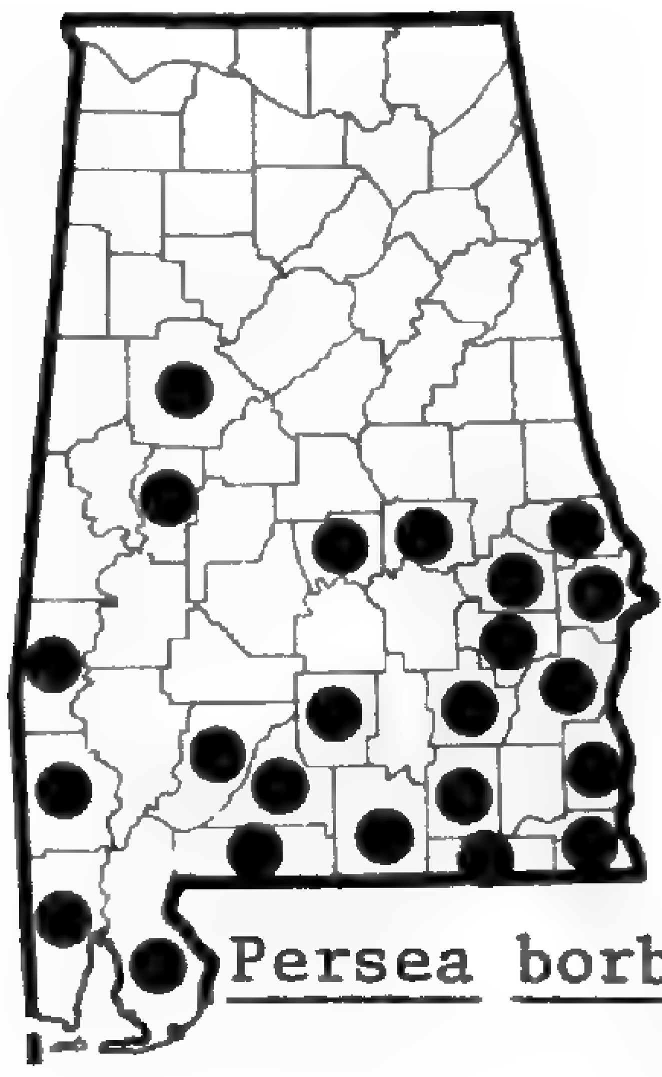
25. LAURACEAE

Cinnamomum camphora

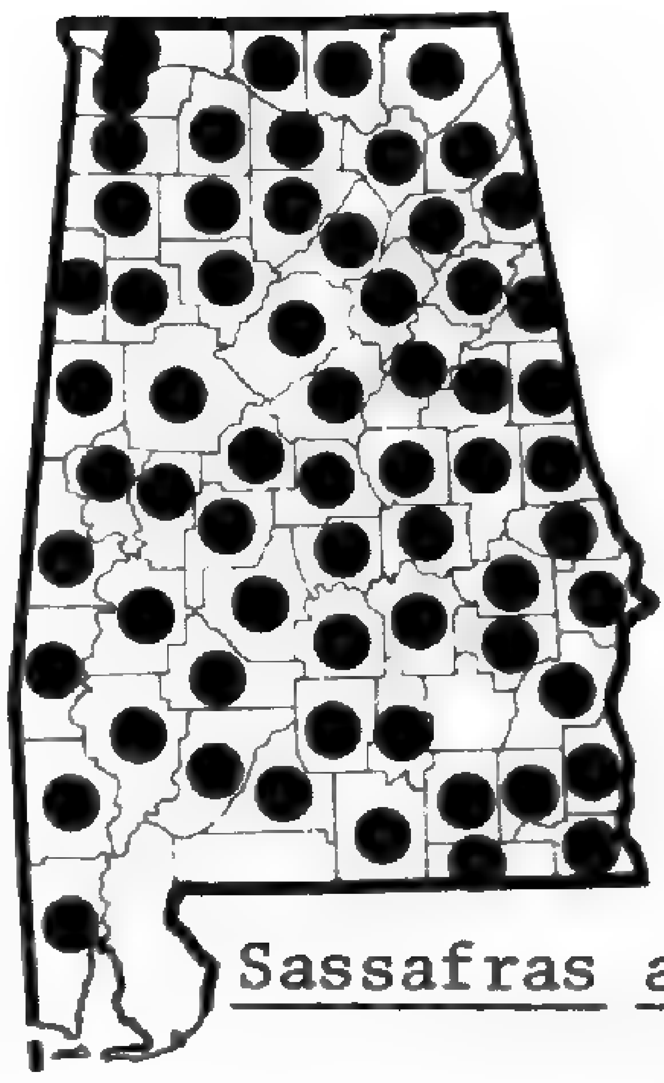


Lindera benzoin

Lindera melissaefolium



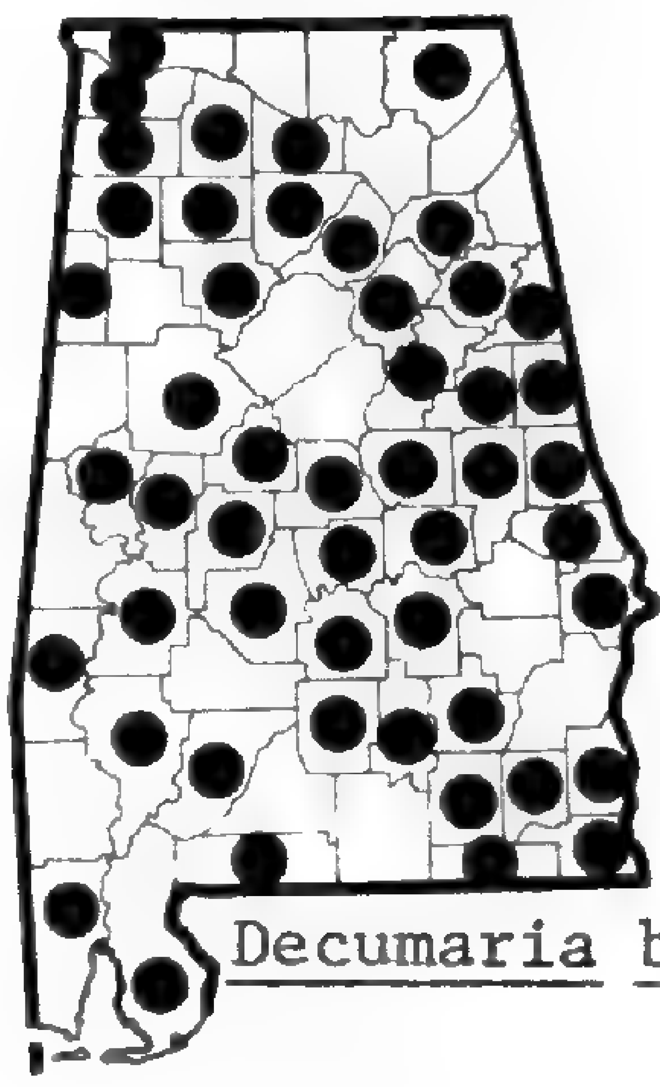
Persea borbonia



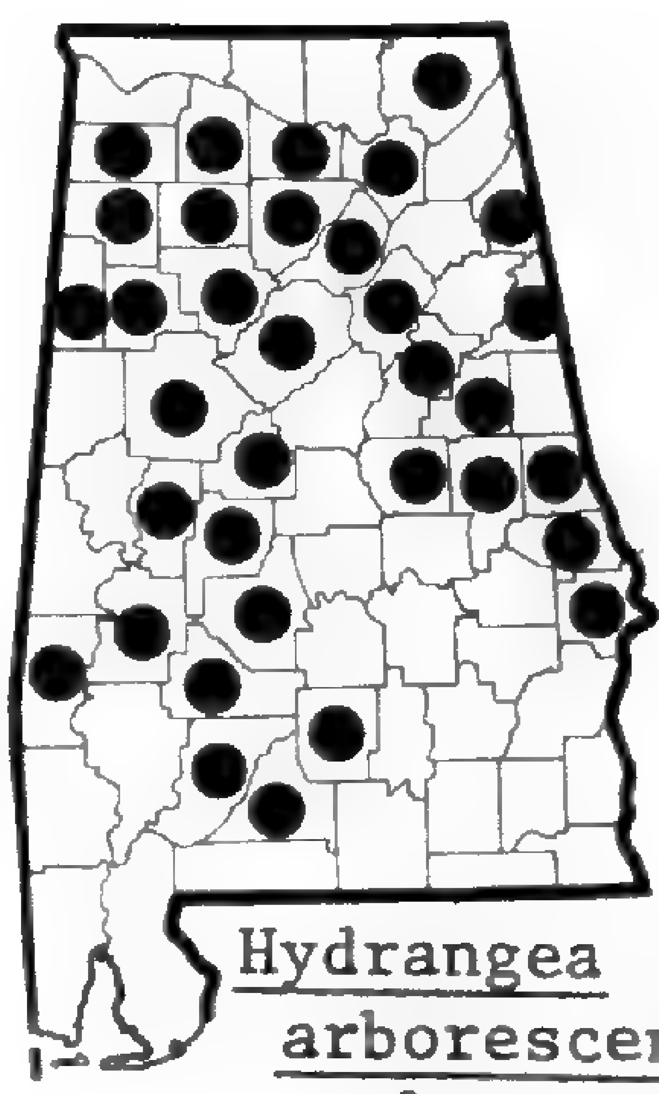
Sassafras albidum

Litsea aestivalis

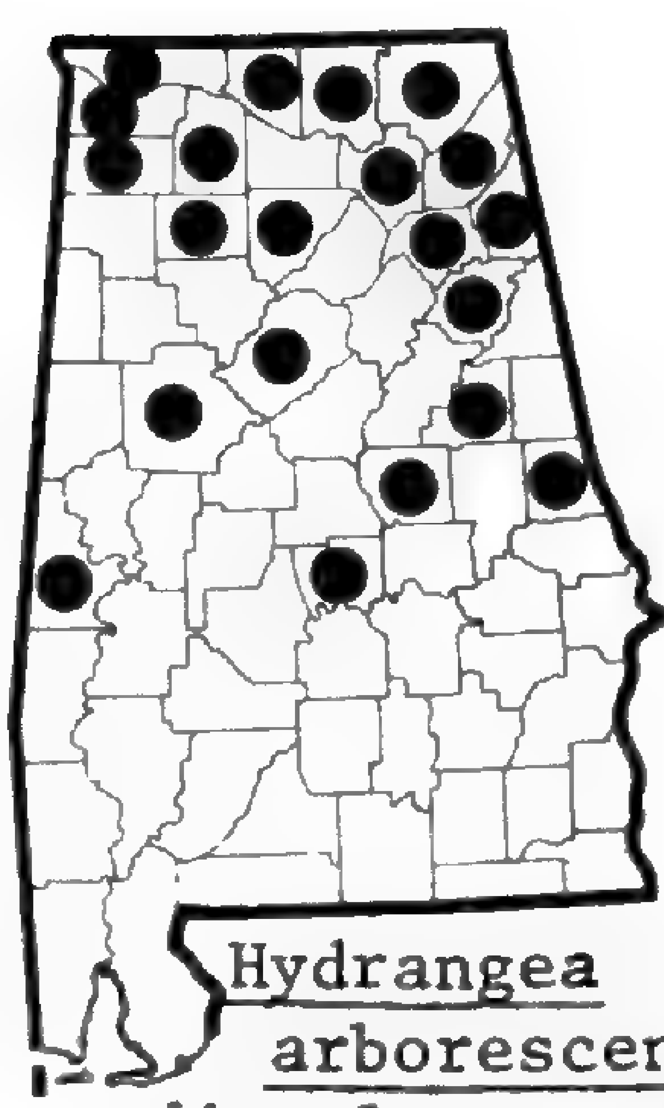
26. SAXIFRAGACEAE



Decumaria barbara



Hydrangea arborescens ssp. arborescens



Hydrangea arborescens ssp. discolor

1. *L. benzoin* (L.) Blume, SPICEBUSH. Spring; summer. Alluvial and rich, low woods; throughout, but infrequent southward. *Benzoin benzoin* (L.) Coult.—M; *B. aestivale* (L.) Nees—H, S.

2. *L. melissaefolium* (Walter) Blume. Spring; summer. Low thicket, extremely rare or extinct in Alabama; CP. *Benzoin melissaefolium* (Walt.)Nees—M, H, S.—Apparently not seen in Alabama since the time of Buckley's residence over 100 years ago.

3. *Persea* Miller

1. *P. borbonia* (L.) Sprengel, RED BAY. Spring; fall. Low, rich woods, infrequent; CP, southern CuP. *P. pubescens* (Pursh) Sarg.—M, H; *Tamala pubescens* (Pursh) Sm., *T. borbonia* (L.) Raf.—S.

4. *Sassafras* Trew *ex* Blackwell, SASSAFRAS

1. *S. albidum* (Nuttall) Nees. Spring; summer. Fencerows, fields, mesic woods; throughout. *S. sassafras* (L.) Karst.—M, S; *S. variifolium* (Sal.) Kuntz.—H.

Litsea aestivalis (L.) Fernald has been listed by Dean (1961), but no specimens have been seen by the writer.

26. SAXIFRAGACEAE

1. Leaves alternate 2
  2. Ovary inferior; fruit a berry .... 5. *Ribes*
  2. Ovary superior; fruit a capsule .... 3. *Itea*
1. Leaves opposite 3
  3. Plant a creeping vine .... 1. *Decumaria*
  3. Plant a shrub 4
    4. Stamens 20 or more; fruit longitudinally dehiscent, not ribbed .... 4. *Philadelphus*
    4. Stamens 10 or less; fruit poricidally dehiscent, ribbed .... 2. *Hydrangea*

1. *Decumaria* L.

1. *D. barbara* L. Spring; summer–fall. Moist woods; throughout.

2. *Hydrangea* L., HYDRANGEA

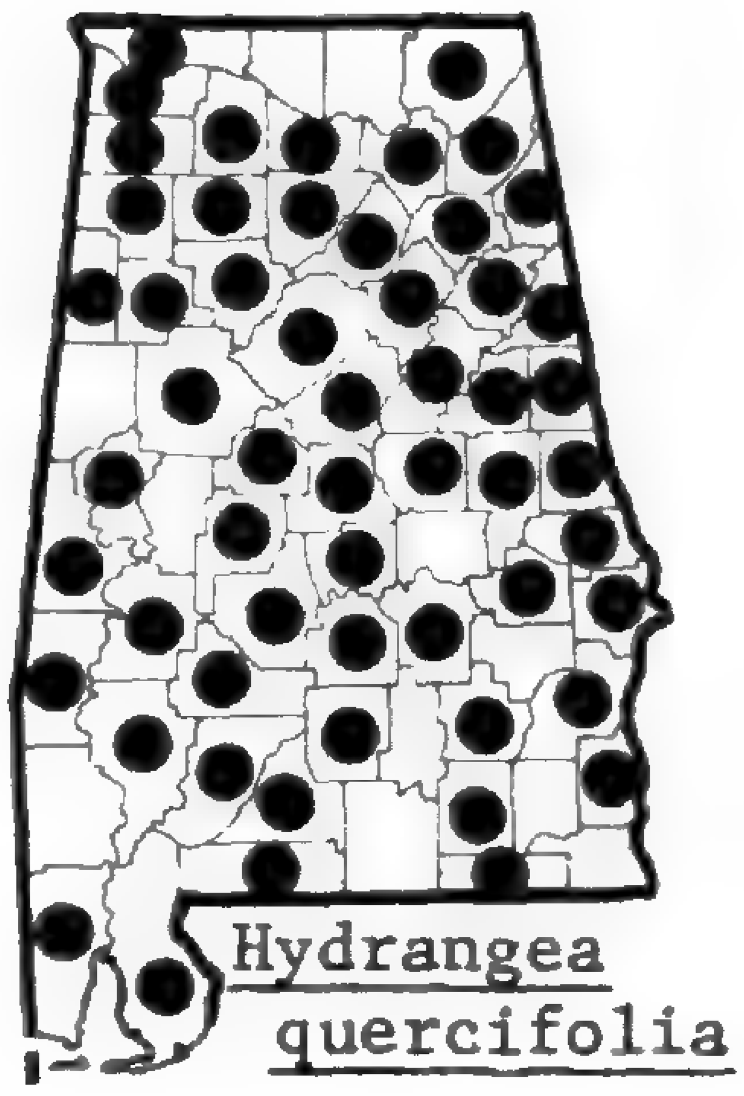
1. Leaves unlobed .... 1. *H. arborescens*
1. Leaves lobed .... 2. *H. quercifolia*

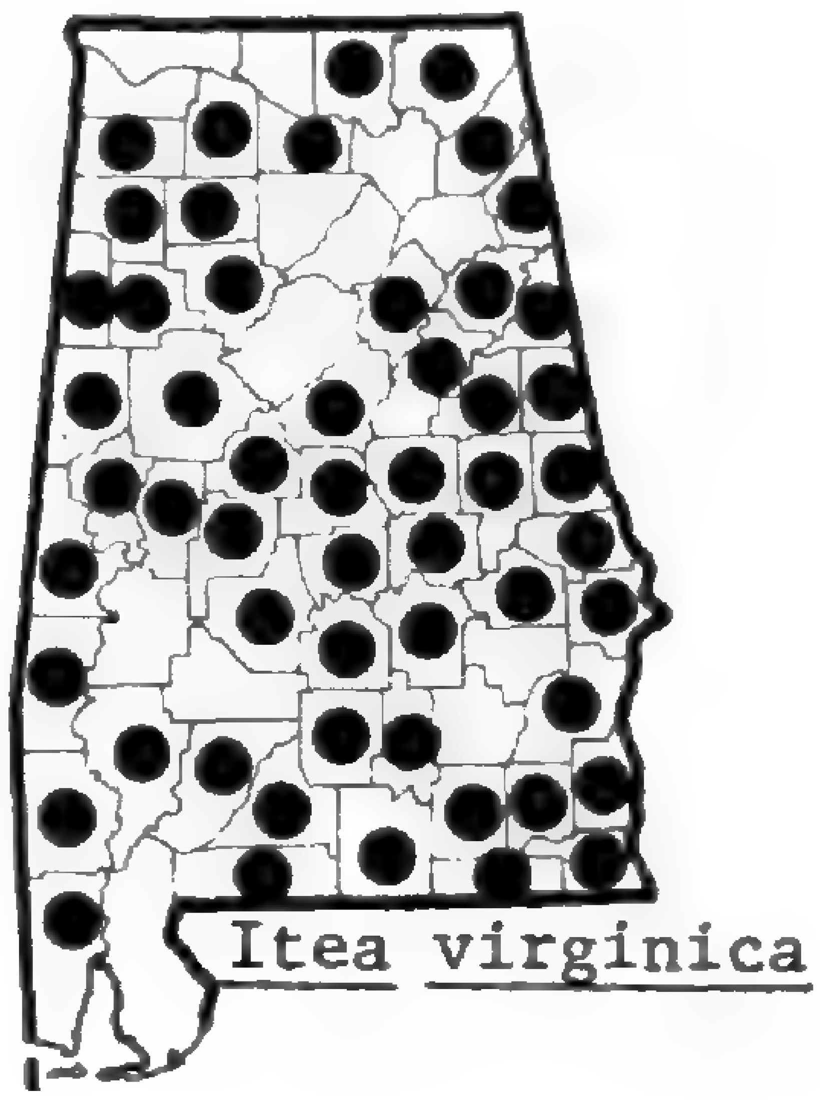
1. *H. arborescens* L., WILD H. Summer; summer–fall.

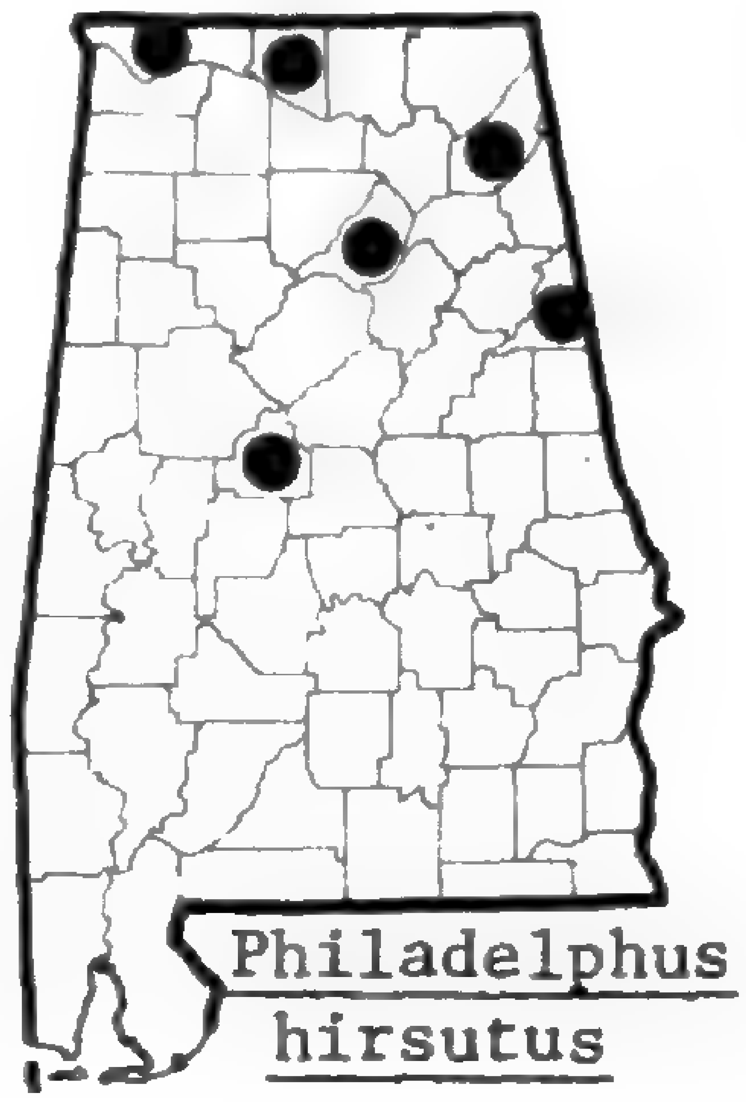
1. Leaves glabrous beneath, or pubescent only on the principal veins .... *H. arborescens* subsp. *arborescens*
1. Leaves pubescent beneath over the lower surfaces .... *H. arborescens* subsp. *discolor*

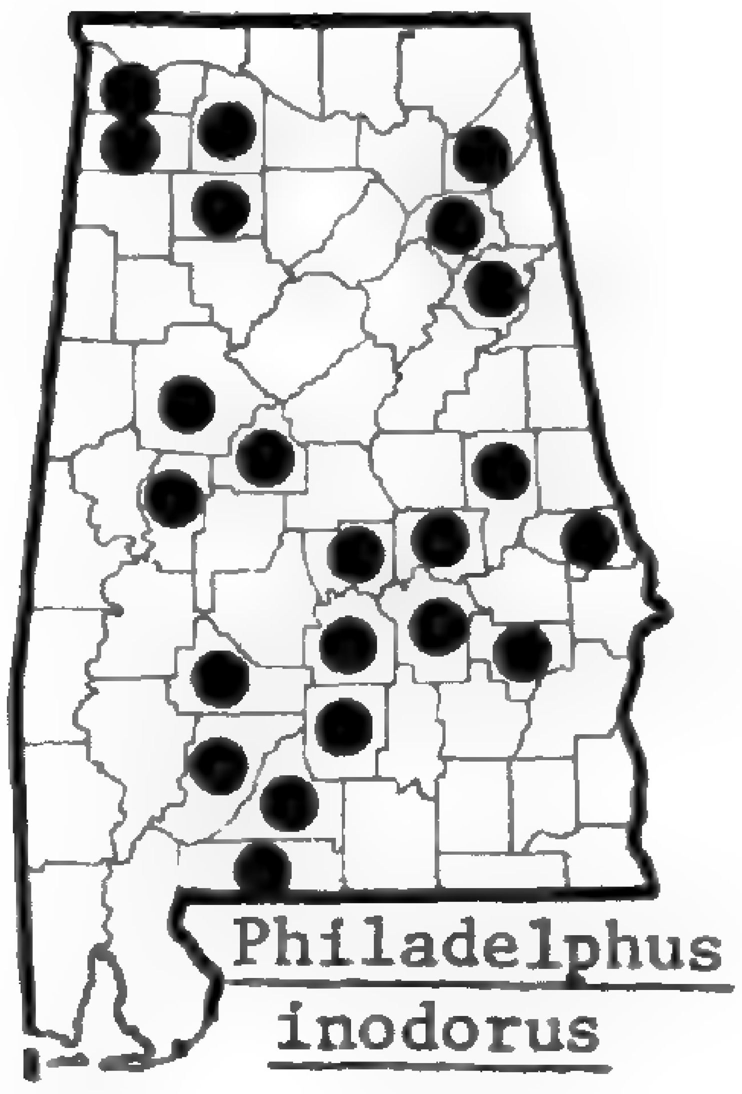
H. arborescens L. subsp. *arborescens*. Rich or low woods; throughout, but infrequent southward.

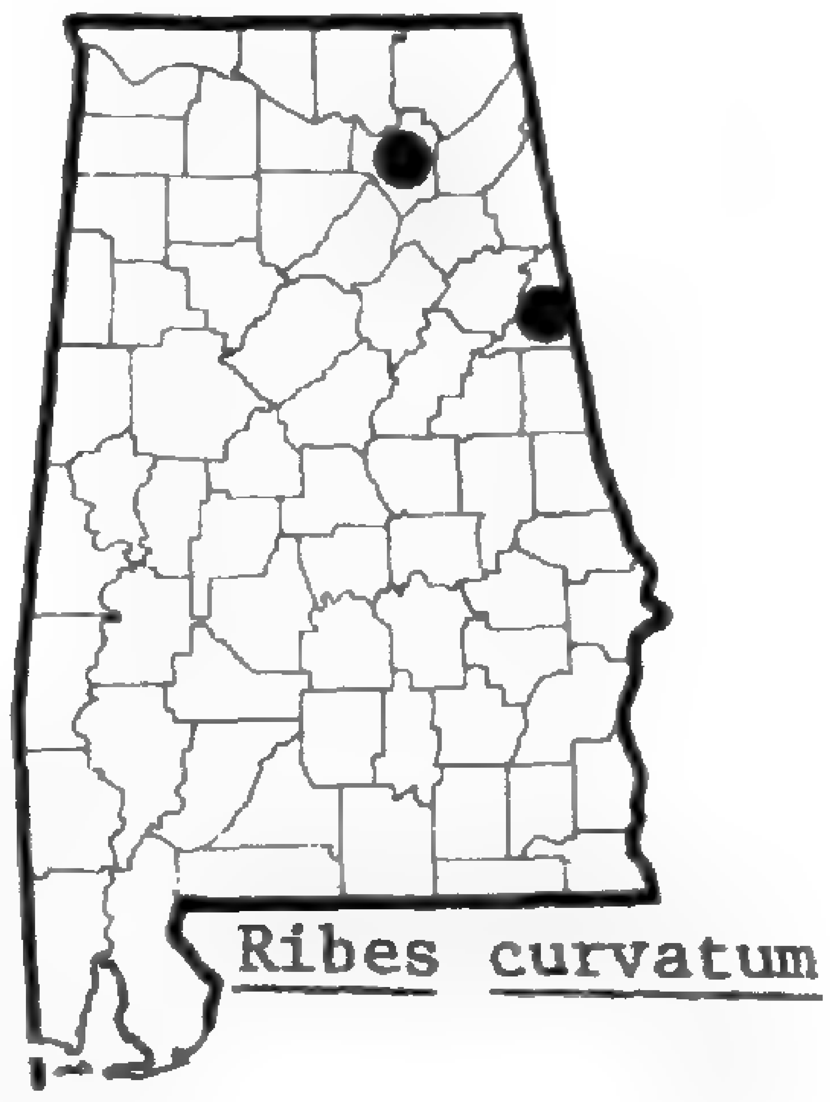
H. arborescens subsp. *discolor* (Seringe) McClintock. Rich woods; throughout, except southern CP. *H. cinerea* Sm.—M, S; *H. arborescens cordata* (Pursh) T. & G.—M.

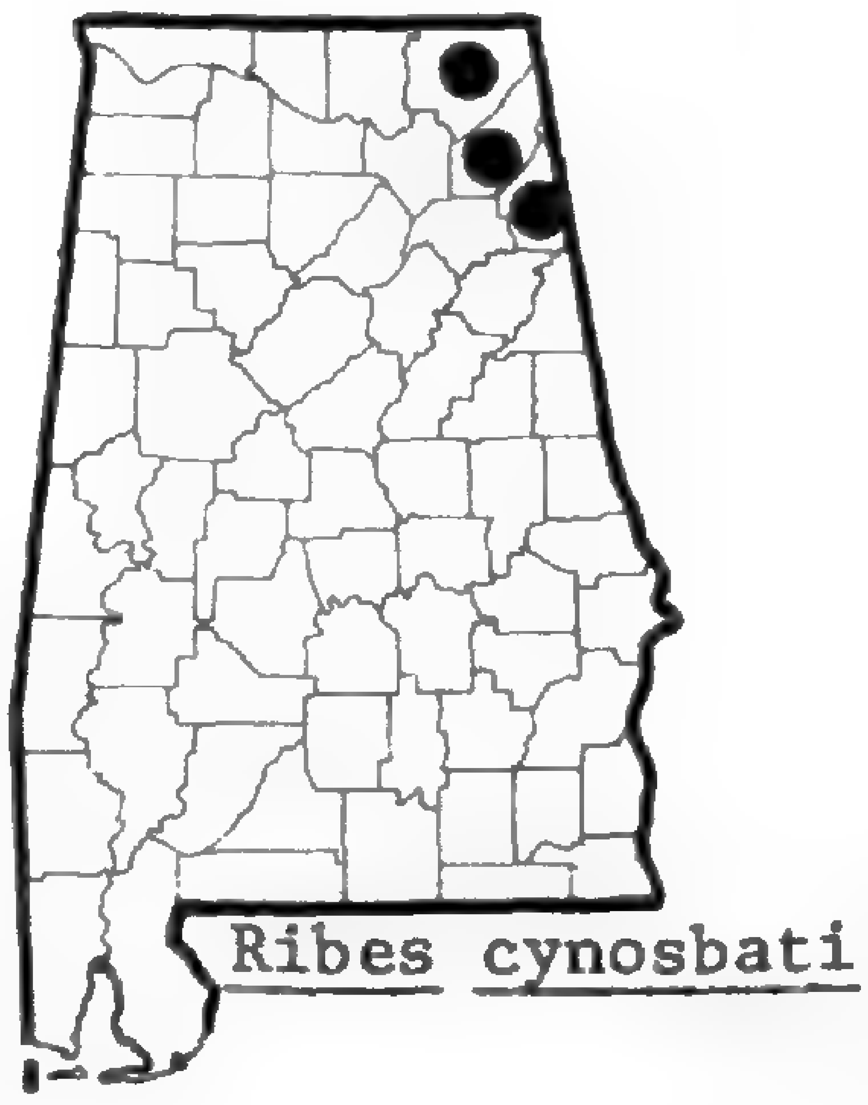

Hydrangea quercifolia


Itea virginica

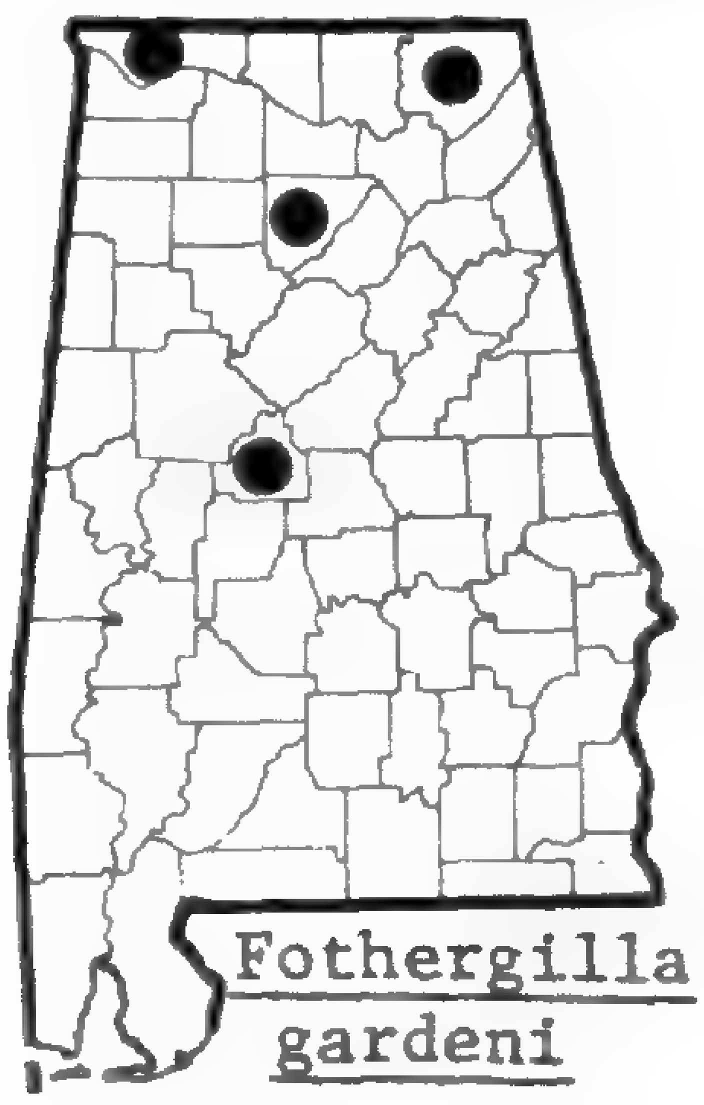

Philadelphus hirsutus

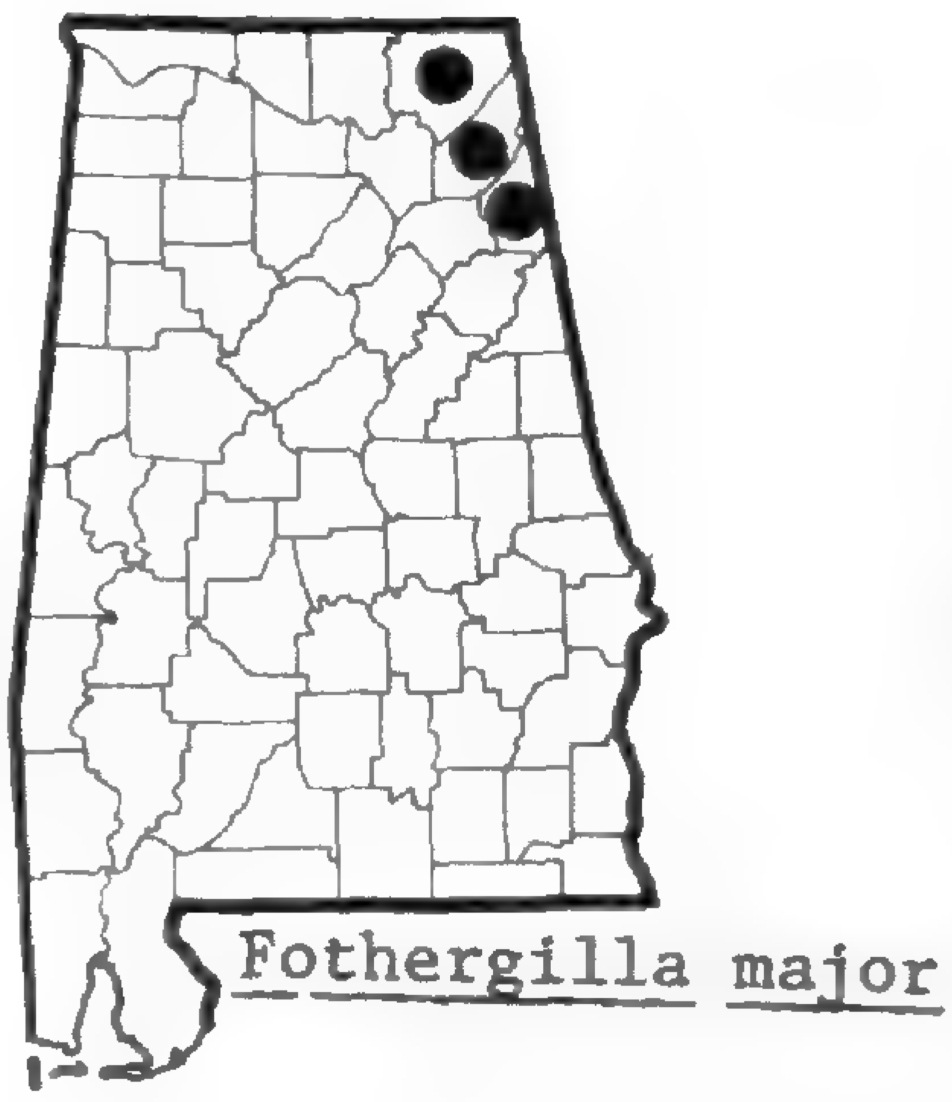

Philadelphus inodorus

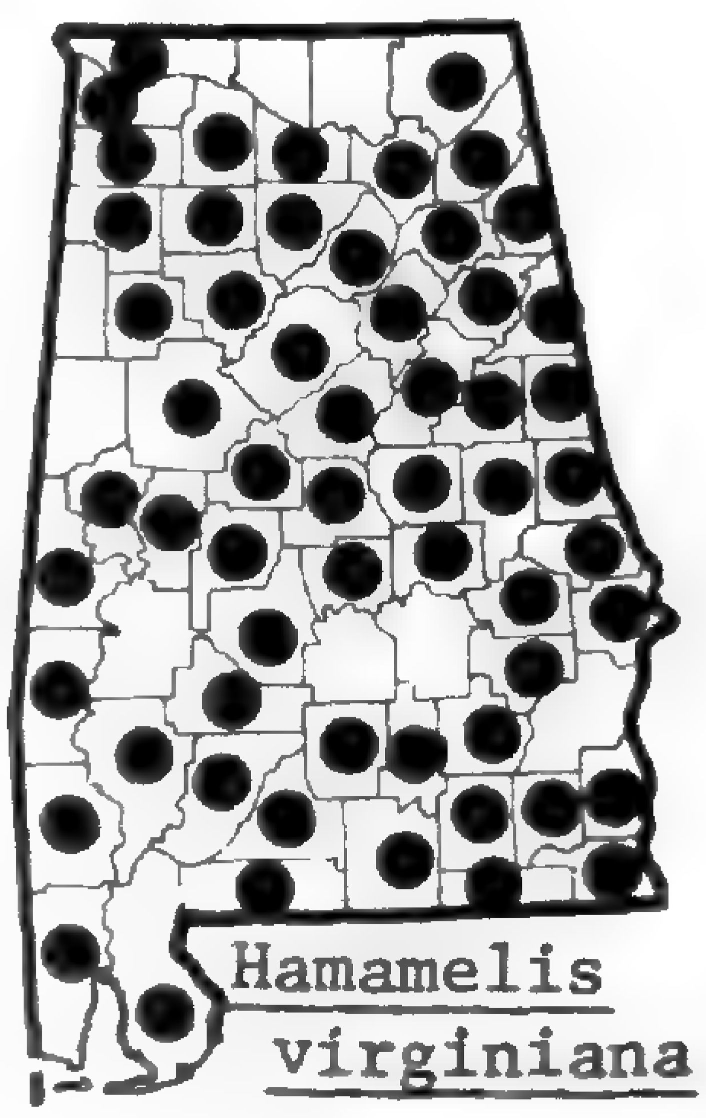

Ribes curvatum


Ribes cynosbati

27. HAMAMELIDACEAE


Fothergilla gardeni


Fothergilla major


Hamamelis virginiana

2. *H. quercifolia* Bartram, Seven-Bark. Late spring–early summer; summer–fall. Rich or mesic woods; throughout.

3. *Itea* L.

1. *I. virginica* L. Spring–early summer; summer–fall. Seepages, ditches, streambanks; throughout.

4. *Philadelphus* L., Mock-Orange

1. Pedicels and hypanthia pubescent .... 1. *P. hirsutus*
1. Pedicels and hypanthia glabrous .... 2. *P. inodorus*

1. *P. hirsutus* Nuttall. Spring; summer. Dry woods, open slopes, infrequent; AM, CuP, HR.

2. *P. inodorus* L. Spring; summer. Rich woods, infrequent; CP, P, CuP, VR. *P. grandiflorus* Willd.—M, S; *P. gloriosus* Bead.—S.

5. *Ribes* L., Gooseberry

1. Hypanthium glandular .... 1. *R. curvatum*
1. Hypanthium spiny, eglandular .... 2. *R. cynosbati*

1. *R. curvatum* Small. Spring; summer. Rocky woods, rare; AM, CuP. *R. curvata* Sm.—M; *Grossularia curvata* (Sm.) Cov. & Britt.—S.

2. *R. cynosbati* L. Spring; summer. Rocky, mesic woods, rare; CuP. *Grossularia cynosbati* L.—S.

Deutzia sp. has been noted as escaped by Dean (1961), without locality.

27. Hamamelidaceae

1. Leaves lobed .... 3. *Liquidambar*
1. Leaves unlobed 2
   2. Flowers and fruit in terminal spikes; petals absent; stamens more than 4 .... 1. *Fothergilla*
   2. Flowers and fruit axillary; petals and stamens 4 .... 2. *Hamamelis*

1. *Fothergilla* Murray

1. Filaments and capsules (including style) more than 10 mm long; leaves glabrous or glabrate above .... 1. *F. gardenii*
1. Filaments and capsules (including style) less than 10 mm long; leaves evidently stellate-pubescent above .... 2. *F. major*

1. *F. gardenii* Murray. Spring; summer–fall. Rocky woods, rare; CP, CuP, HR. *F. carolina* (L.) Britt.—M.

2. *F. major* (Sims) Lodd. Spring; summer–fall. Alluvial woods, rare; CuP.

The Alabama populations of this genus are in need of critical study.

2. *Hamamelis* L., Witch-Hazel

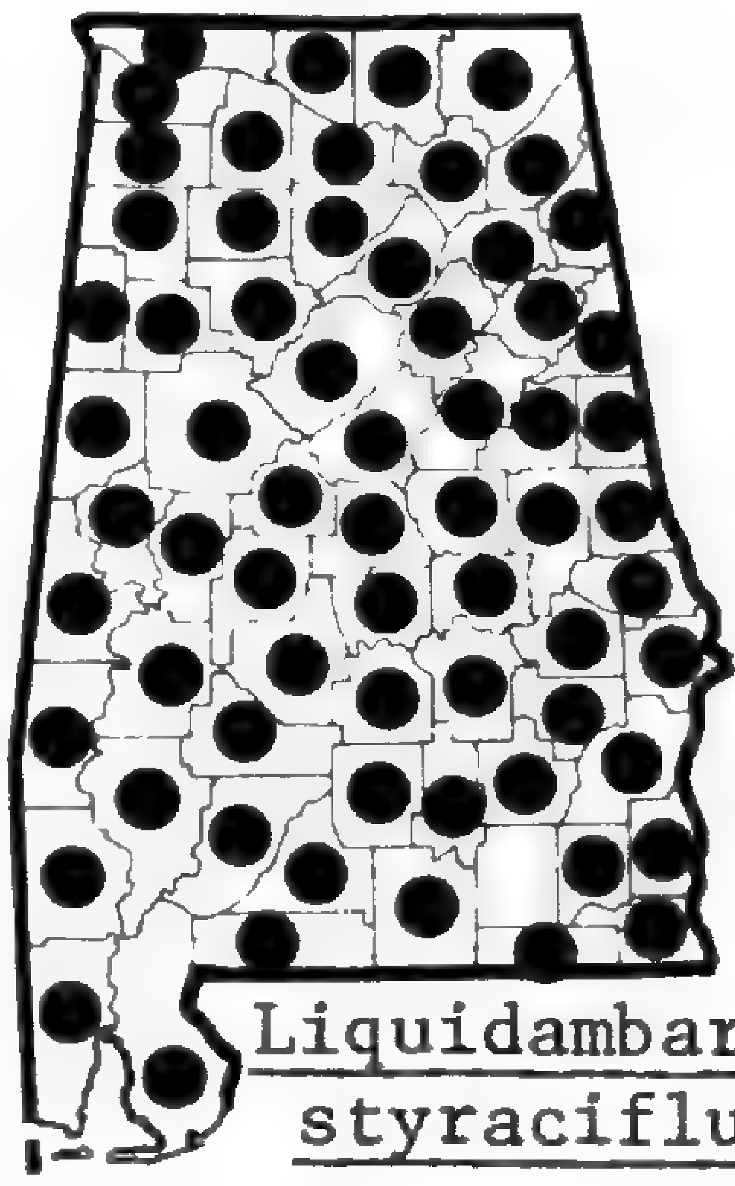
1. *H. virginiana* L. Fall–winter; fall. Dry, mesic and low woods; throughout.

3. *Liquidambar* L., Sweet Gum

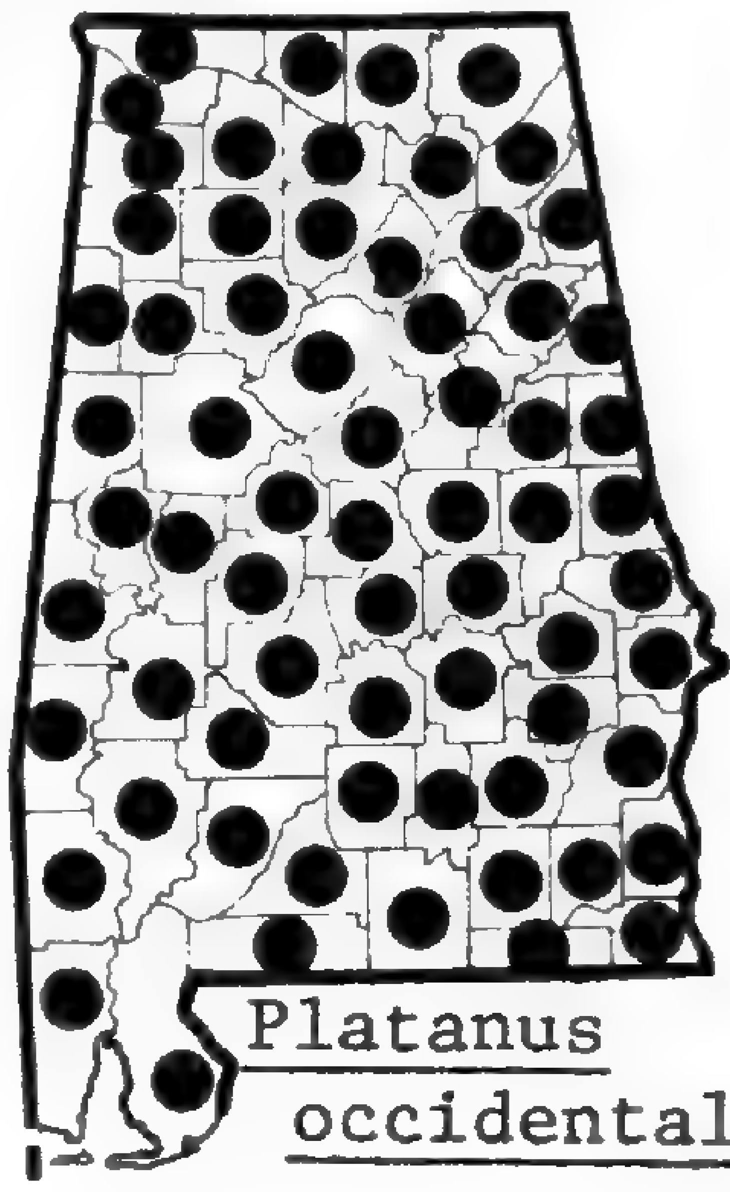
1. *L. styraciflua* L. Spring; fall. Deciduous woods, fields, fencerows; throughout.

28. PLATANACEAE

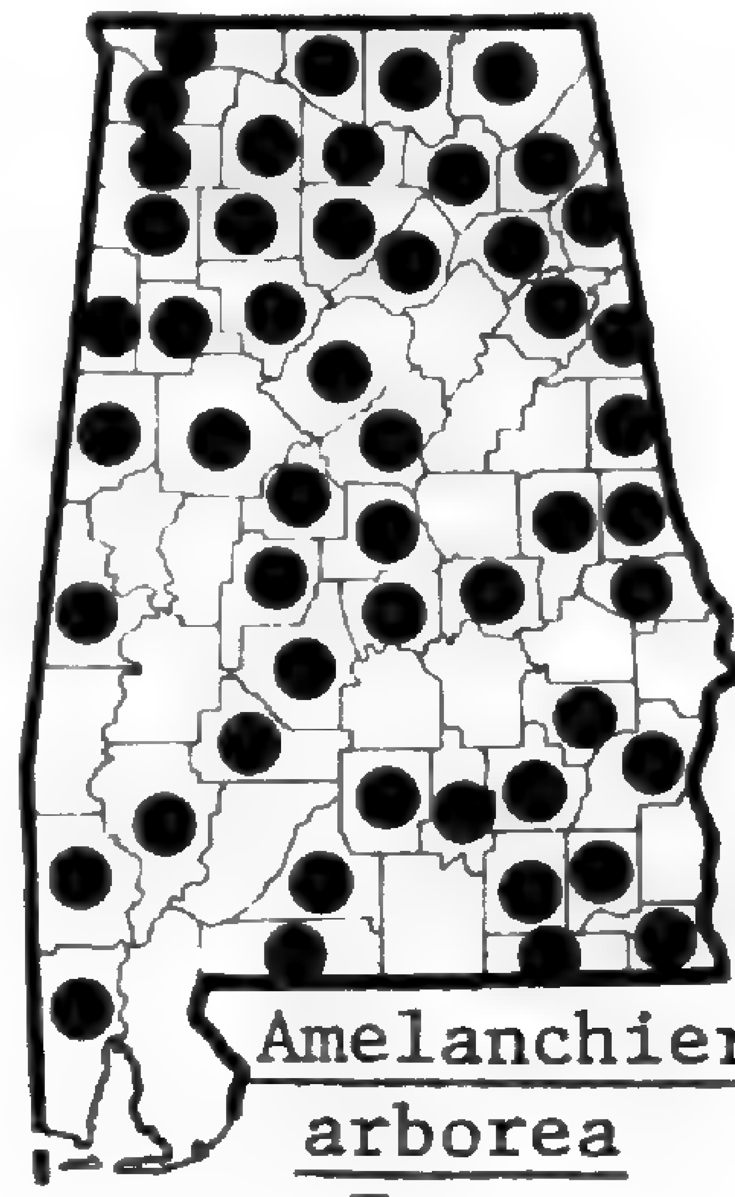
29. ROSACEAE



Liquidambar styraciflua

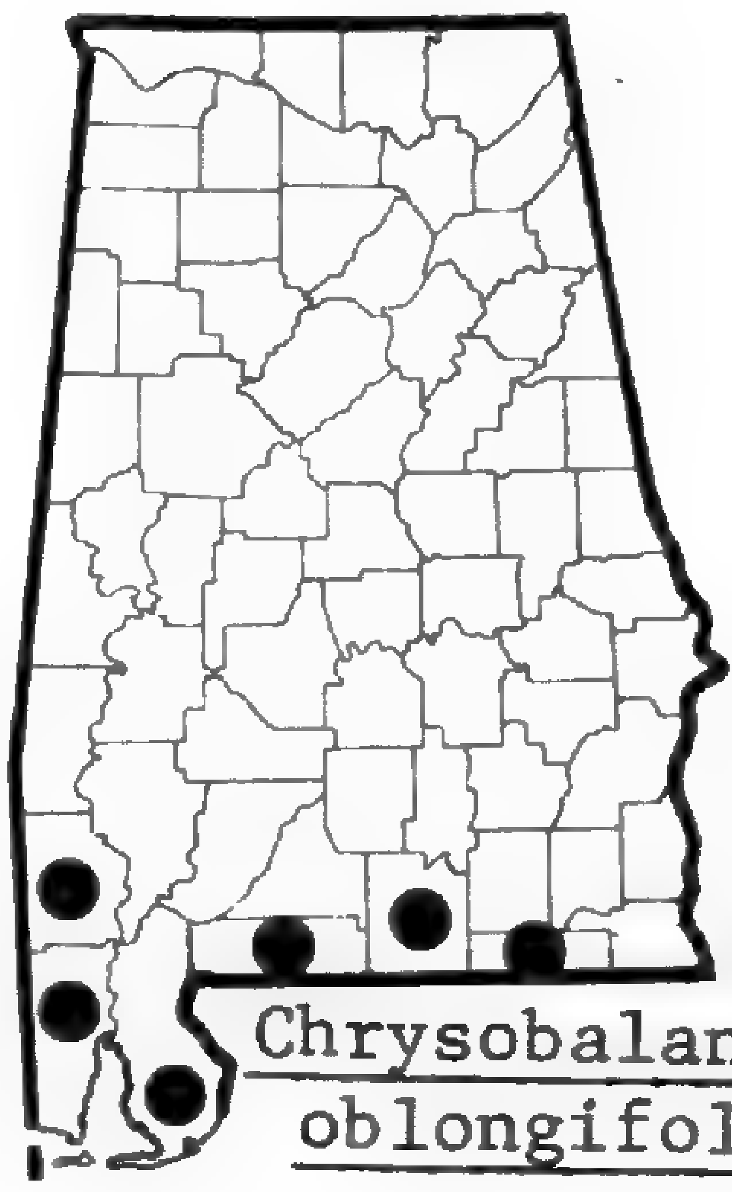


Platanus occidentalis



Amelanchier arborea Fern.

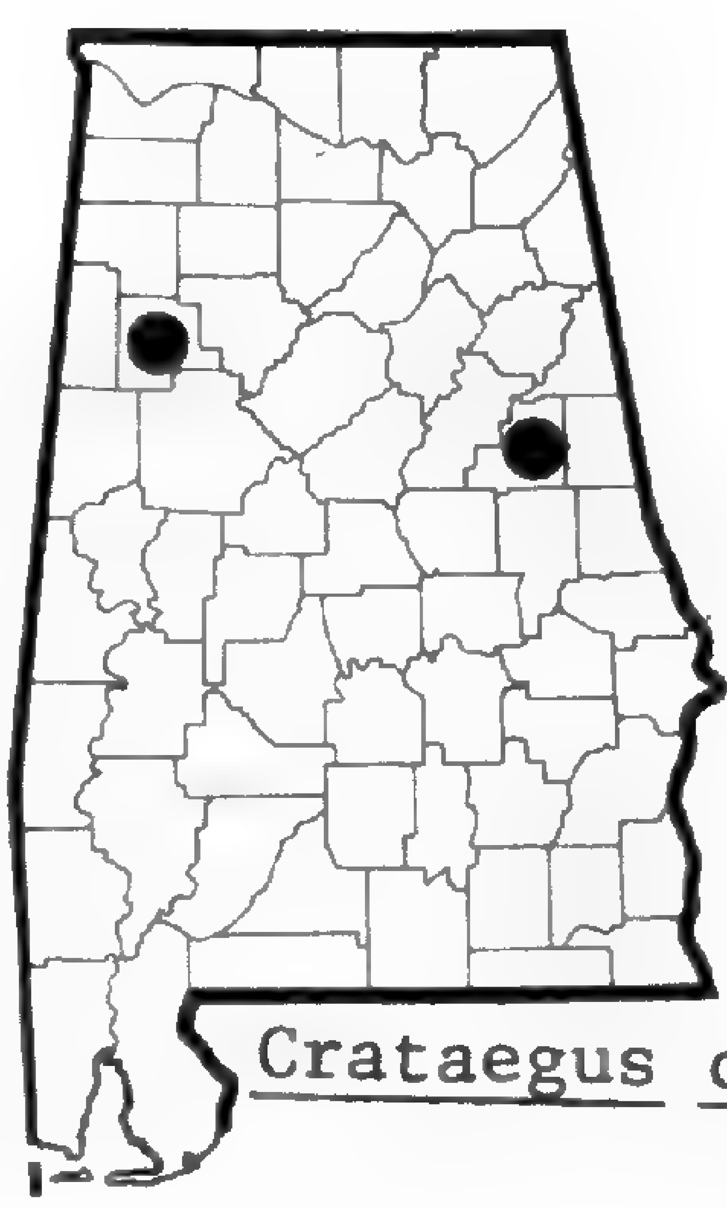
Amelanchier canadensis



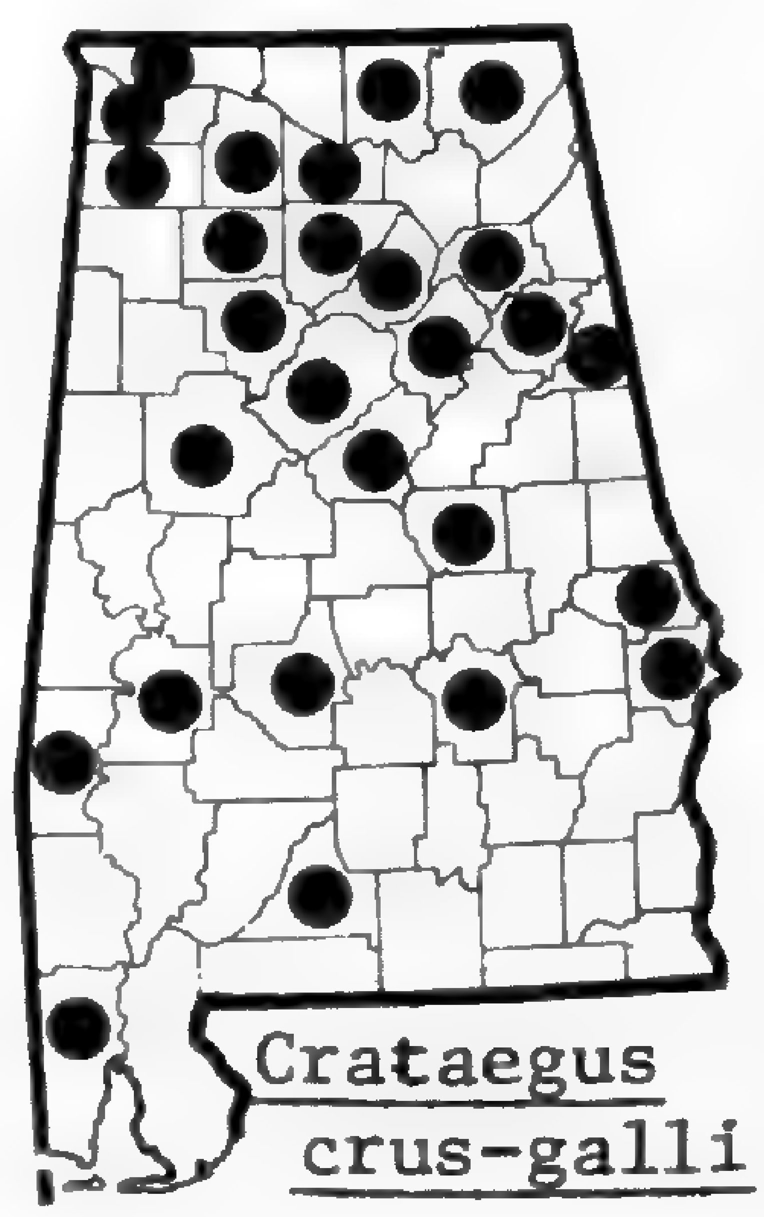
Chrysobalanus oblongifolius

Crataegus aestivalis (Walt.)

Crataegus brachyacantha



Crataegus coccinea



Crataegus crus-galli

28. Platanaceae

1. *Platanus* L., Sycamore

1. *P. occidentalis* L. Spring; fall. Low woods; throughout.

29. Rosaceae

1. Leaves pinnately compound 2
  2. Flower perigynous, ovaries and fruit enclosed within hypanthium; fruit not drupaceous ..... 10. *Rosa*
  2. Flower hypogynous, ovaries and fruit borne above calyx on elongated torus; fruit an aggregate of drupelets ..... 11. *Rubus*
1. Leaves simple, palmately compound, or absent at anthesis 3
  3. Leaves palmately compound ..... 11. *Rubus*
  3. Leaves simple, or absent at anthesis 4
    4. Plant in flower 5
      5. Corolla absent ..... 5. *Neviusia*
      5. Corolla present 6
        6. Ovary inferior, or partially so 7
          7. Inflorescence racemose ..... 1. *Amelanchier*
          7. Inflorescence corymbose or axillary-solitary 8
            8. Inflorescence a compound corymb or axillary-solitary 9
              9. Plant thornless; leaves crenate, unlobed ..... 12. *Sorbus*
              9. Plant with thorns or leaves lobed 10
                10. Leaves evergreen ..... 8. *Pyracantha*
                10. Leaves deciduous ..... 3. *Crataegus*
            8. Inflorescence a simple corymb 11
              11. Petals white; leaves entire to serrulate ..... 9. *Pyrus*
              11. Petals pink, often fading to white; leaves coarsely crenate or serrate to lobed ..... 4. *Malus*
        6. Ovary superior 12
          12. Pistil 1 13
            13. Flowers in racemes, umbellate fascicles, or axillary-solitary; petals white or pink ..... 7. *Prunus*
            13. Flowers in panicles; petals yellow-green ..... 2. *Chrysobalanus*
          12. Pistils 2 or more 14
            14. Leaves lobed; flowers more than 2 cm broad; petals purple ..... 11. *Rubus*
            14. Leaves unlobed or flowers less than 1 cm broad; petals white 15
              15. Flowers in panicles or compound corymbs ..... 13. *Spiraea*
              15. Flowers in simple corymbs 16
                16. Leaves cuneate ..... 13. *Spiraea*
                16. Leaves rounded to truncate ..... 6. *Physocarpus*
    4. Plant in fruit 17
      17. Fruit an aggregate of drupelets ..... 11. *Rubus*
      17. Fruit not an aggregate of drupelets 18
        18. Fruit a pome 19
          19. Inflorescence a raceme ..... 1. *Amelanchier*
          19. Inflorescence a corymb 20
            20. Corymbs compound 21
              21. Midrib pubescent beneath with tawny trichomes ..... 12. *Sorbus*
              21. Midrib not pubescent beneath with tawny trichomes 22
                22. Leaves evergreen ..... 8. *Pyracantha*
                22. Leaves deciduous ..... 3. *Crataegus*
            20. Corymbs simple 23
              23. Endocarp indurate, bony 24
                24. Leaves evergreen ..... 8. *Pyracantha*
                24. Leaves deciduous ..... 3. *Crataegus*
              23. Endocarp cartilaginous or chartaceous 25

25. Leaves entire to serrulate; flesh of fruit gritty .... 9. *Pyrus*
25. Leaves coarsely crenate or serrate to lobed; flesh of fruit not gritty .... 4. *Malus*
18. Fruit follicular or drupaceous 26
26. Fruit solitary in fruiting calyx 27
27. Inflorescences terminating principal stems; leaves evergreen .... 2. *Chrysobalanus*
27. Inflorescences axillary or terminating short side branches; leaves deciduous or evergreen .... 7. *Prunus*
26. Fruits commonly 2 or more per fruiting calyx 28
28. Leaves 3-veined from base .... 6. *Physocarpus*
28. Leaves pinnately veined, not 3-veined from base 29
29. Inflorescence axillary-solitary or cymose .... 5. *Neviusia*
29. Inflorescence corymbose .... 13. *Spiraea*

1. *Amelanchier* Medicus, Sarvice-Berry

1. Sepal bases and hypanthium neck glabrous .... 1. *A. arborea*
1. Sepal bases and hypanthium neck pubescent .... 2. *A. canadensis*

1. *A. arborea* (Michaux f.) Fernald. Spring; spring–summer. Upland, mesic and alluvial woods; throughout. *A. botryapium* (L. f.) DC.—M; *A. canadensis* (L.) Medic.—H, S; *A. alabamensis* Britt.—S.

2. *A. canadensis* Medicus. Spring; spring–summer. Hedgerow, rare; CP.

Amelanchier sanguinea (Pursh) DC. and *A. arborea* var. *laevis* (Wiegand) Ahles have been reported from Alabama, but no specimens have been seen by the writer.

2. *Chrysobalanus* L.

1. *C. oblongifolius* Michaux, Gopher-Apple, Sweet-Shrub. Spring–early summer; fall. Sandy woods; OCP. *Geobalanus oblongifolius* (Michx.) Sm.—S.

3. *Crataegus* L., Hawthorn

1. Leaves predominantly cuneate to attenuate 2
2. Sepals glandular-serrate 3
3. Glands on petioles sessile 4
4. Flowers usually 2–3 in an inflorescence .... 6. *C. flava*
4. Flowers usually solitary .... 11. *C. uniflora*
3. Glands on petioles stalked 5
5. Leaves serrate to base .... 9. *C. punctata*
5. Leaves not serrate to base .... 11. *C. uniflora*
2. Sepals entire or only remotely glandular-serrate 6
6. Leaves usually 3-lobed apically, spatulate .... 10. *C. spathulata*
6. Leaves not 3-lobed apically, not spatulate 7
7. Branches of inflorescence pubescent .... 9. *C. punctata*
7. Branches of inflorescence glabrous 8
8. Leaves lustrous above, rarely lobed; fruit more than 9 mm long 9
9. Pyrenes usually 2; inflorescence compound, usually more than 3-flowered .... 4. *C. crus-galli*
9. Pyrenes usually 3–5; inflorescence simple, 1–3-flowered 10
10. Leaves pubescent beneath .... 1. *C. aestivalis*
10. Leaves glabrous beneath .... 2. *C. brachyacantha*
8. Leaves dull above, often lobed; fruit less than 9 mm long .... 12. *C. viridis*
1. Leaves predominantly rounded, truncate or cordate 11
11. Veins running to the sinuses as well as to the lobe apices 12
12. Leaves lobed; inflorescence glabrous or glabrate .... 8. *C. phaenopyrum*

12. Leaves dissected; inflorescence pubescent .... 7. *C. marshallii*
11. Veins not running to the sinuses 13
13. Sepals glandular-serrate 14
14. Petioles conspicuously glandular with sessile glands .... 6. *C. flava*
14. Petioles not glandular, or remotely glandular with stalked glands .... 3. *C. coccinea*
13. Sepals not glandular-serrate, or only remotely so .... 5. *C. flabellata*

1. *C. aestivalis* (Walter) Torrey & Gray. Spring; summer. Sandy woods, infrequent; OCP. *C. rufula* Sarg.—H; *C. tomentosa chapmani* Bead.—M.

2. *C. brachyacantha* Sargent & Engelm., Pomette-Bleue. Flowers, fruits not seen. Reported from OCP.—This taxon is so distinct that report of its occurrence by Dean (1961) should be considered reliable.

3. *C. coccinea* L. Spring; fall. Upland woods, rare; AM, CuP. *C. mollis* (T. & G.) Scheele, *C. rotundifolia* (Ehrh.) Borck.—M.

4. *C. crus-galli* L. Spring; fall. Thickets, fencerows, deciduous woods; throughout, but rare southward. *C. signata* Bead., *C. harbisonii* Bead., *C. mohrii* Bead.—S; *C. mohri* Bead.—M.

5. *C. flabellata* (Bosc) K. Koch. Spring; fall. Thickets, deciduous woods, infrequent; throughout. *C. intricata* Lang., *C. populifolia* Walt., *C. macrosperma* Ashe, *C. pruinosa* (Wendl.) K. Koch—S; *C. triflora* Chapm., *C. silvicola* Bead., *C. boyntoni* Bead., *C. biltmoreana* Bead.—M.

6. *C. flava* Aiton. Spring; summer–fall. Thickets, fencerows, upland woods; CP, P, AM, CuP, VR. *C. michauxii* Pers.—S, H; *C. floridana* Sarg.—S; *C. elliptica* Ait.—M.

7. *C. marshallii* Eggleston. Spring; late summer–fall. Low woods; throughout. *C. apiifolia* (Marsh.) Michx.—M, H.

8. *C. phaenopyrum* (L. f.) Medicus. Spring; fall. Low or mesic woods, infrequent to rare; CP, CuP, VR.

9. *C. punctata* Jacquin. Spring; fall. Rocky woods; CP (rare), CuP. *C. collina* Chapm.—M, S.

10. *C. spathulata* Michaux. Spring; fall. Thickets, fencerows, deciduous woods; throughout.

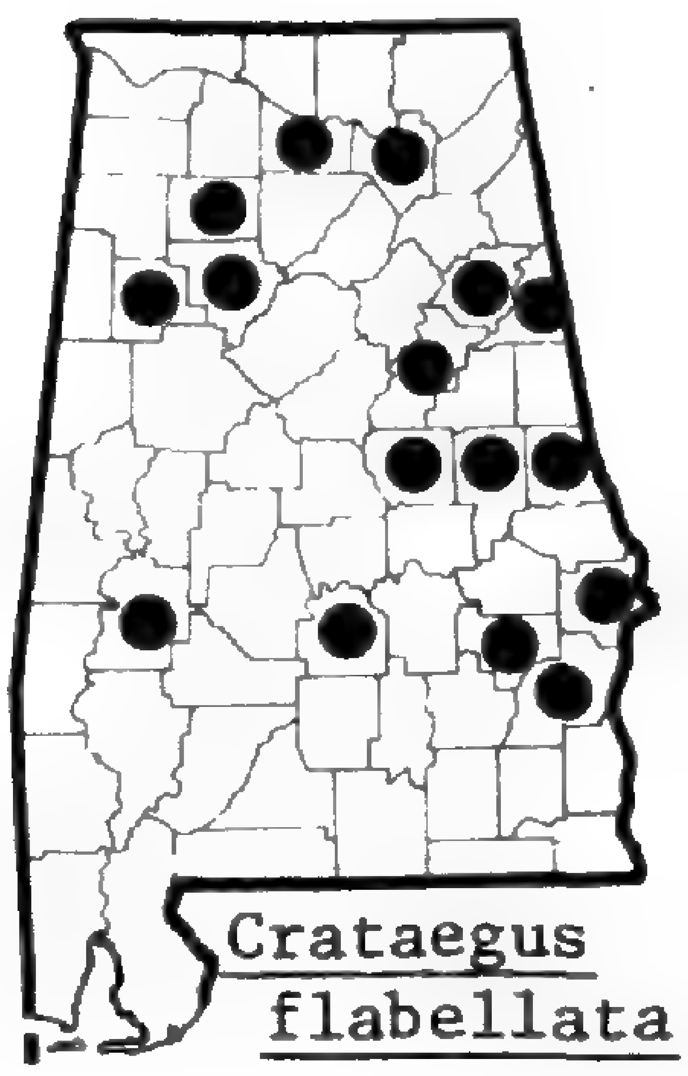
11. *C. uniflora* Muenchh. Spring–early summer; late summer–fall. Dry thickets, fencerows, rights-of-way, woods; CP, P, AM, CuP, VR.

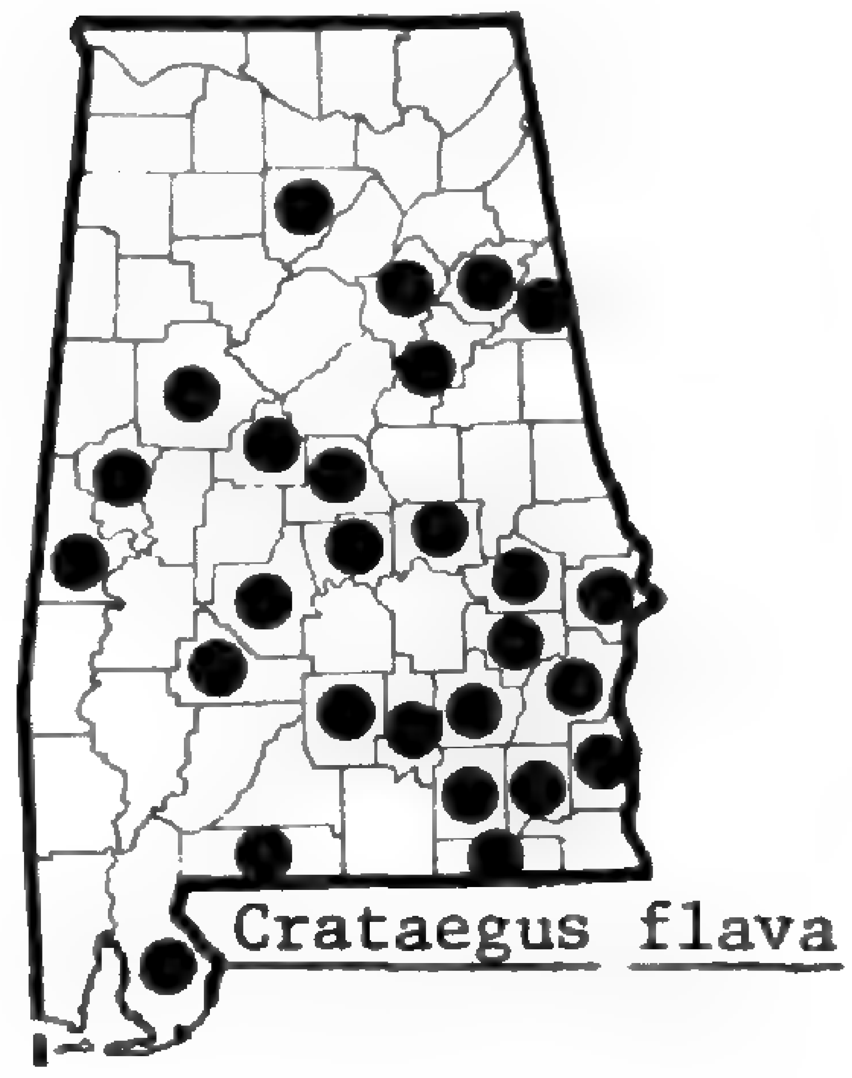
12. *C. viridis* L. Spring; fall. Low woods, rare; CP, VR, HR.

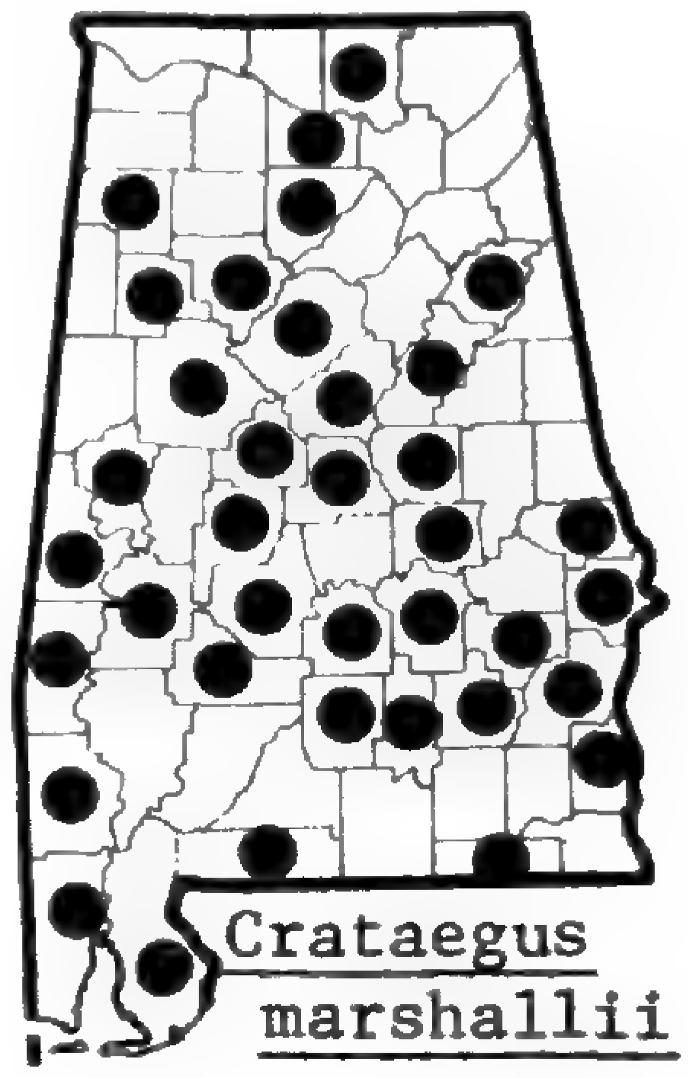
Taxa of uncertain status in Alabama include *Crataegus armentalis* Bead., *C. sargenti* Bead., *C. mollis* (T .& G.) Scheele, *C. triflora* Chapm., *C. austromontana* Bead., and *C. mendosa* Bead. Reports of *C. calpodendron* (Ehrh.) Medic. from Alabama may be based upon misdetermination of *C. punctata* Jacq.

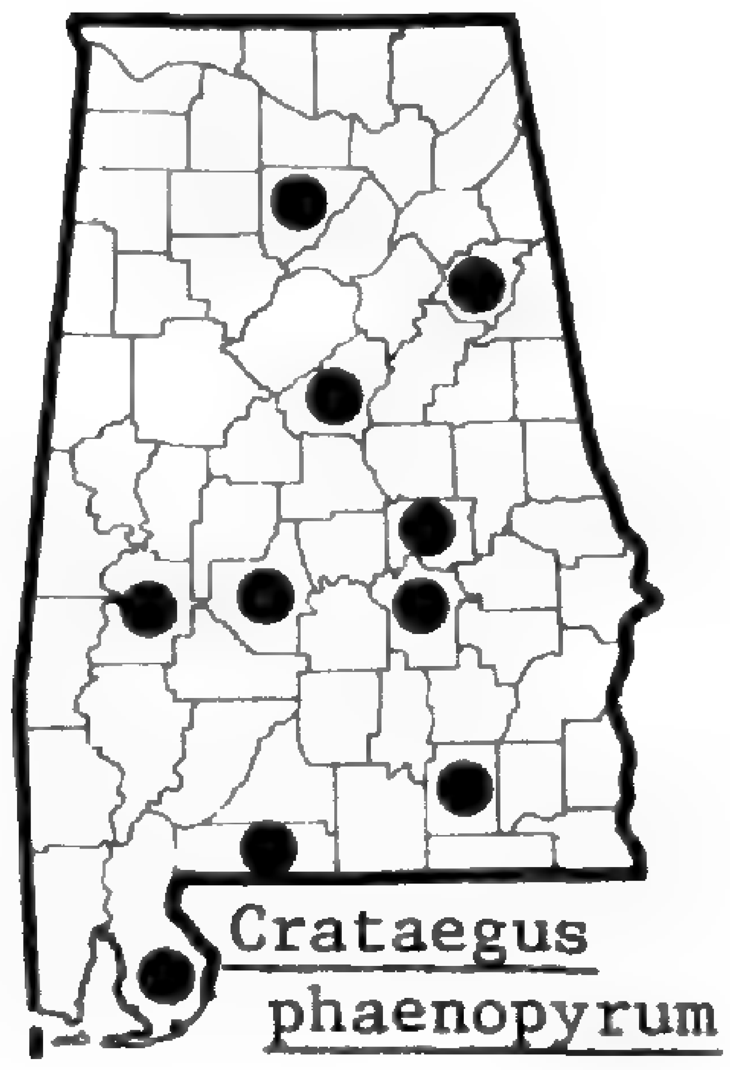
4. *Malus* Miller, Apple

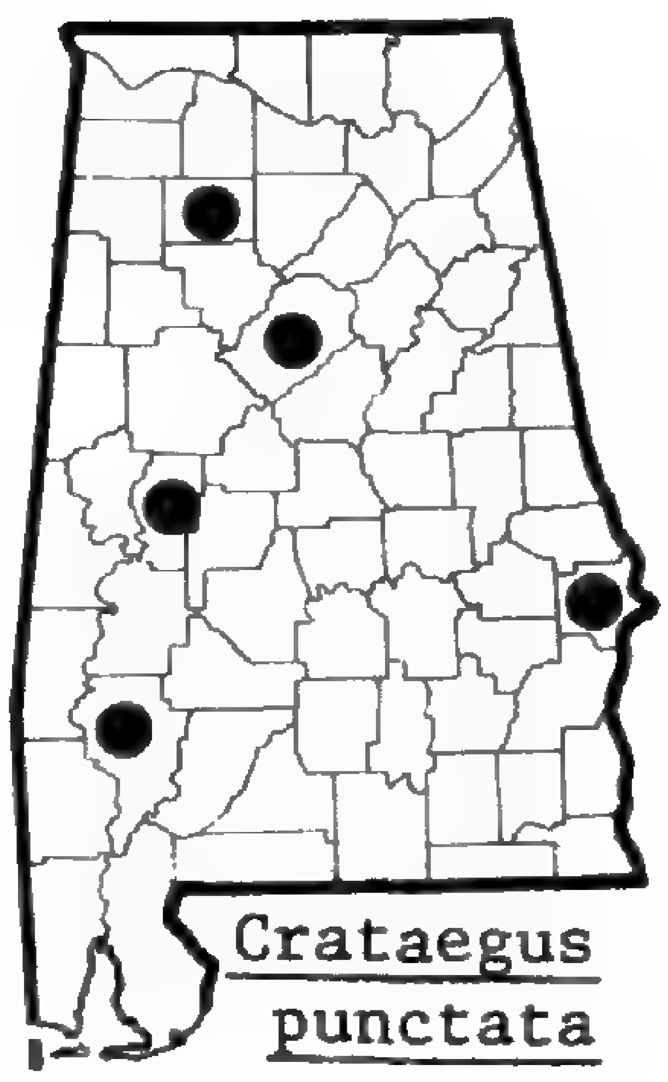
1. Calyx glabrous abaxially; leaves folded in bud 2
2. Some leaves crenate, not lobed .... 1. *M. angustifolia*
2. All leaves serrate, often basally lobed .... 2. *M. coronaria*
1. Calyx pubescent abaxially; leaves convolute in bud .... 3. *M. pumila*

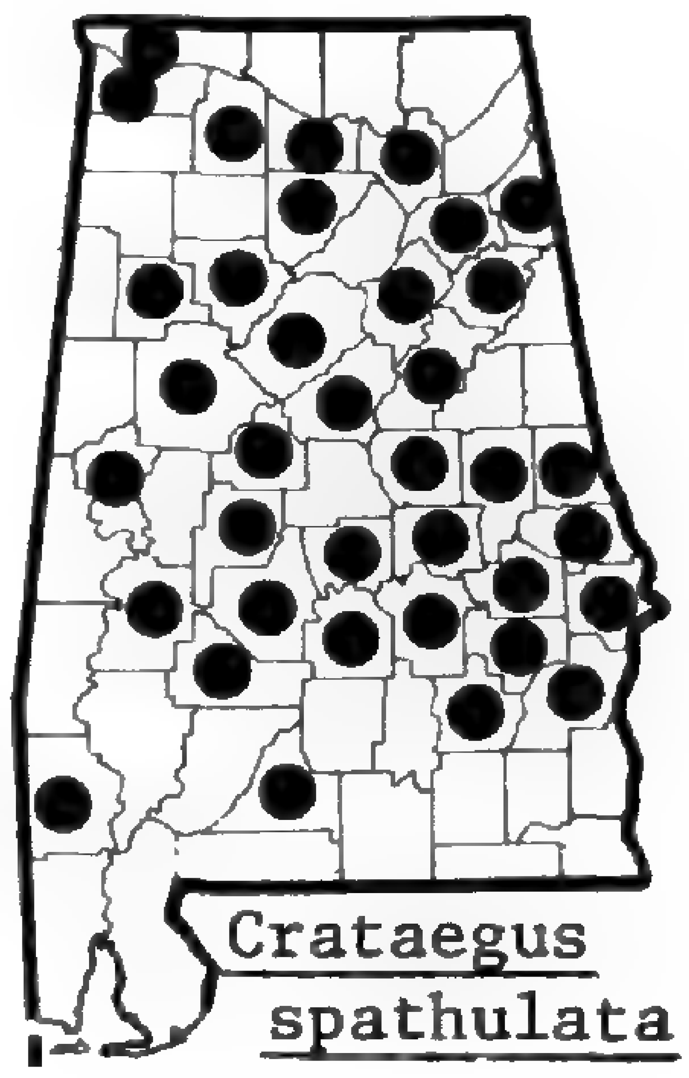

Crataegus flabellata

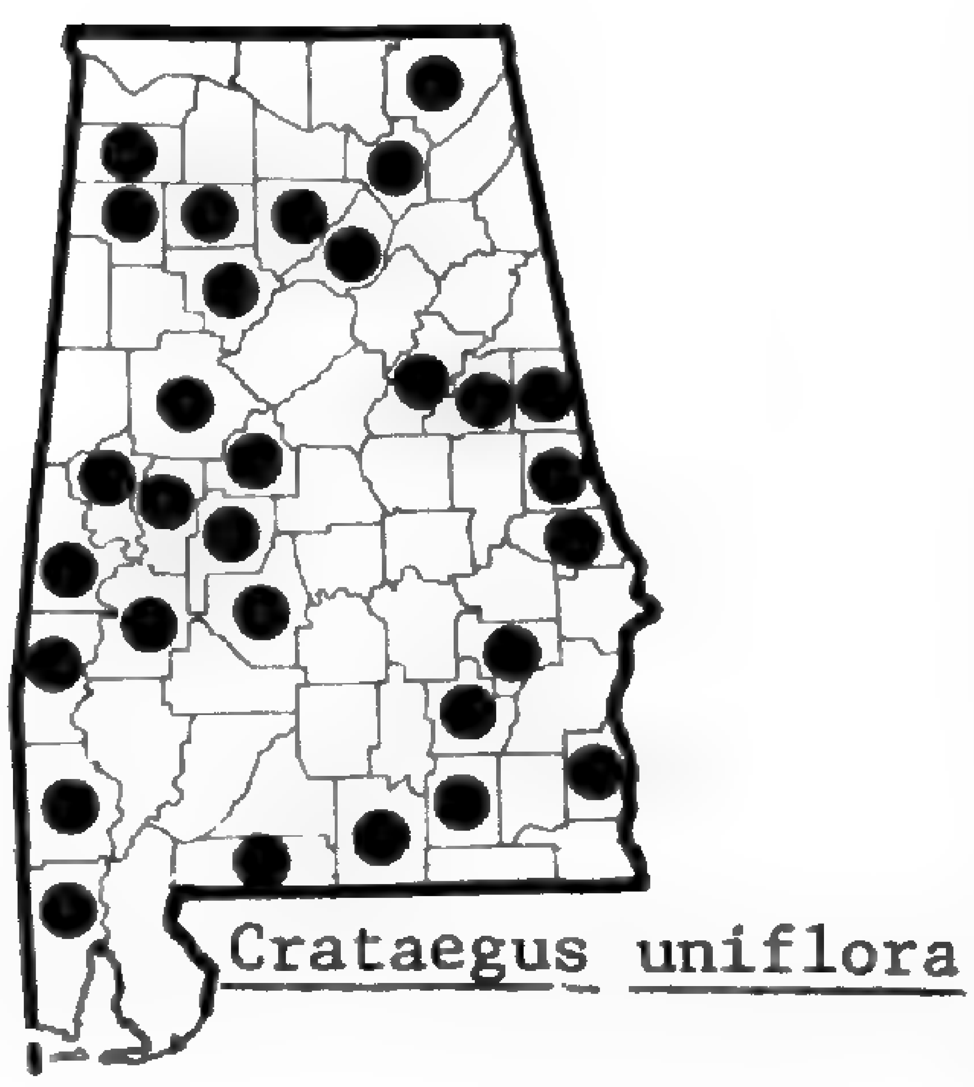

Crataegus flava

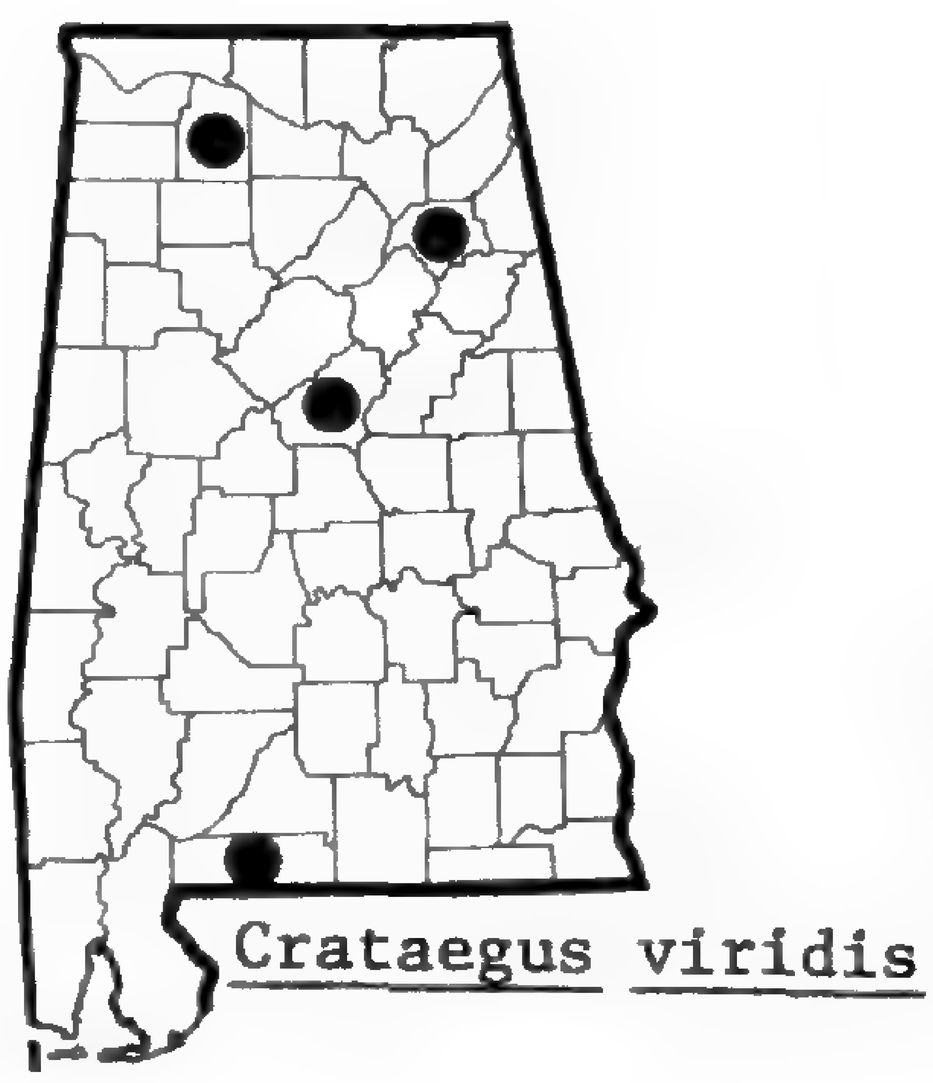

Crataegus marshallii

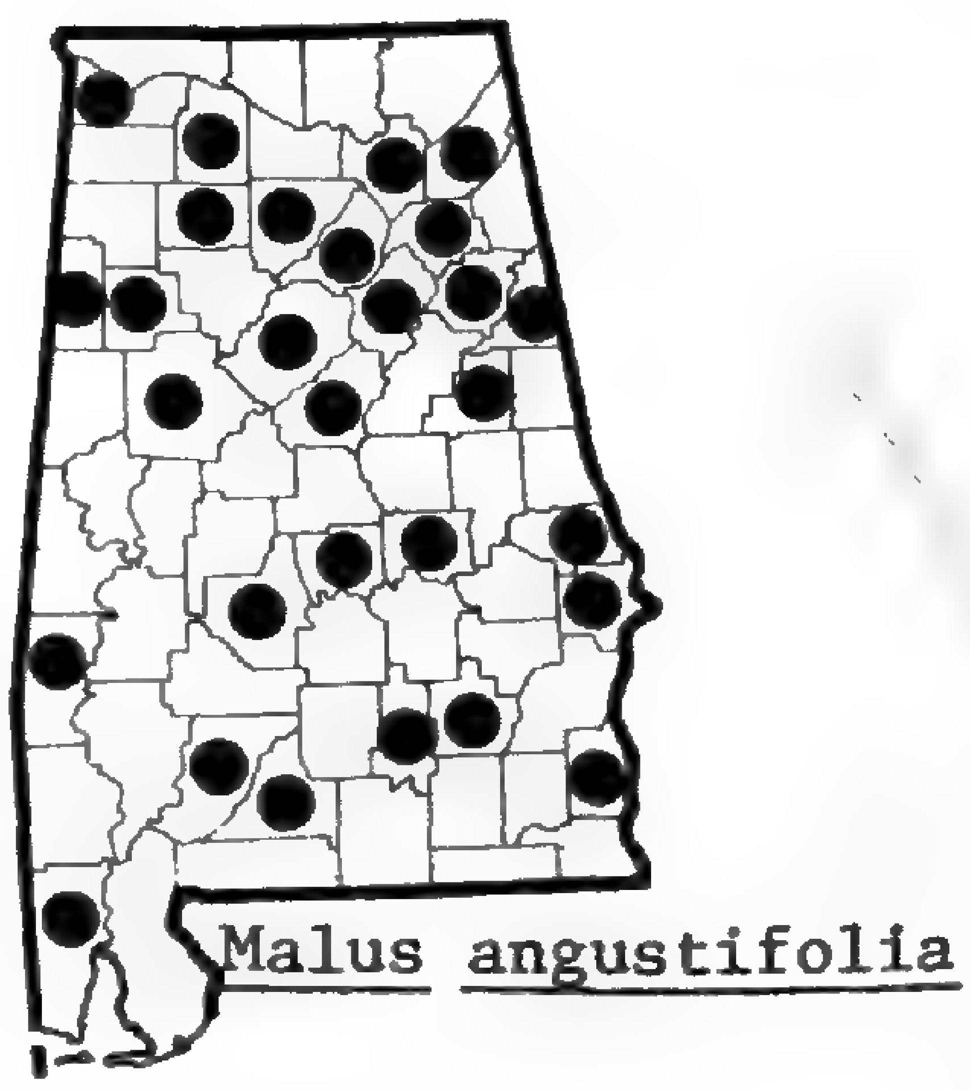

Crataegus phaenopyrum


Crataegus punctata


Crataegus spathulata


Crataegus uniflora


Crataegus viridis


Malus angustifolia

1. *M. angustifolia* (Aiton) Michaux, CRAB-APPLE. Spring; summer–fall. Upland thickets, woods; throughout.

2. *M. coronaria* (L.) Miller, CRAB-APPLE. Spring; summer–fall. Upland thickets, woods, infrequent to rare; CP, AM, CuP. *M. glaucescens* Rehd., *M. bracteata* Rehd.—S.

3. *M. pumila* Miller, COMMON A. Spring; summer–fall. Occasional escape; throughout.

Species 1 and 2 are in need of concurrent biosystematic evaluation.

5. *Neviusia* Gray

1. *N. alabamensis* Gray. Spring; fall. Rich woods over calcareous substrata, very rare; southern CuP, reported from HR.—One of the rarest and most celebrated taxa in Alabama. Known elsewhere from Arkansas and Missouri (Steyermark, 1963).

6. *Physocarpus* Maximowicz, NINEBARK

1. *P. opulifolius* (L.) Maximowicz. Spring; summer–fall. Rocky or alluvial woods, rare; P, CuP, VR, reported from HR. *P. stellatus* (Rydb.) Rehd.—H; *Opulaster opulifolius* (L.) Kuntze—M, H, S; *O. alabamensis* Rydb.—H, S; *O. intermedius* Rydb., *O. australis* Rydb.—S.

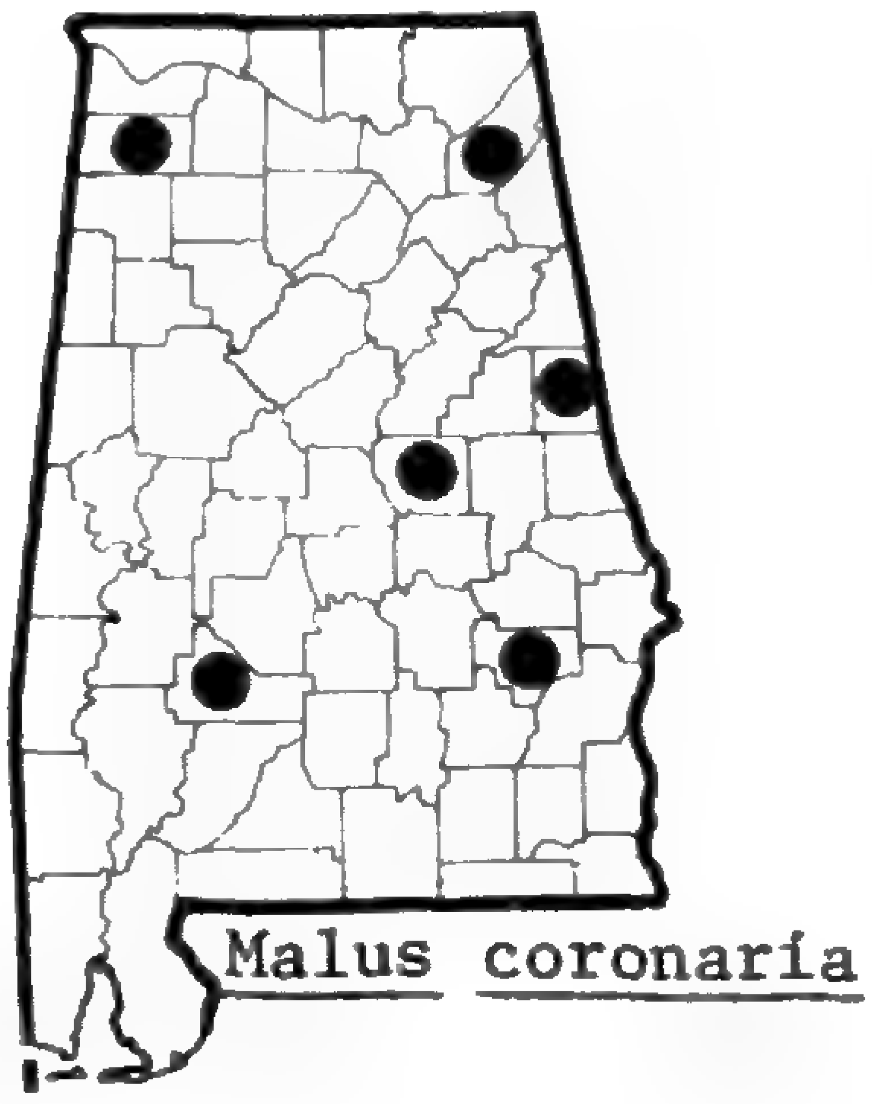
7. *Prunus* L.

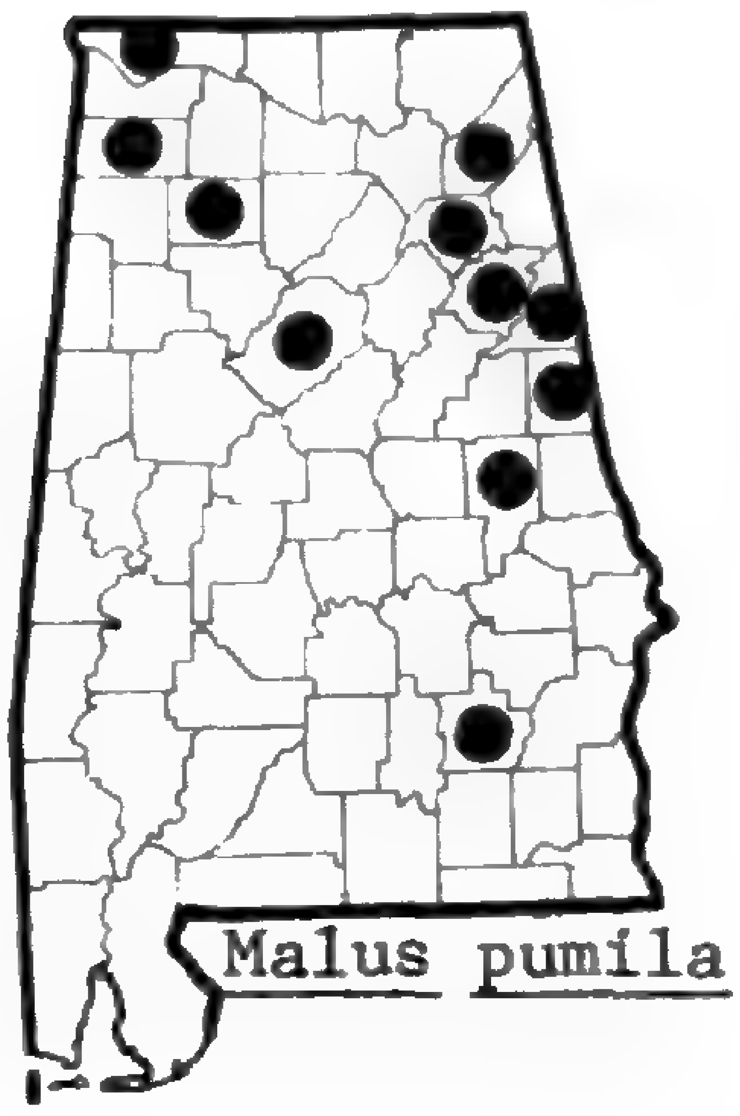
1. Inflorescence racemose 2
 2. Leaves evergreen; petioles not glandular .... 3. *P. caroliniana*
 2. Leaves deciduous; petioles usually glandular distally with 1–2 sessile glands .... 5. *P. serotina*
1. Inflorescence fasciculate or axillary 3
 3. Pedicels 2 mm or less long .... 4. *P. persica*
 3. Pedicels more than 5 mm long 4
  4. Leaves absent; plant in flower 5
   5. Petals averaging 7.5 mm or more in length .... 1. *P. americana*
   5. Petals averaging less than 7 mm in length .... 2. *P. angustifolia* or 6. *P. umbellata*
  4. Leaves present or plant in fruit 6
   6. Teeth of leaf margin conspicuously glandular .... 2. *P. angustifolia*
   6. Teeth of leaf margin not conspicuously glandular 7
    7. Leaves abruptly acuminate, usually doubly serrate; stone more than 1 cm long .... 1. *P. americana*
    7. Leaves acute or gradually acuminate, simply serrate; stone less than 1 cm long .... 6. *P. umbellata*

There are no apparent characteristics which will differentiate flowering individuals of *P. angustifolia* Marshall from those of *P. umbellata* Ell.

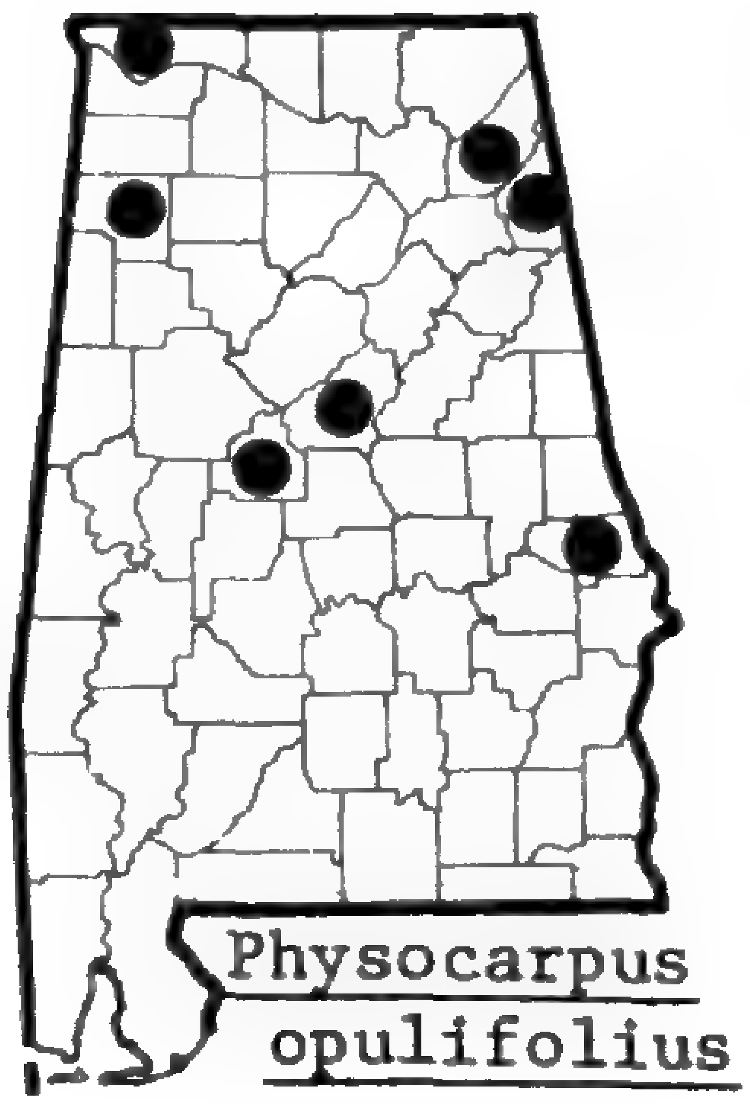
1. *P. americana* Marshall, WILD PLUM. Spring; summer.

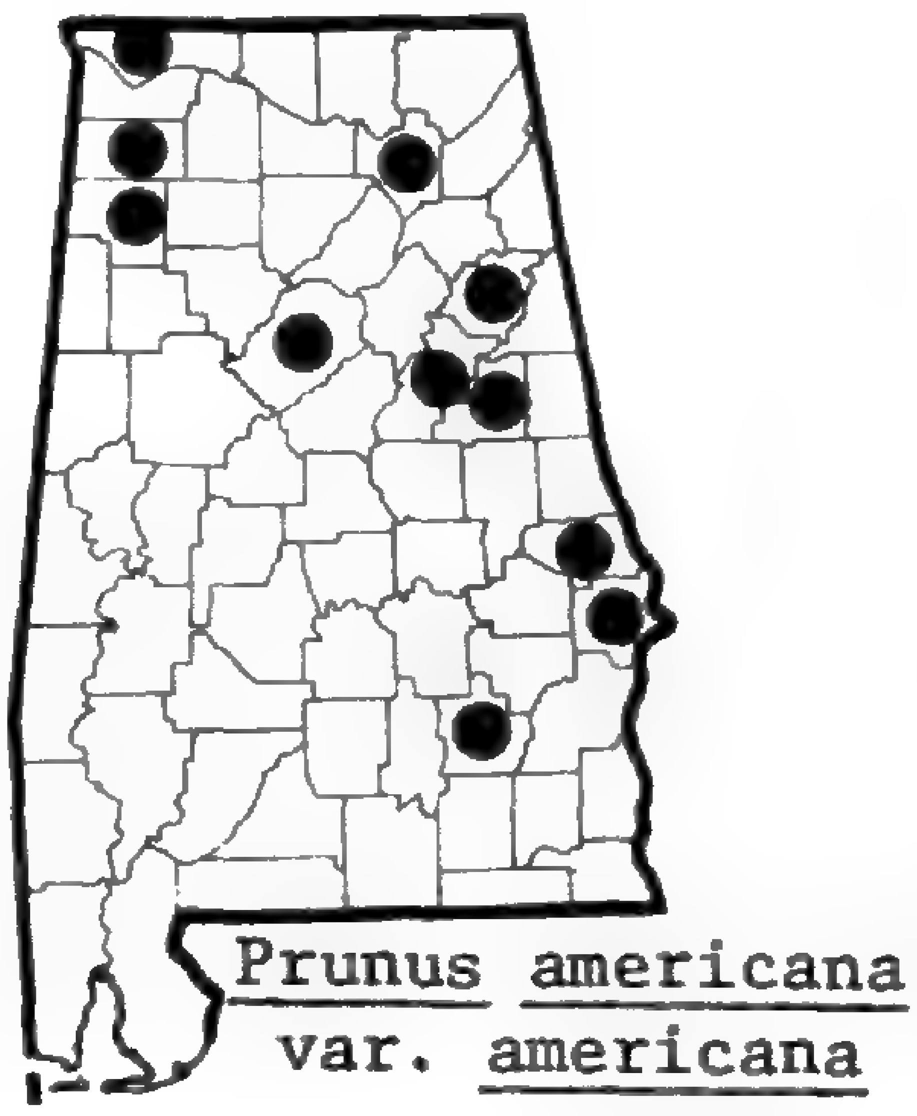
1. Pedicels and calyx tubes glabrous; leaves glabrous beneath or pubescent only near the principal veins .... *P. americana* var. *americana*
1. Pedicels and calyx tubes pubescent; leaves densely pubescent beneath .... *P. americana* var. *lanata*

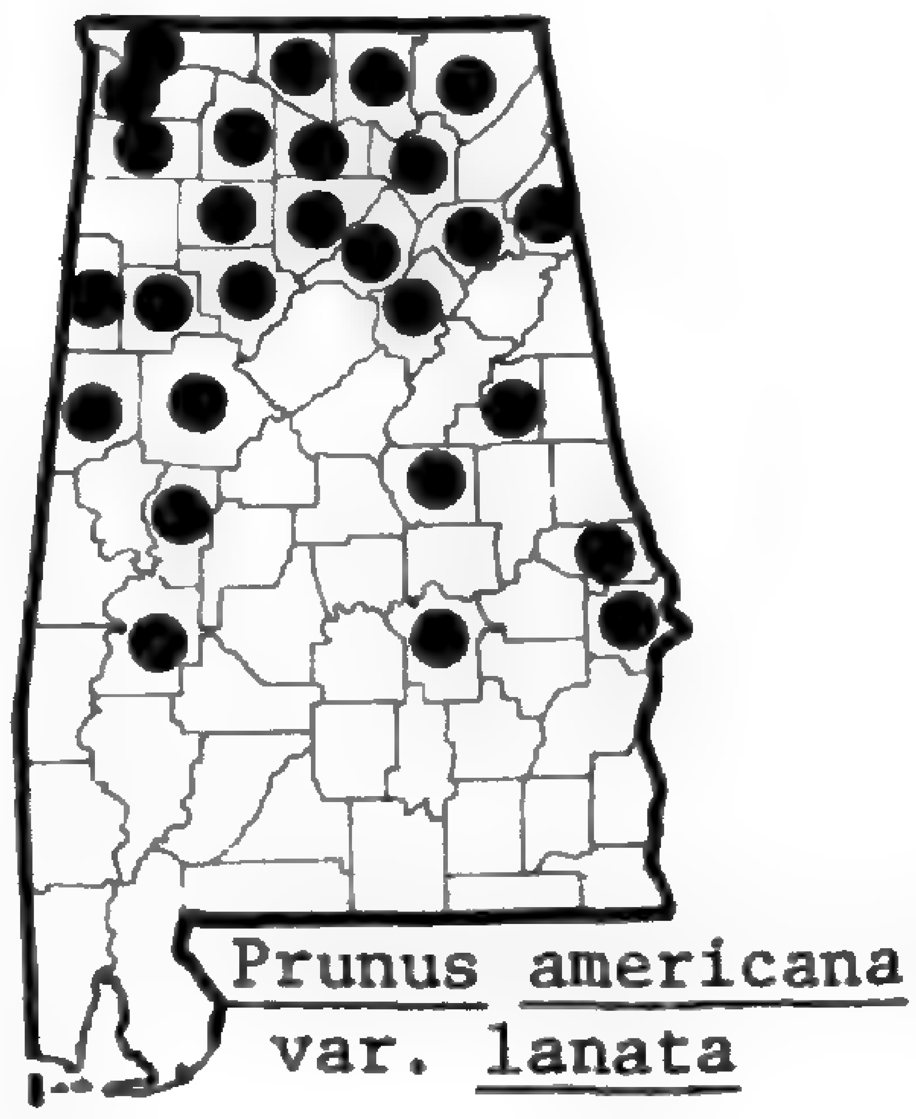

Malus coronaria

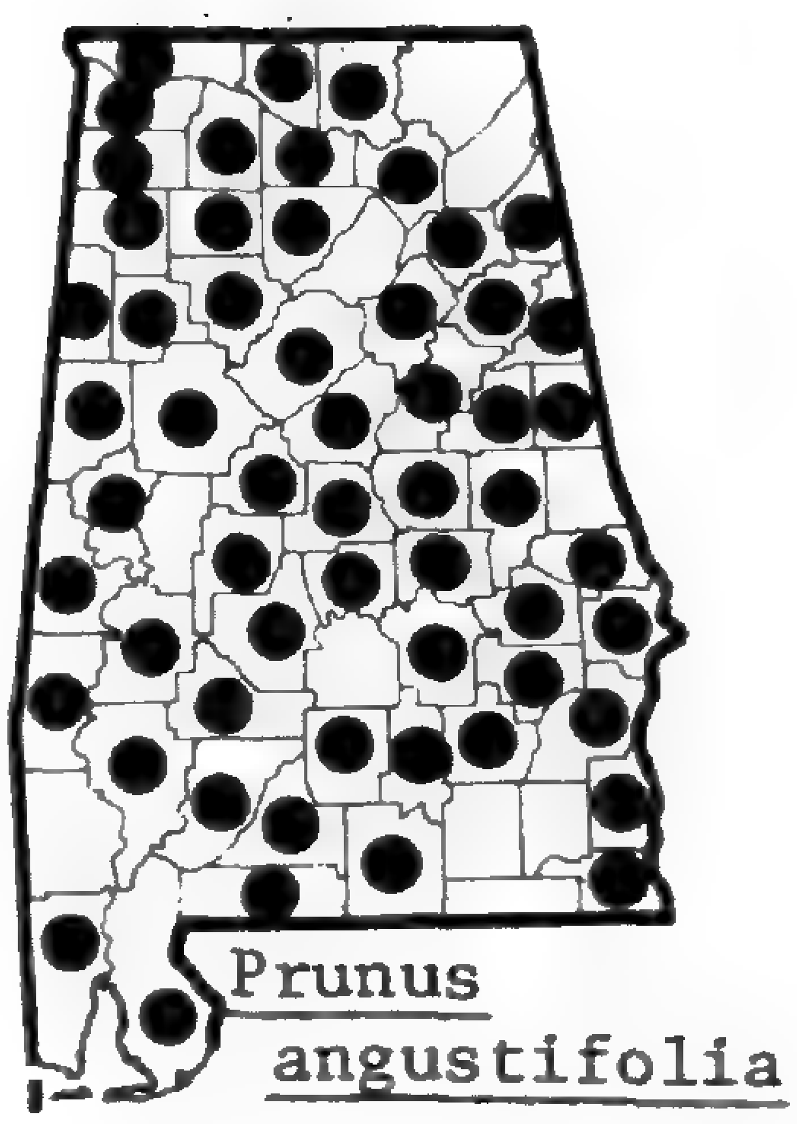

Malus pumila

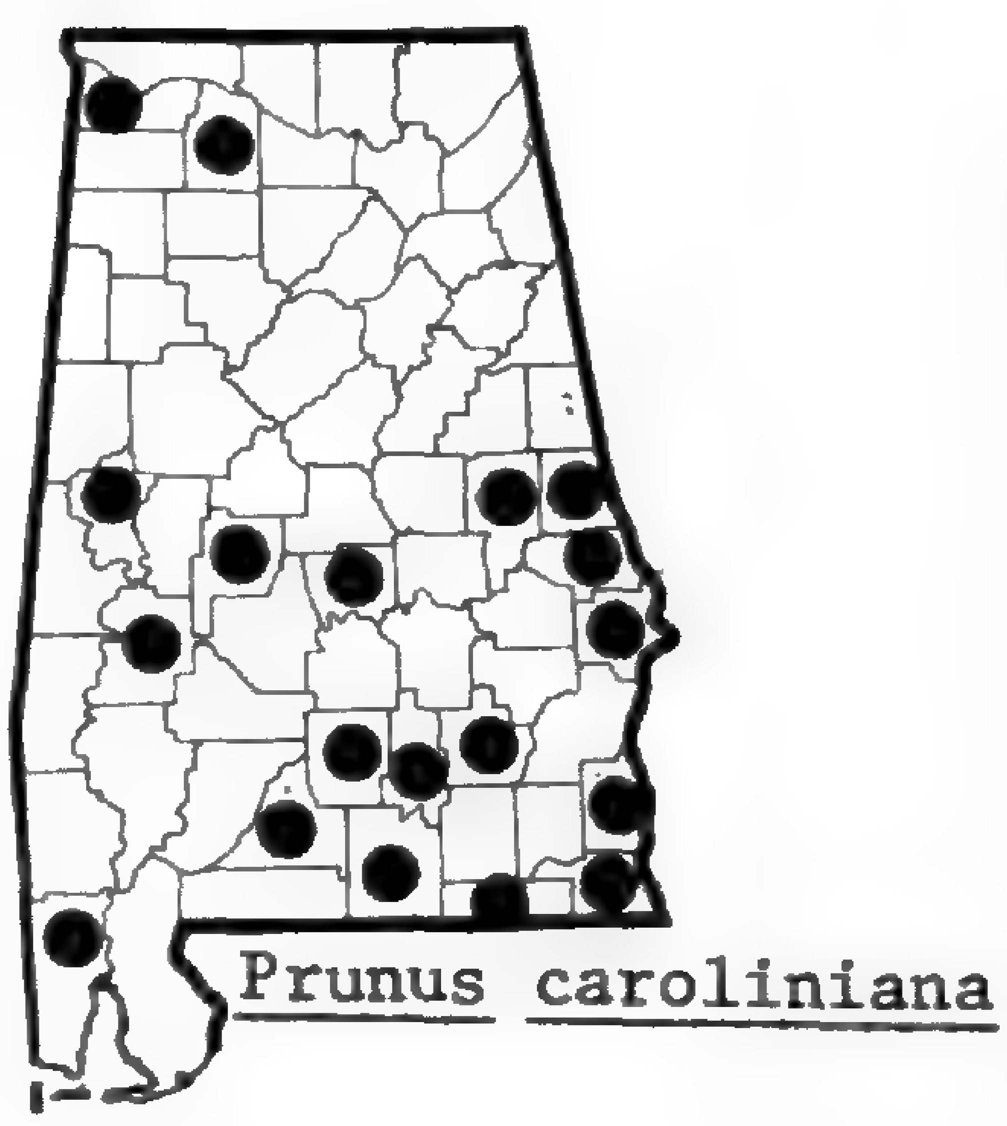

Neviusia
alabamensis

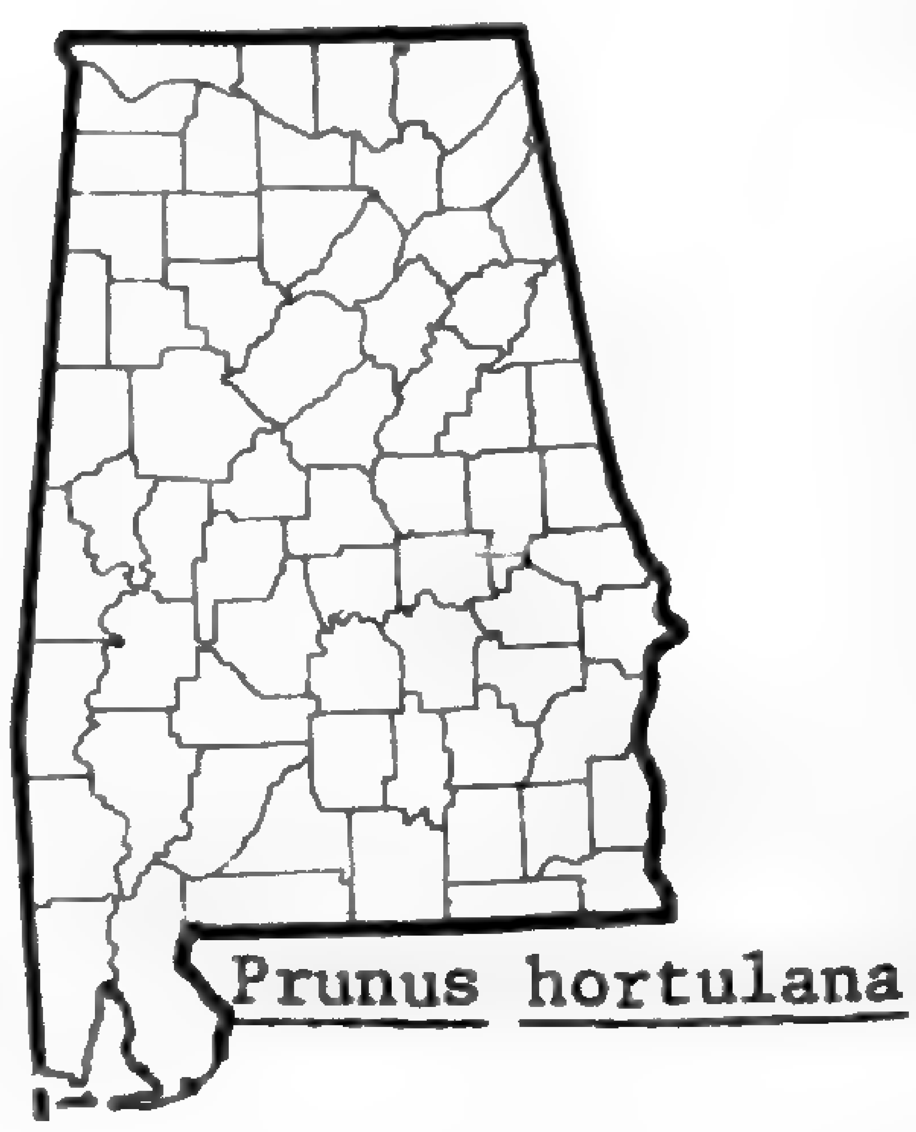

Physocarpus
opulifolius


Prunus americana
var. americana


Prunus americana
var. lanata


Prunus
angustifolia


Prunus caroliniana


Prunus hortulana

P. americana Marshall var. *americana*. Thickets, trash piles, deciduous woods; throughout.

P. americana Marshall var. *lanata* Sudworth. Thickets, trash piles, deciduous woods; throughout. *P. lanata* (Sudw.) Mackz. & Bush.—H; *P. mexicana* Watson—S.

2. *P. angustifolia* Marshall, CHICKSAW PLUM. Spring; late spring–early summer. Thickets (often of its own making), rights-of-way, woodland borders; throughout.

3. *P. caroliniana* Aiton, LAUREL CHERRY. Spring; fall. Fencerows, low woods, native and escaped from cultivation; CP, P, HR. *Laurocerasus caroliniana* (Mill.) Roem.—S.

4. *P. persica* (L.) Batsch., PEACH. Spring; summer. Fencerows, rights-of-way, trash heaps, woods borders; escaped throughout. *Amygdalus persica* L.—S.

5. *P. serotina* Ehrhart, BLACK CHERRY, WILD CHERRY. Spring; summer.

1. Leaves glabrous beneath, except often more or less pubescent near the veins; rachis of inflorescence glabrous .... *P. serotina* subsp. *serotina*
1. Leaves pubescent beneath over the entire blade; rachis of inflorescence pubescent .... *P. serotina* subsp. *hirsuta*

P. serotina Ehrhart subsp. *serotina*. Woods, fencerows, fields; throughout. *P. serotina neo-montana* (Sm.) Sudw.—M; *Padus virginiana* (L.) Mill.—S.

P. serotina Ehrhart subsp. *hirsuta* (Elliott) McVaugh. Rocky woods, infrequent; CP, AM, southern CuP, VR. *P. serotina* var. *alabamensis* (Mohr) Little—RAB; *P. alabamensis* Mohr—M, H; *P. australis* Bead.—H; *Padus alabamensis* (Mohr) Sm., *Padus australis* Bead.—S.

6. *P. umbellata* Elliott, HOG PLUM, SLOE PLUM. Spring; summer. Upland thickets, woodland borders; throughout, but more common southeastward. *P. injucunda* Sm.—M, S; *P. mitis* Bead.—S.

Prunus hortulana Bailey has been reported (as a waif?) from Mobile County. *Prunus gracilis* Engelm. & Gray cited by Mohr (1901) is of uncertain status.

8. *Pyracantha* Roemer, FIRETHORN

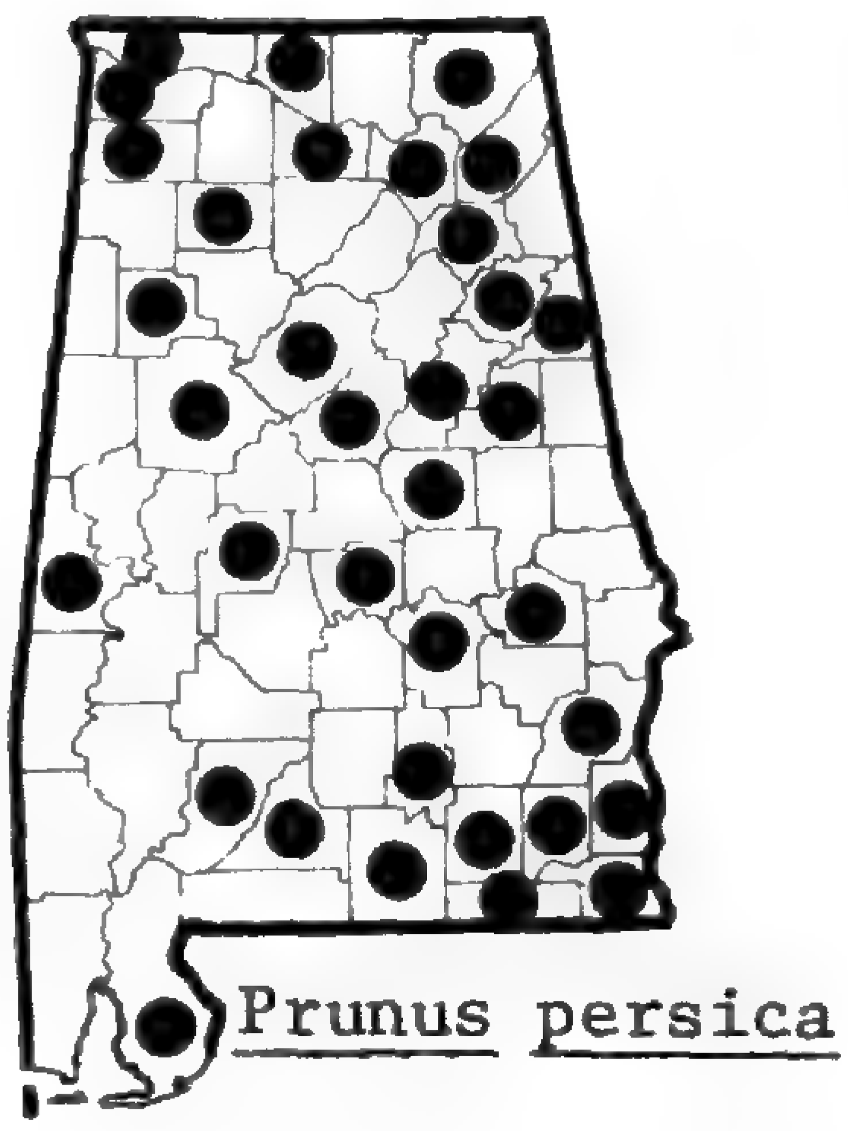
1. *P. coccinea* Roemer. Spring–summer; fall–winter. Fencerows, rights-of-way, infrequently escaped; CP. *Cotoneaster pyracantha* (L.) Spach—M, S.

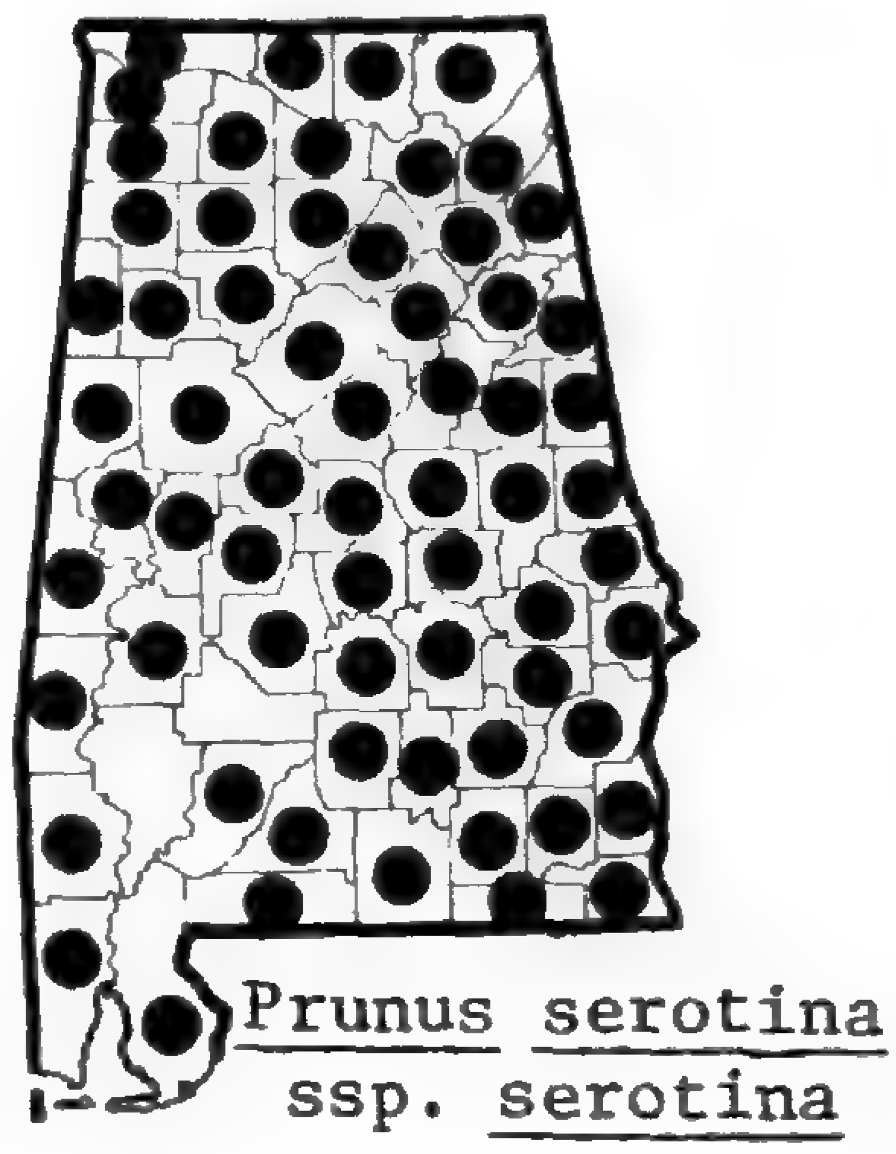
9. *Pyrus* L., PEAR

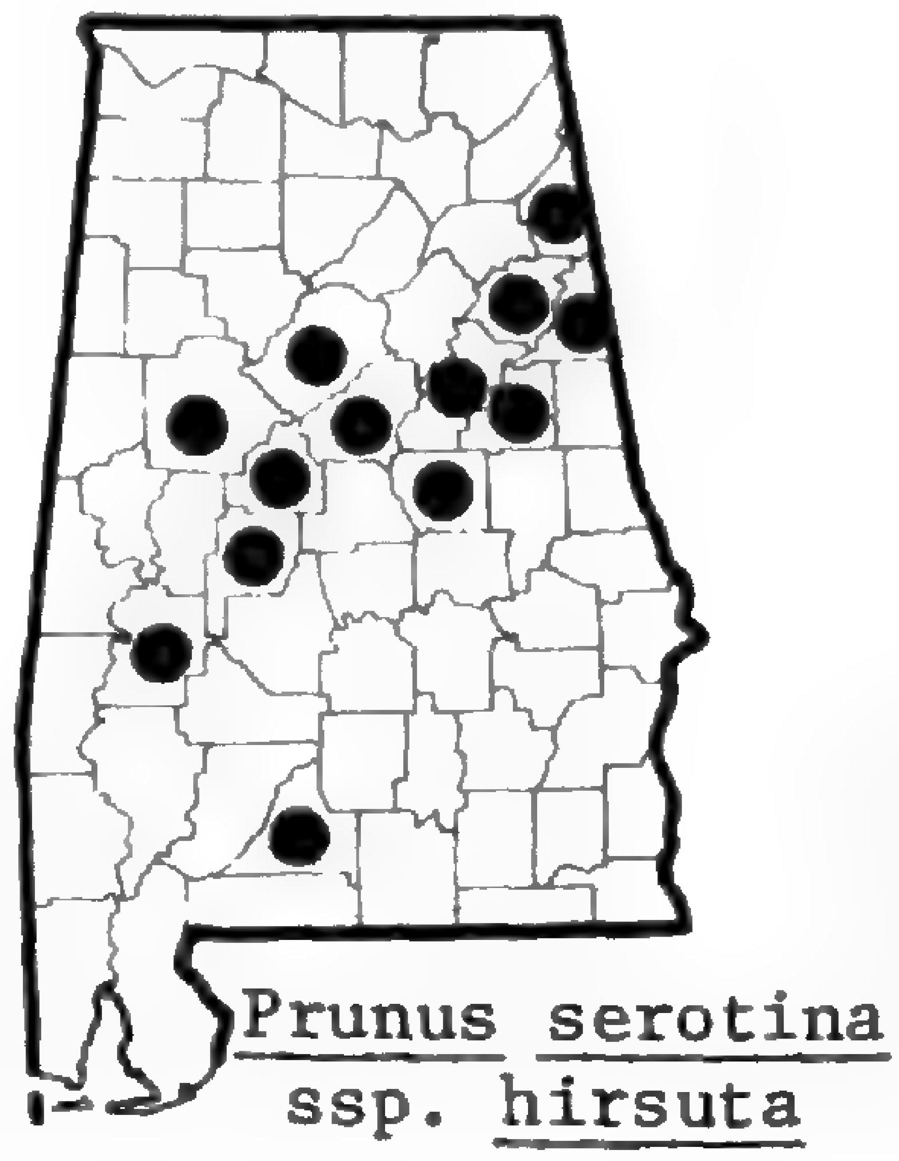
1. *P. communis* L. Spring; summer–fall. Occasionally escaped; throughout.

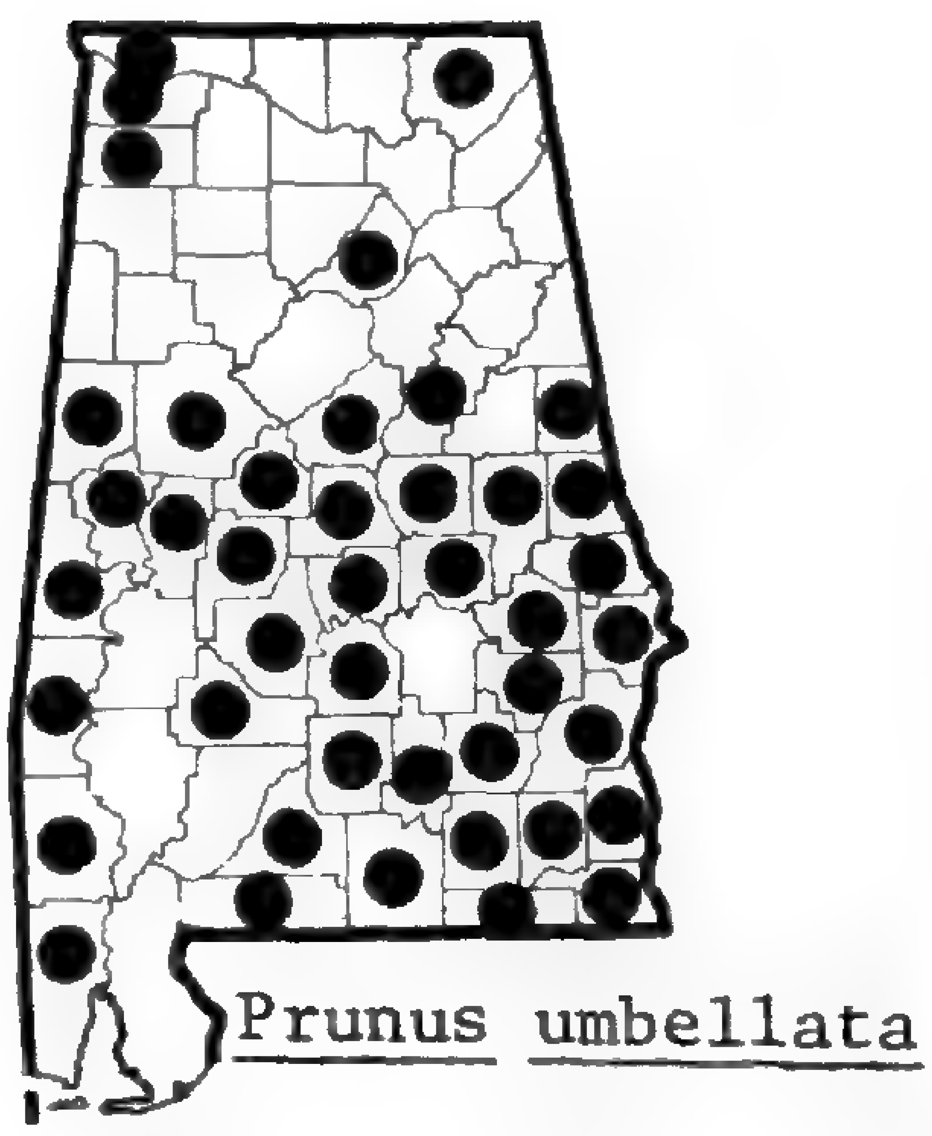
10. *Rosa* L., ROSE

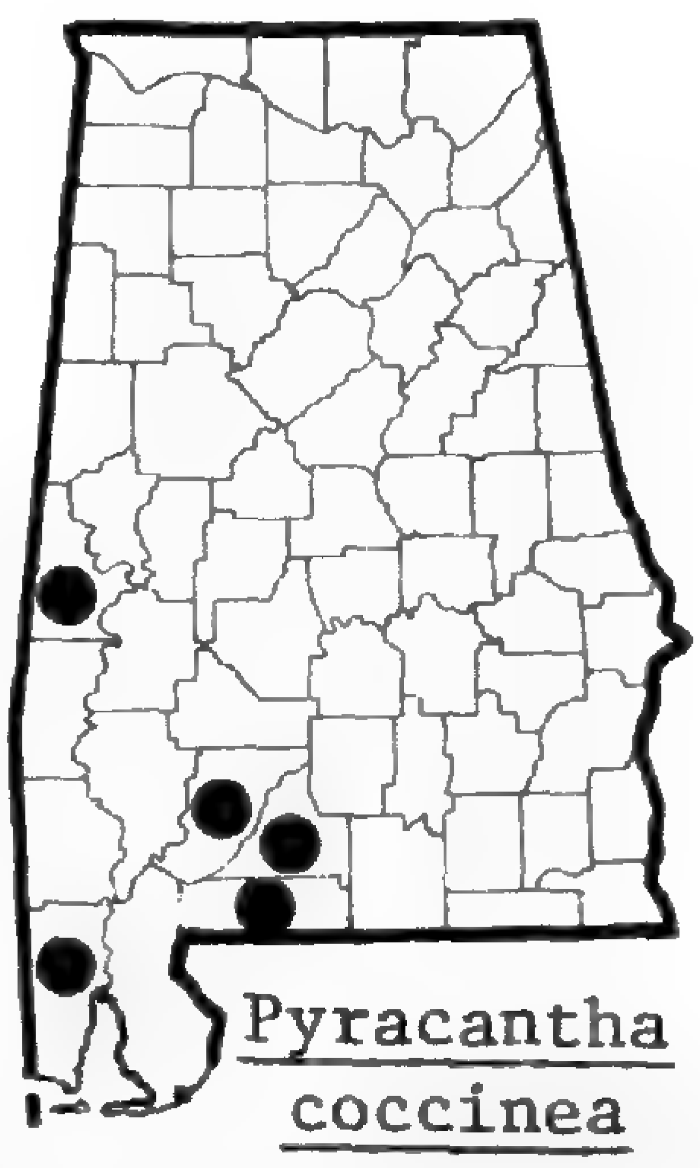
1. Leaf rachises stipitate-glandular 2
   2. Stipules pectinate 3
      3. Leaflets glandular over the lower surfaces .... 3. *R. eglanteria*
      3. Leaflets glandular beneath only along the midrib, or not at all 4
         4. Stipules free from petiole for more than ½ their lengths; sepals 1.5 cm long or longer .... 1. *R. bracteata*
         4. Stipules adnate to petiole for more than ½ their lengths; sepals 1 cm long or shorter 5

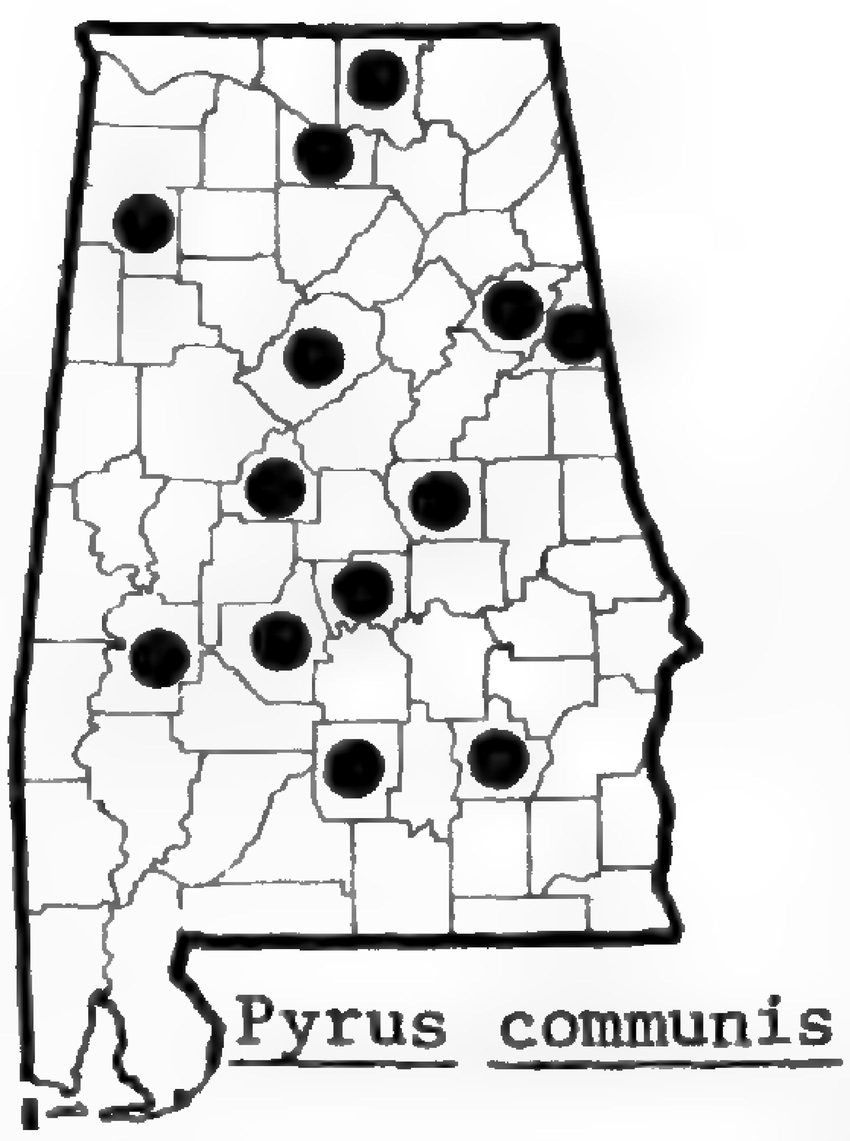

Prunus persica

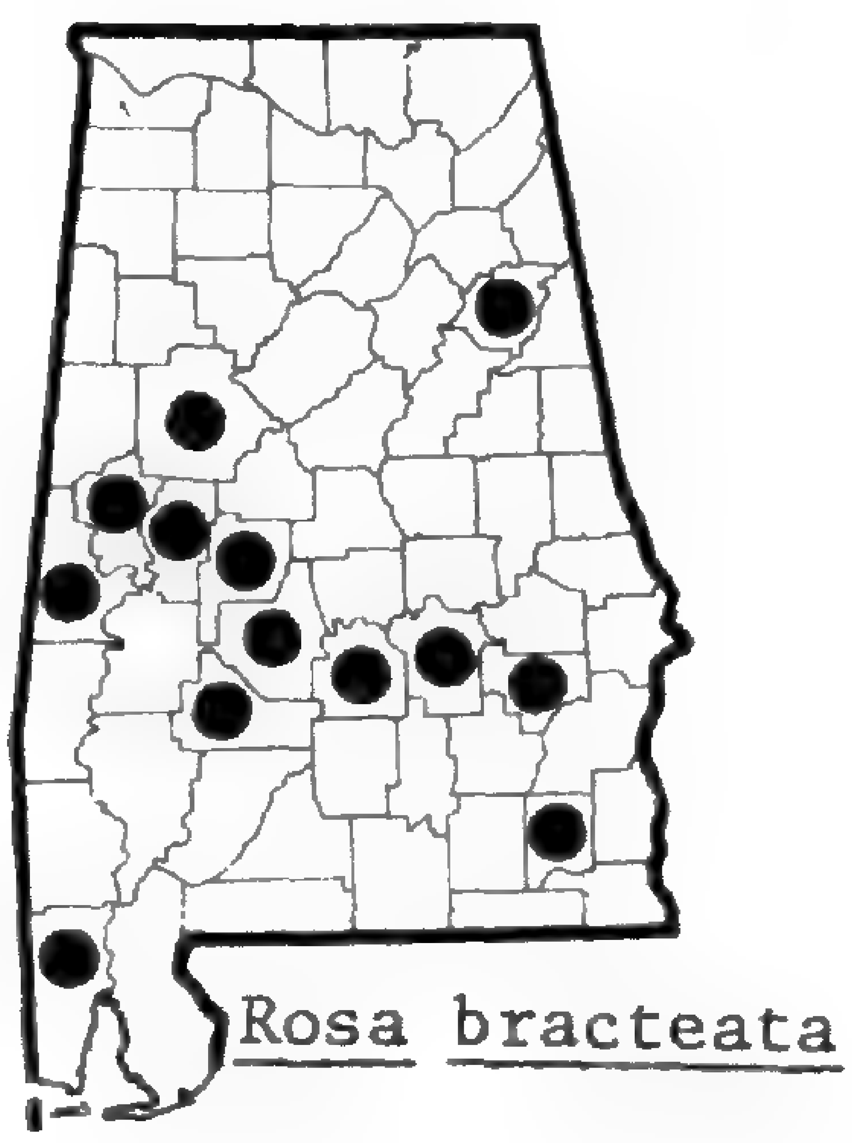

Prunus serotina
ssp. serotina


Prunus serotina
ssp. hirsuta

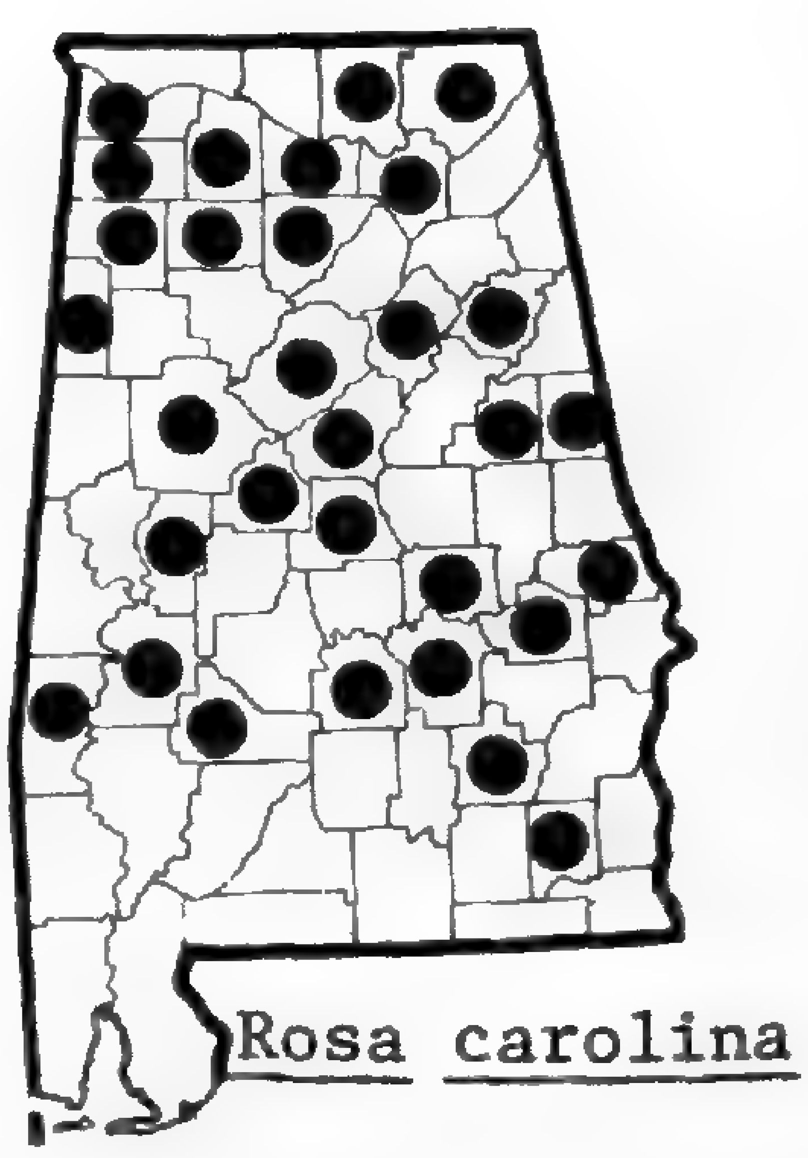

Prunus umbellata


Pyracantha
coccinea


Pyrus communis


Rosa bracteata


Rosa canina


Rosa carolina

5. Leaflets tomentose beneath .... 5. *R. multiflora*
5. Leaflets glabrous beneath, or pubescent only near the midvein .... 8. *R. wichuraiana*
2. Stipules entire or with glandular margins, not pectinate 6
6. Leaflets glandular over the lower surfaces .... 3. *R. eglanteria*
6. Leaflets glandular beneath only along the midrib, or not at all, except sometimes marginally 7
7. Flowers and fruits solitary .... 2. *R. carolina*
7. Flowers and fruits 2 or more in an inflorescence .... 7. *R. setigera*
1. Leaf rachises not stipitate-glandular 8
8. Stipules pectinate .... 5. *R. multiflora*
8. Stipules entire or with glandular margins, not pectinate 9
9. Stipules adnate to petiole for less than ½ their lengths .... 4. *R. laevigata*
9. Stipules adnate to petiole for more than ½ their lengths 10
10. Infrastipular spines retrorsely arching .... 6. *R. palustris*
10. Infrastipular spines straight .... 2. *R. carolina*

1. *R. bracteata* Wendland, Macartney R. Spring–fall; summer–fall. Fencerows, waste places, old homesites, persistent after or rarely spreading from cultivation, occasional; throughout.

2. *R. carolina* L., Wild R. Spring–early summer; summer–fall. Upland woods, thickets, fencerows; throughout. *R. humilis* Marsh.—H, M.

3. *R. eglanteria* L., Eglantine Sweetbriar R. Spring–summer; fall. Waste places, infrequent; P, AM, CuP. *R. rubiginosa* L.—M, S.

4. *R. laevigata* Michaux, Cherokee R. Spring; fall. Reported as naturalized; CP.

5. *R. multiflora* Thunberg, Multiflora R. Spring; summer–fall. Fencerows, waste places, naturalized; throughout.

6. *R. palustris* Marshall, Swamp R. Spring–summer; fall. Low ground, rare, CP, VR. *R. virginiana* Mill.—S.

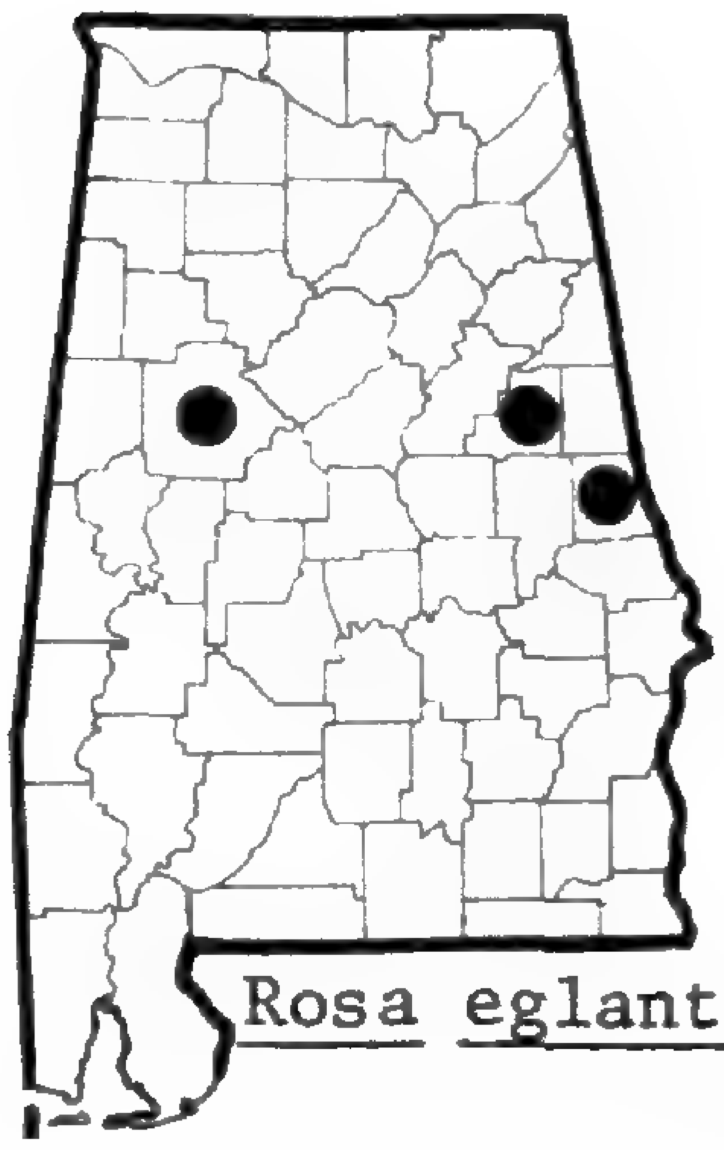
7. *R. setigera* Michaux, Prairie R. Spring; fall. Thickets, rights-of-way, infrequent; inner CP, CuP, VR, HR. *R. rubifolia* Brown—S.

8. *R. wichuraiana* Crepin. Spring; fall. Roadsides, old homesites, waste places, persistent or spreading; throughout.

Rosa canina L. (Dog R.) and *R. moschata* Herrm. (Musk R.) have been reported as persistent or rarely spreading.

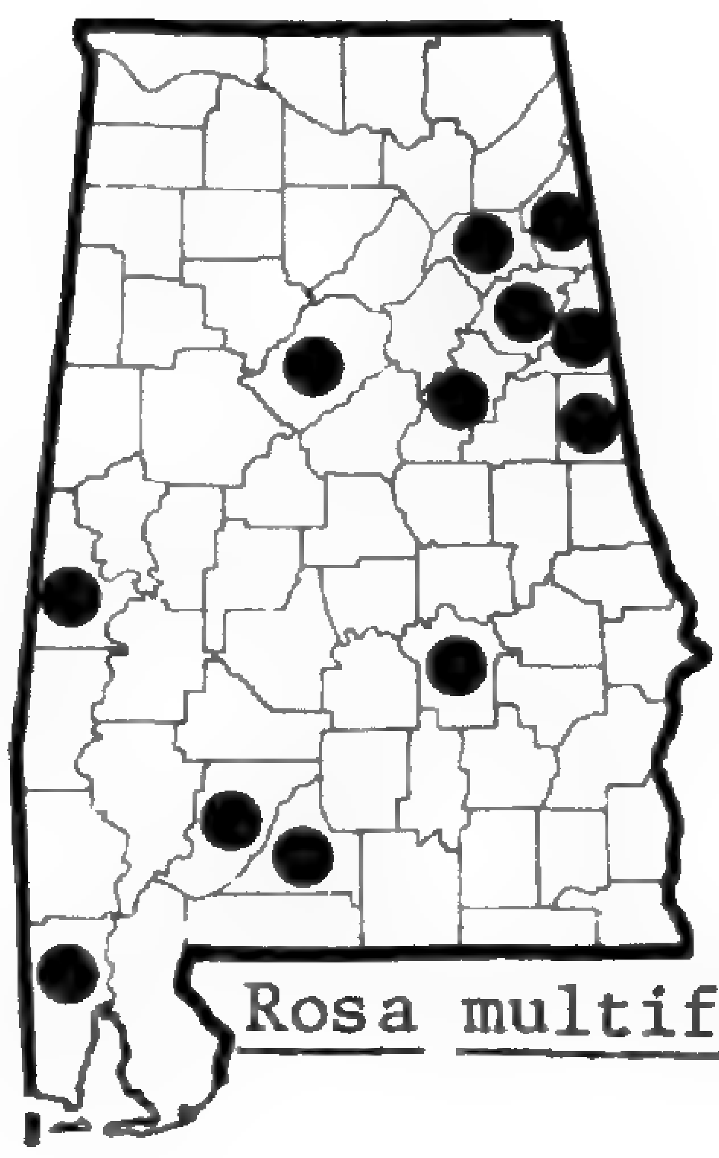
11. *Rubus* L.

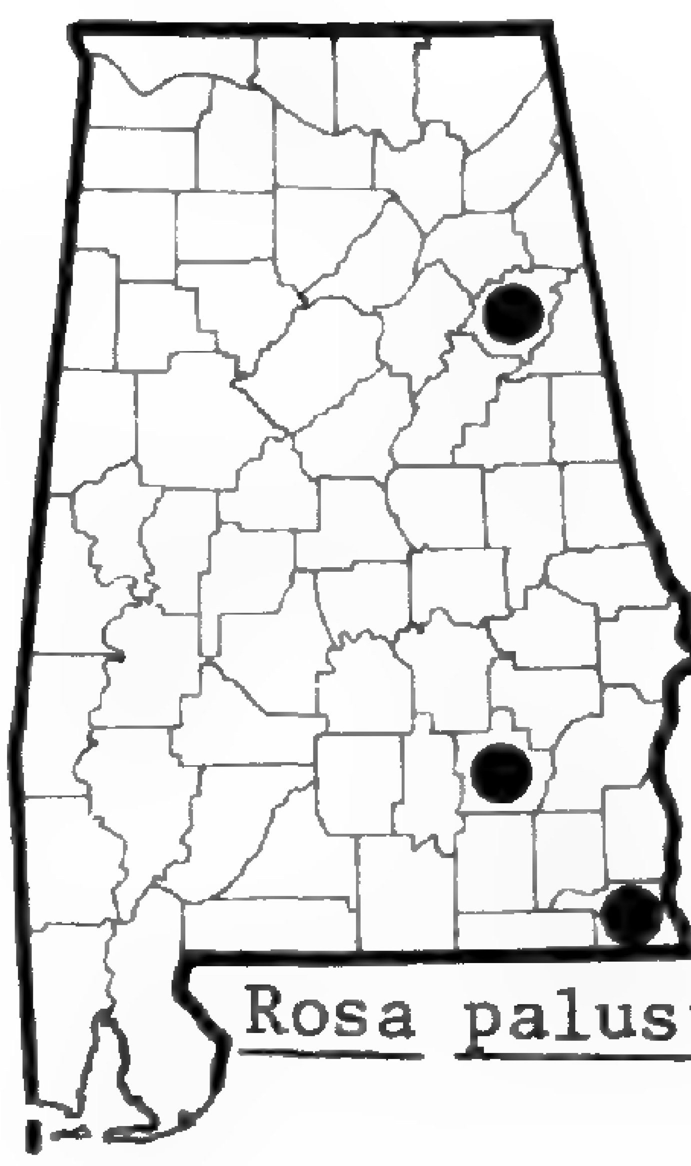
1. Leaves simple .... 8. *R. odoratus*
1. Leaves compound 2
2. Petals shorter than the sepals; fruit separating from torus at maturity .... 7. *R. occidentalis*
2. Petals longer than the sepals; fruit adhering tightly to torus at maturity 3
3. Leaves white- or gray-tomentose beneath .... 4. *R. cuneifolius*
3. Leaves not white- or gray-tomentose beneath 4
4. Stems trailing 5
5. Flowers and fruits solitary 6
6. Stems hispid, or pedicels evenly retrorsely-spiny; leaves semi-evergreen .... 9. *R. trivalis*
6. Stems not hispid; pedicels pubescent to remotely retrorsely-spiny; leaves deciduous .... 5. *R. flagellaris*
5. Flowers and fruits commonly 3 or more per inflorescence 7
7. Stems hispid, at least remotely so .... 6. *R. hispidus*

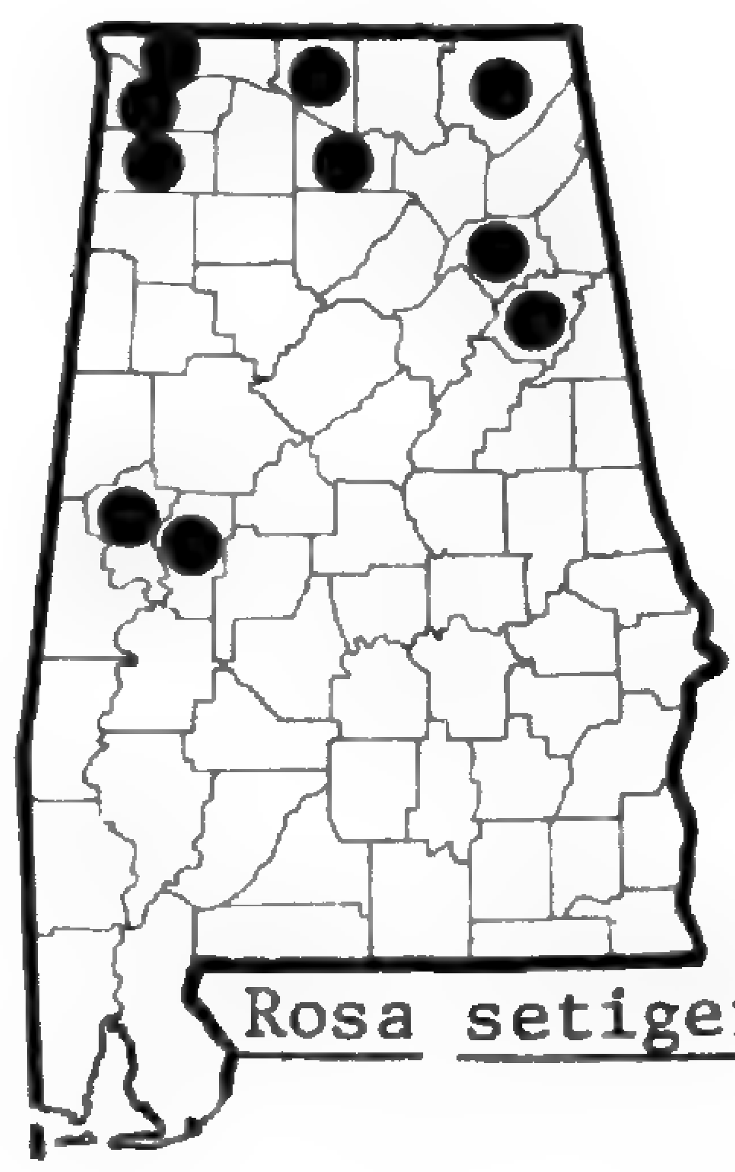

Rosa eglanteria

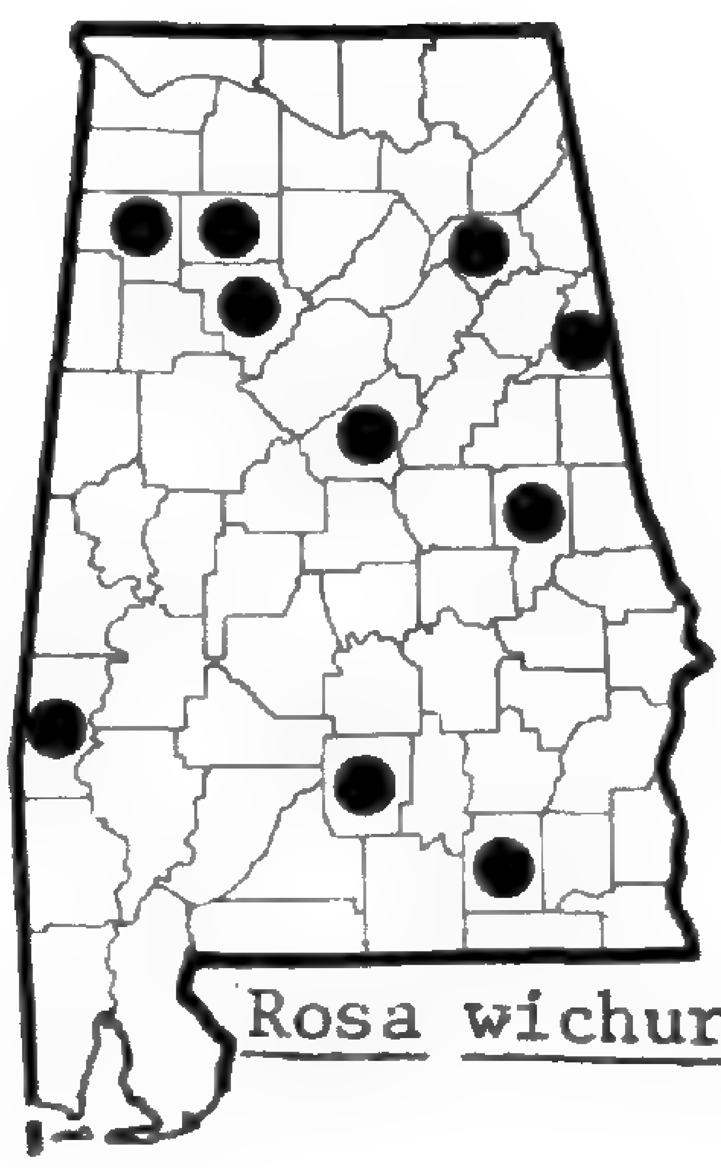

Rosa laevigata


Rosa moschata

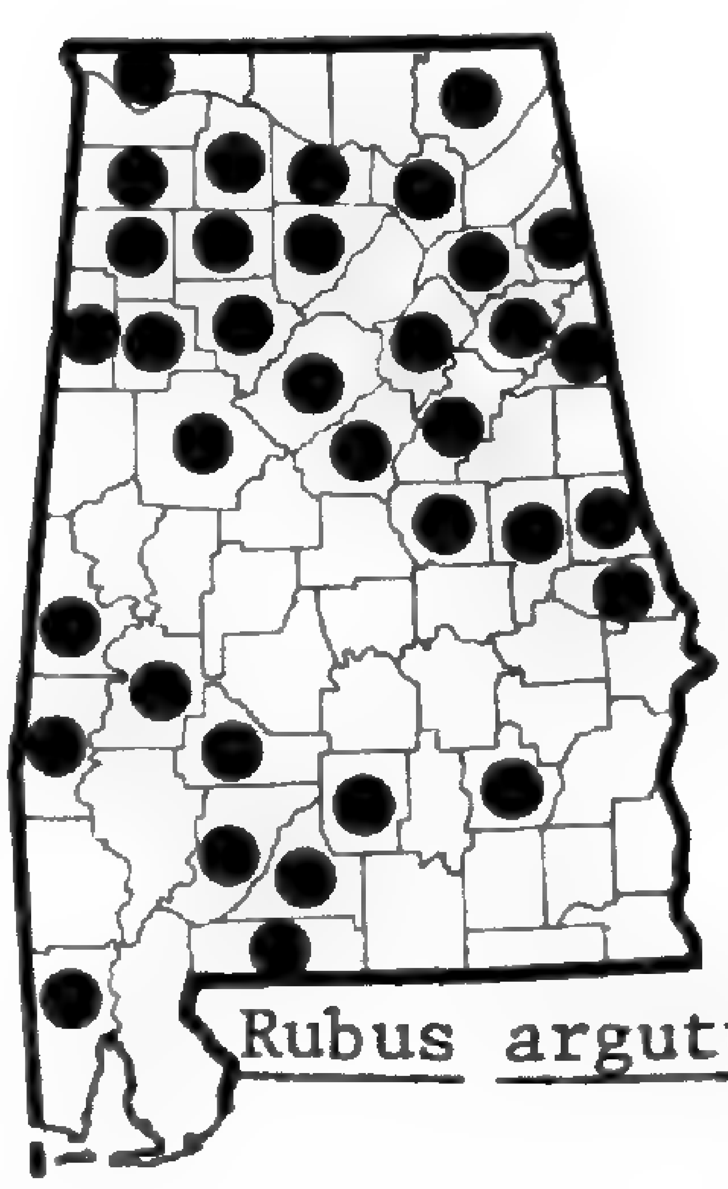

Rosa multiflora


Rosa palustris


Rosa setigera


Rosa wichuraiana


Rubus allegheniensis


Rubus argutus

7. Stems retrorsely spiny, not hispid .... 5. *R. flagellaris*
4. Stems erect or arching 8
8. Pedicels stipitate-glandular .... 1. *R. allegheniensis*
8. Pedicels not stipitate-glandular 9
9. Leaves glabrous or glabrate beneath, except along the principal veins .... 3. *R. betulifolius*
9. Leaves velvety-pubescent over the lower surfaces .... 2. *R. argutus*

1. *R. allegheniensis* Porter, BLACKBERRY. Spring; late spring–early summer. Opening, rare; AM. *R. nigrobaccus* Bail.—S.

2. *R. argutus* Link, BLACKBERRY. Spring; late spring–early summer. Fields, openings in woods, fencerows, roadsides, thickets; throughout, but becoming infrequent southward. *R. argutus floridus* (Tratt.) Bail.—M; *R. floridus* Tratt.—H, S.

3. *R. betulifolius* Small, BLACKBERRY. Spring; late spring–early summer. Thickets, fencerows, roadsides, infrequent; CP.

4. *R. cuneifolius* Pursh, BLACKBERRY. Spring; late spring–summer. Fields, roadsides, fencerows; throughout, but more common southeastward.

5. *R. flagellaris* Willd., DEWBERRY. Spring; spring–early summer. Fields, rights-of-way, upland woods; throughout, but more common northeastward. *R. enslenii* Tratt., *R. invisus* (Bail.) Britt.—M, S; *R. rhodophyllus* Rydb., *R. baileyanus* Britt.—S.

6. *R. hispidus* L., DEWBERRY. Low woods, rare; CP, reported from P, CuP, *R. continentalis* (Focke) Bail.—S.

7. *R. occidentalis* L., RASPBERRY. Mesic or rich woods, rare; CuP, VR, HR.

8. *R. odoratus* L. Late spring–early summer; summer. Rocky woods, rare; reported from CuP (Jackson Co.) by Dean (1961). *Rubacer odoratum* (L.) Rydb.—S.—This species is so distinctive that the report of its occurrence should justify its inclusion here.

9. *R. trivialis* Michaux, DEWBERRY. Spring. Roadsides, rights-of-way, open low ground; CP, P, AM, CuP. *R. lucidus* Rydb.—S.

12. *Sorbus* L.

1. *S. arbutifolia* (L.) Heynhold. Spring; late summer–fall. Swamp ecotones, low woods, seepages; CP, P, AM, CuP. *Aronia arbutifolia* (L.) Ell.—M, S; *A. arbutifolia* (L.) Pers.—H; *S. arbutifolia* var. *atropurpurea* (Britt.) Schneid.—RAB. Two color forms of the mature fruit exist: Red and bluish-black.

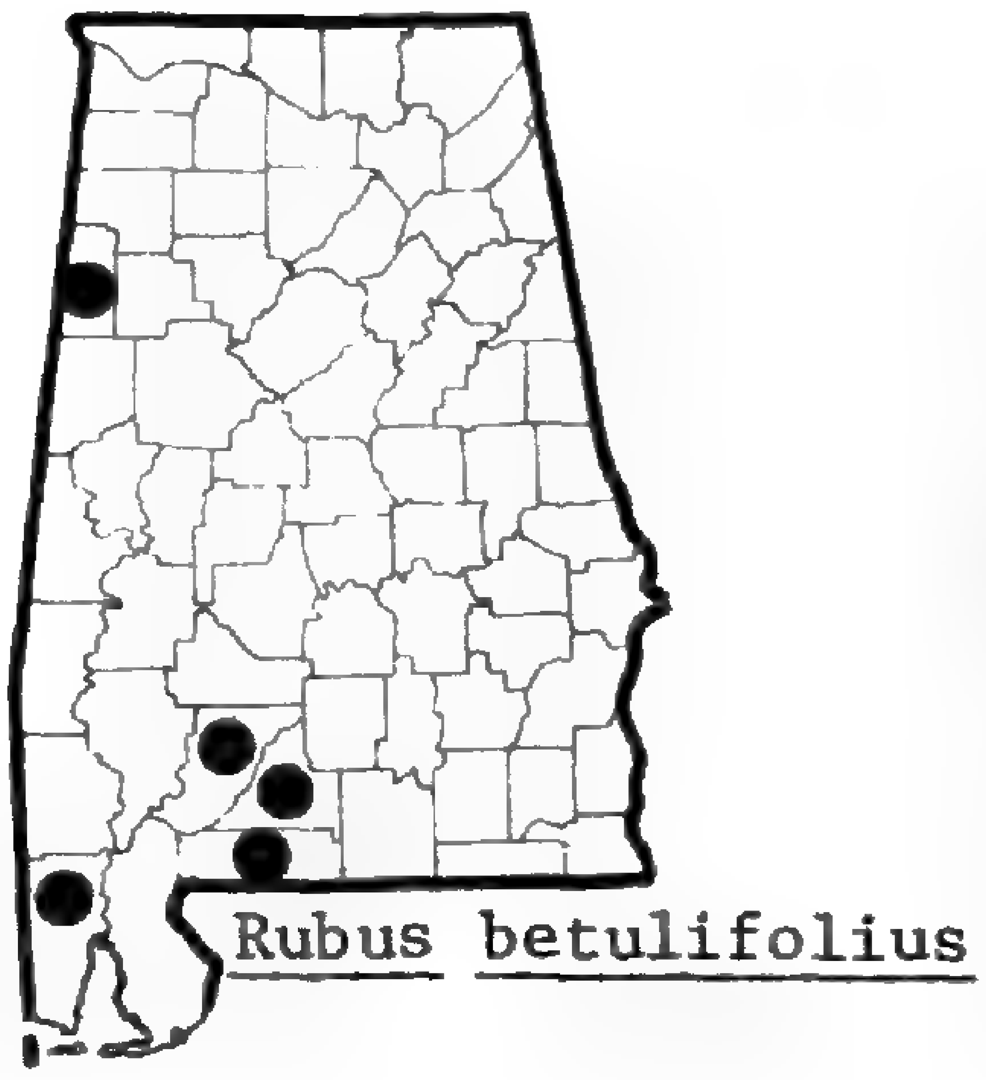
13. *Spiraea* L., SPIRAEA

1. Inflorescence pedunculate .... 3. *S. tomentosa*
1. Inflorescences not pedunculate 2
2. Flowers in umbel-like racemes on current season's growth .... 1. *S. cantoniensis*
2. Flowers in sessile umbels on last season's or older growth .... 2. *S. thunbergii*

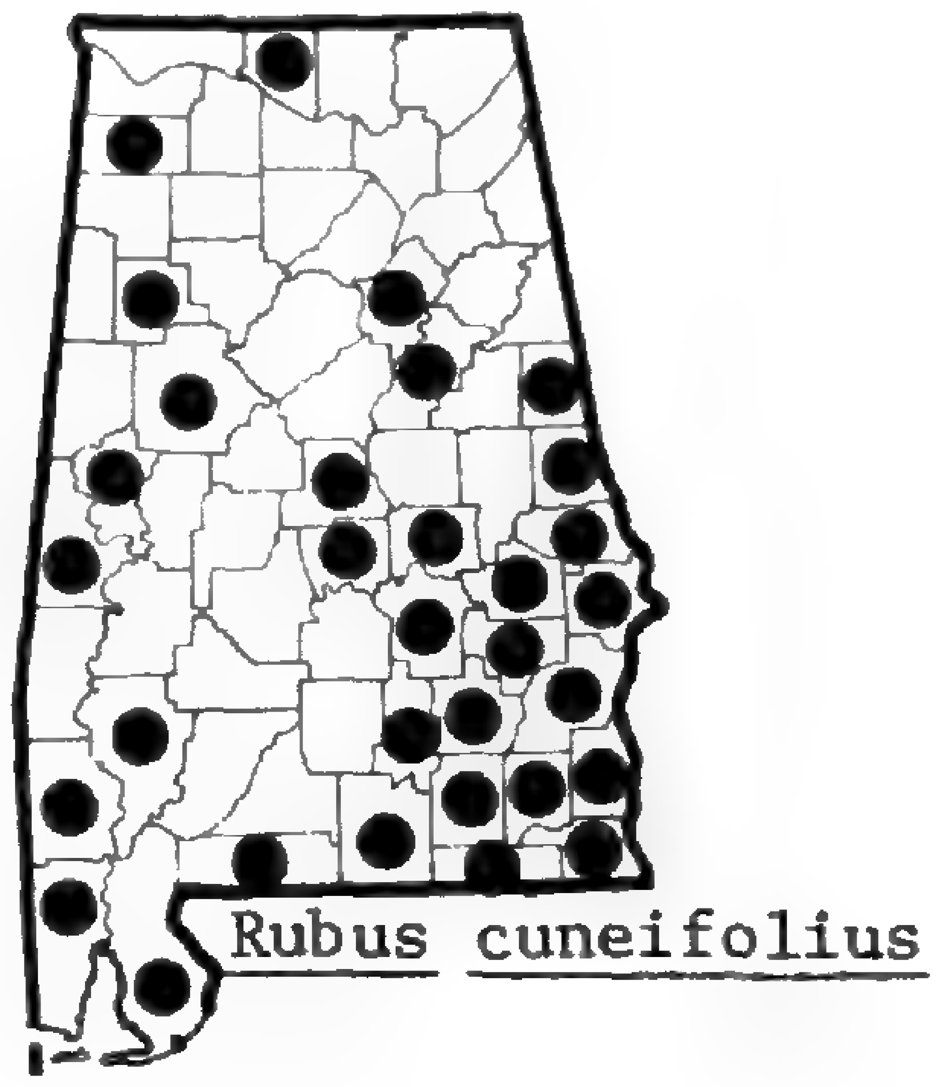
1. *S. cantoniensis* Loureiro. Flowers, fruit not seen in Alabama. Escaped to roadside; VR.

2. *S. thunbergii* Siebold. Spring; fruit not seen in Alabama. Escaped to roadsides; southeastern CP, CuP (rare).

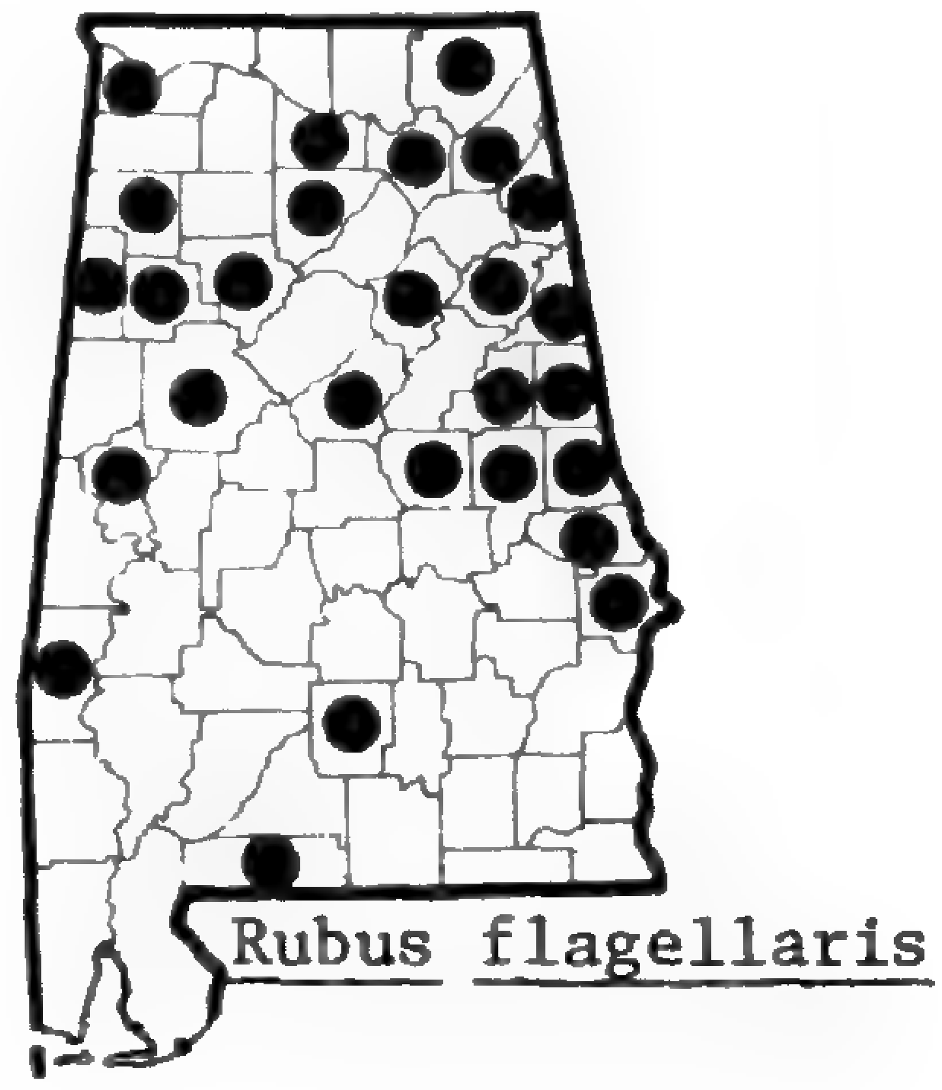
3. *S. tomentosa* L. Summer; fall. Habitat not specified, very rare; HR.



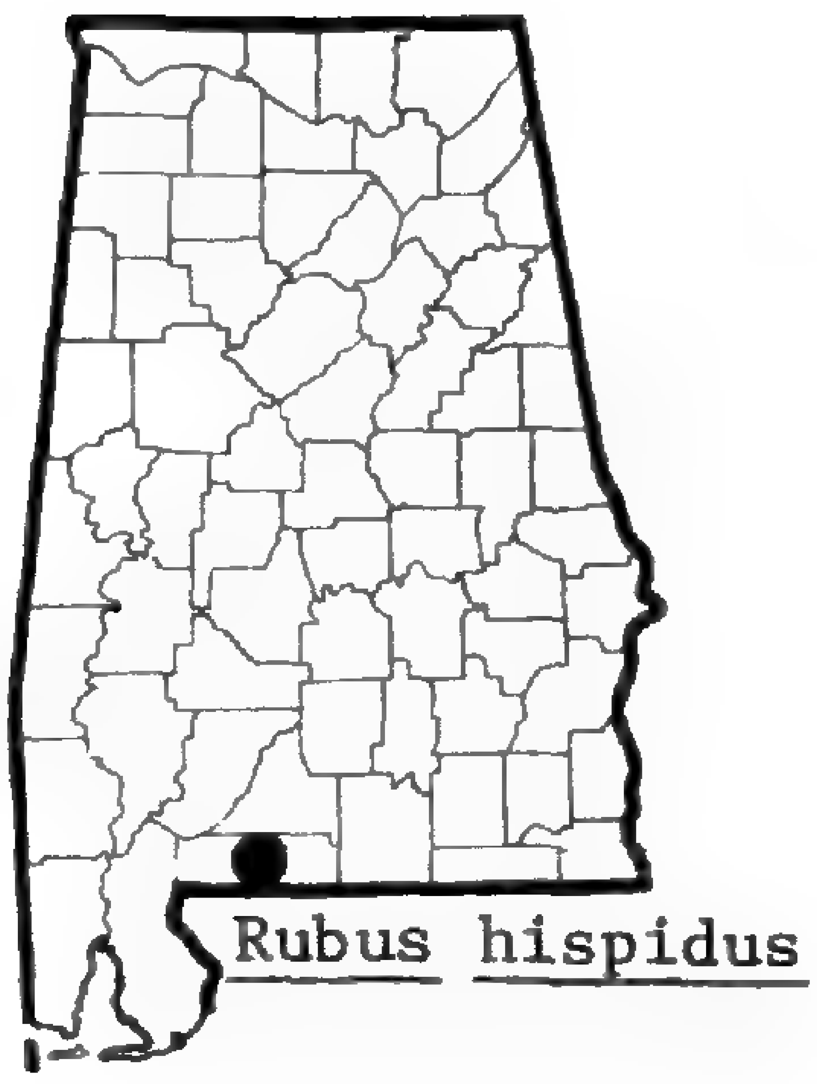
Rubus betulifolius



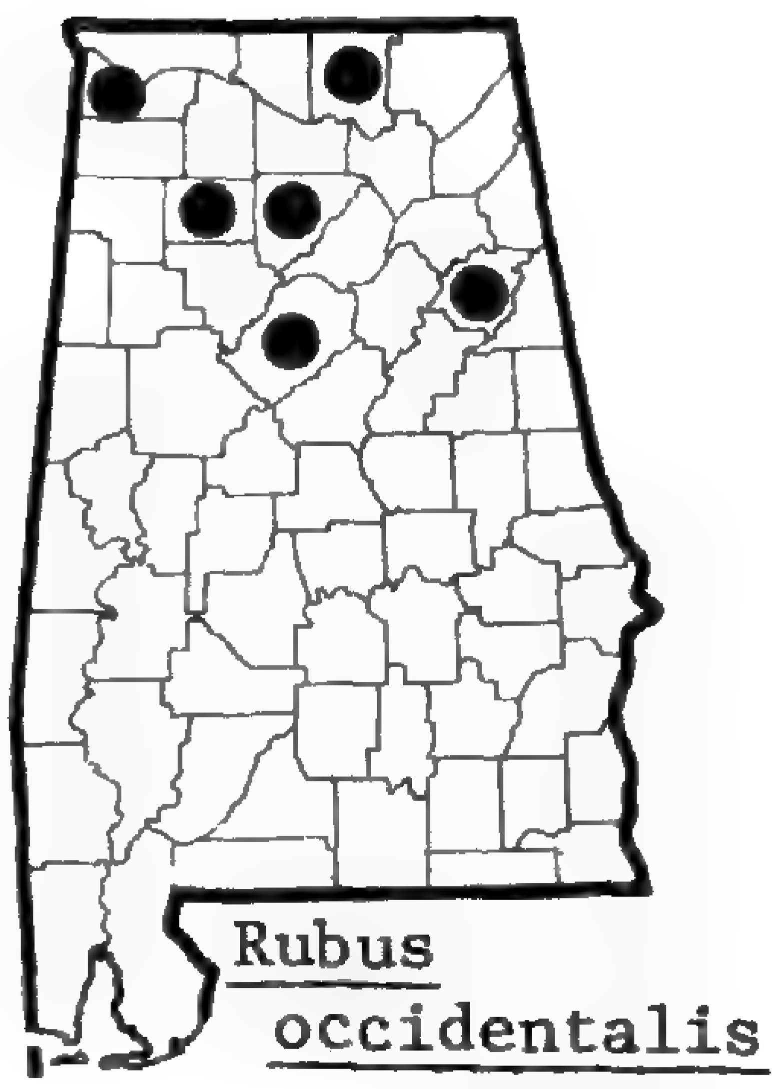
Rubus cuneifolius



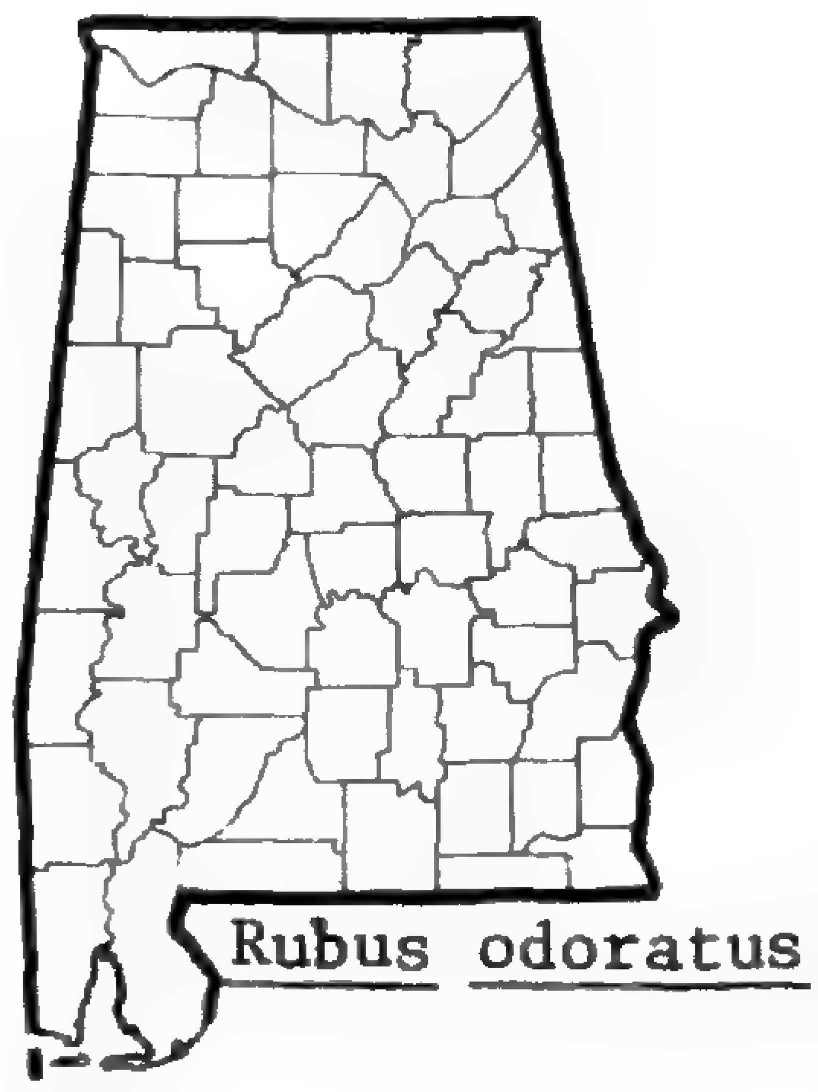
Rubus flagellaris



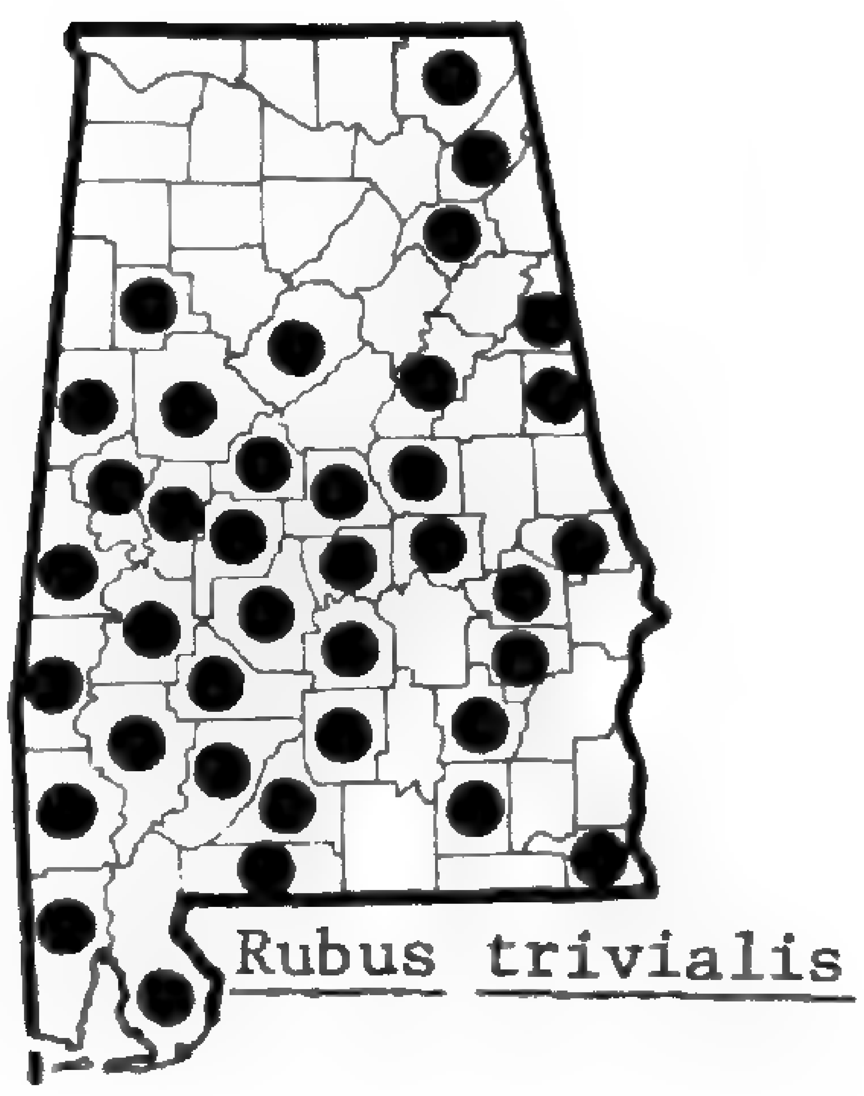
Rubus hispidus



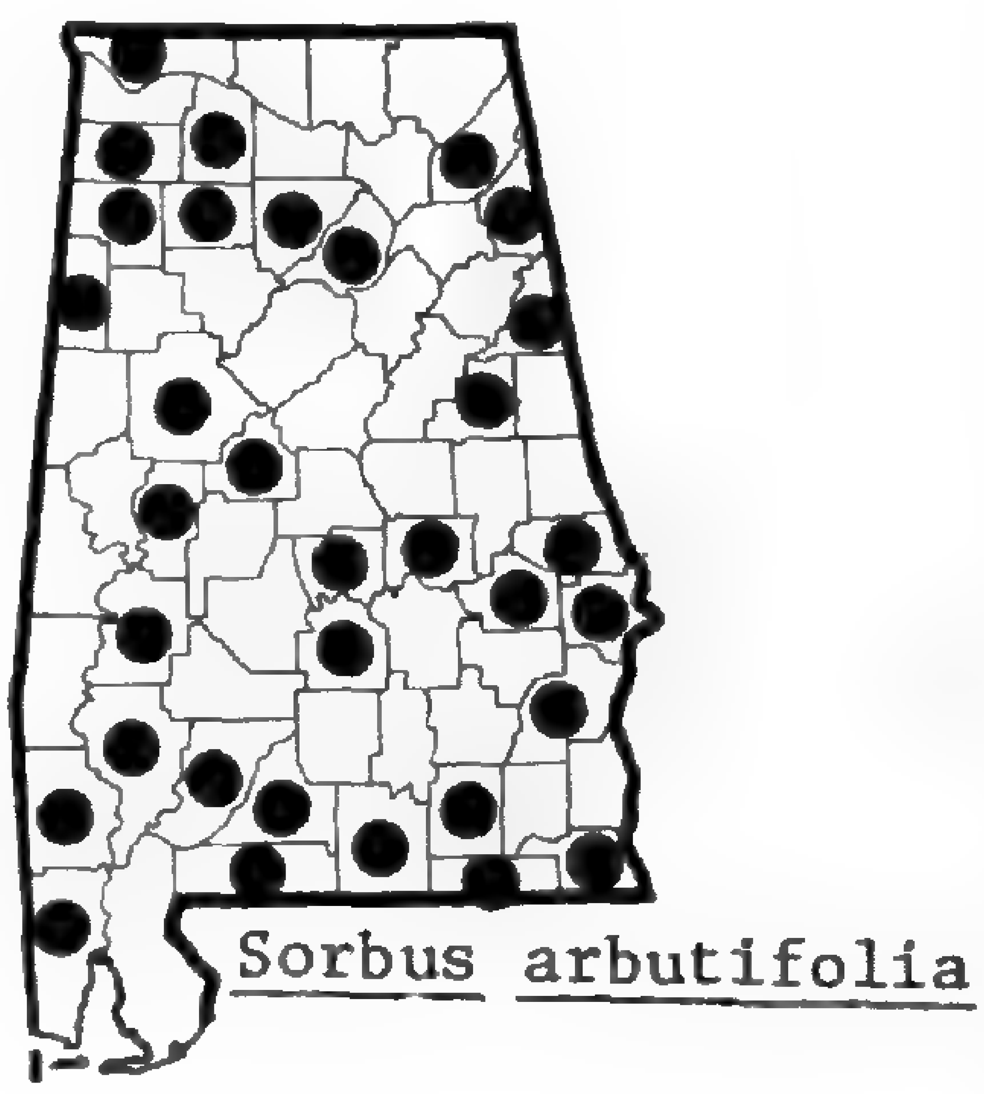
Rubus occidentalis



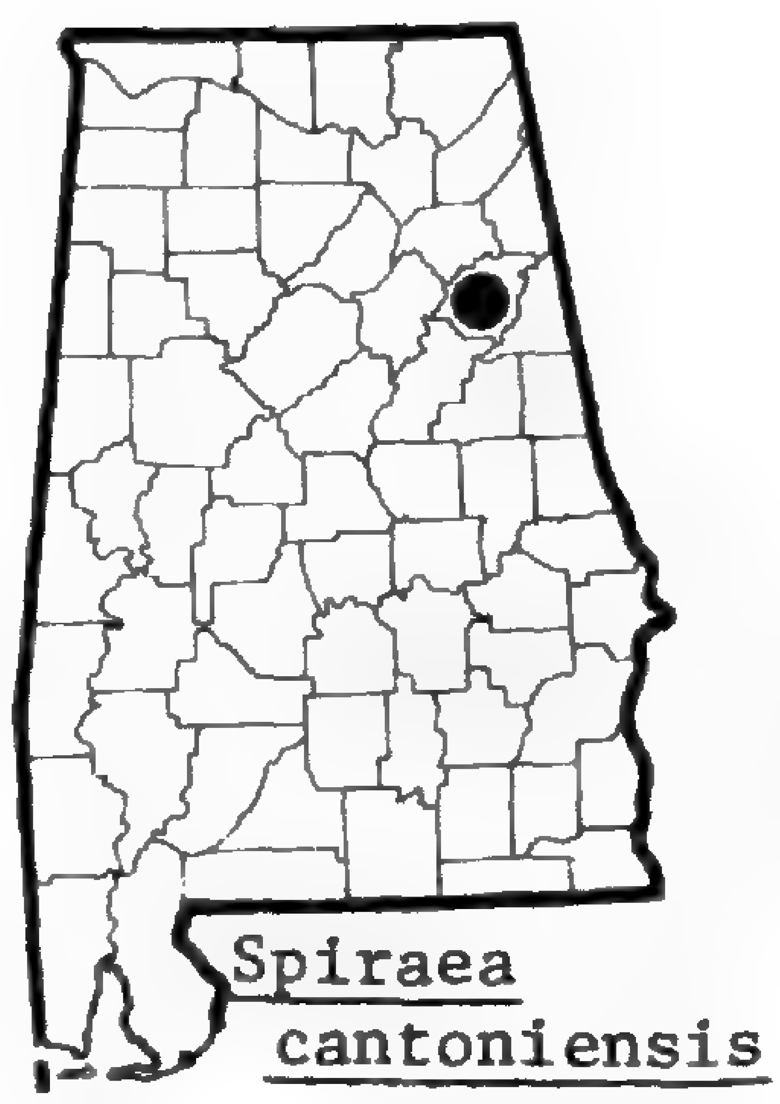
Rubus odoratus



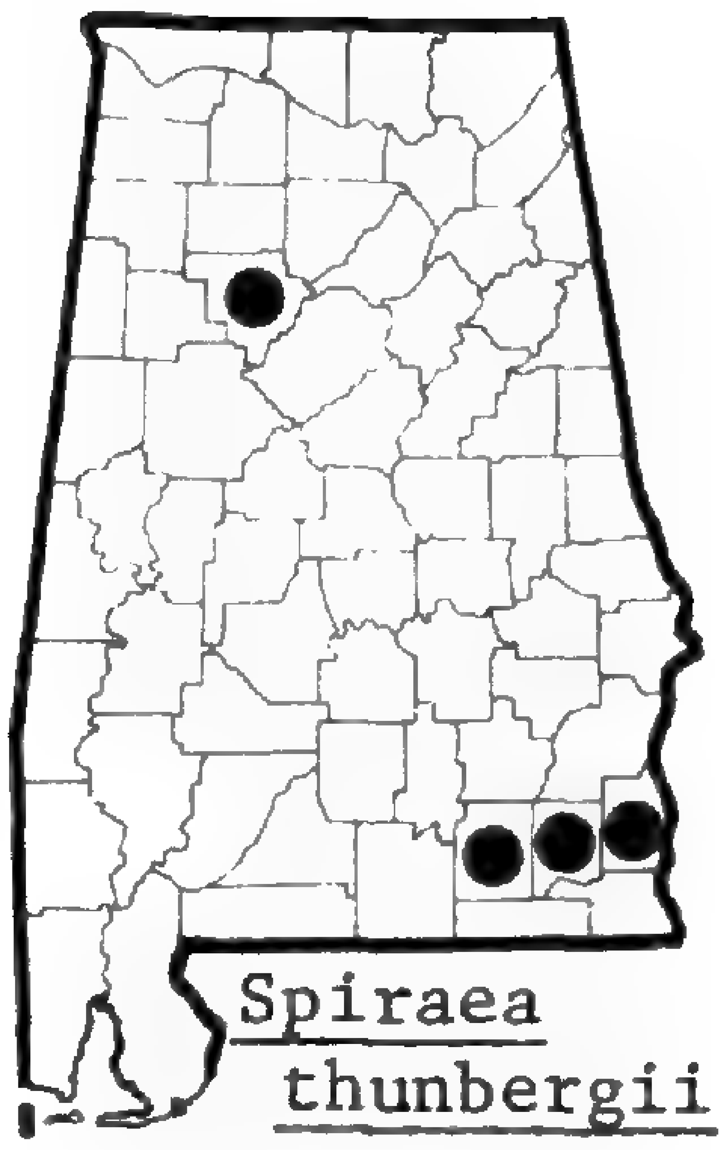
Rubus trivialis



Sorbus arbutifolia



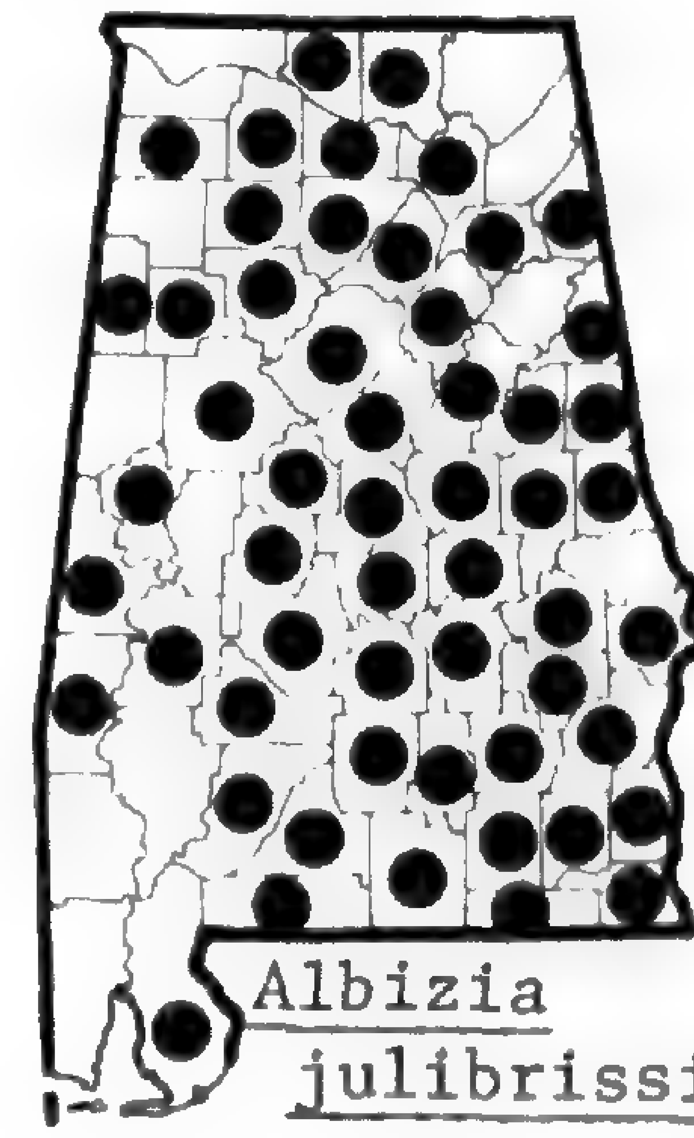
Spiraea cantoniensis



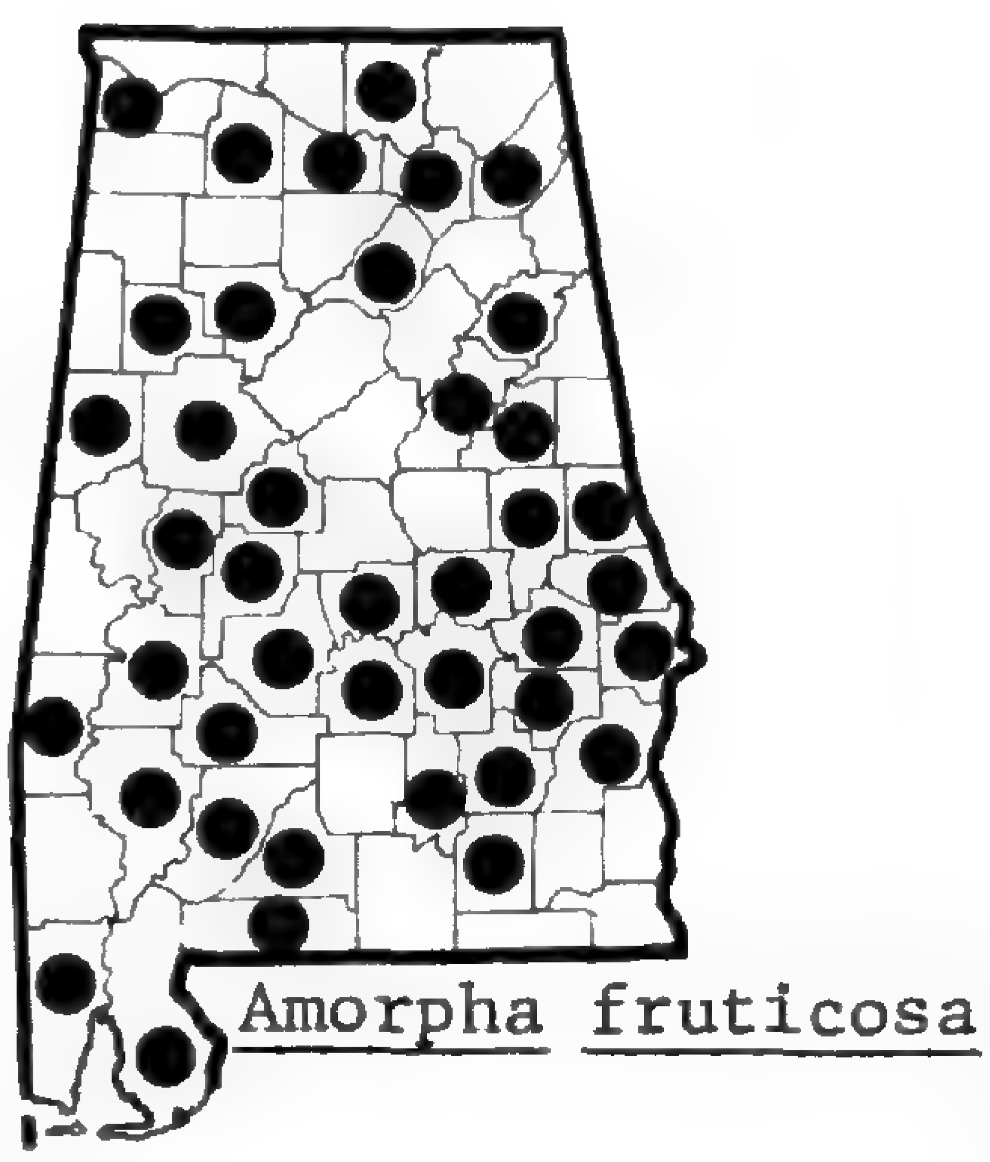
Spiraea thunbergii

Spiraea tomentosa

30. FABACEAE



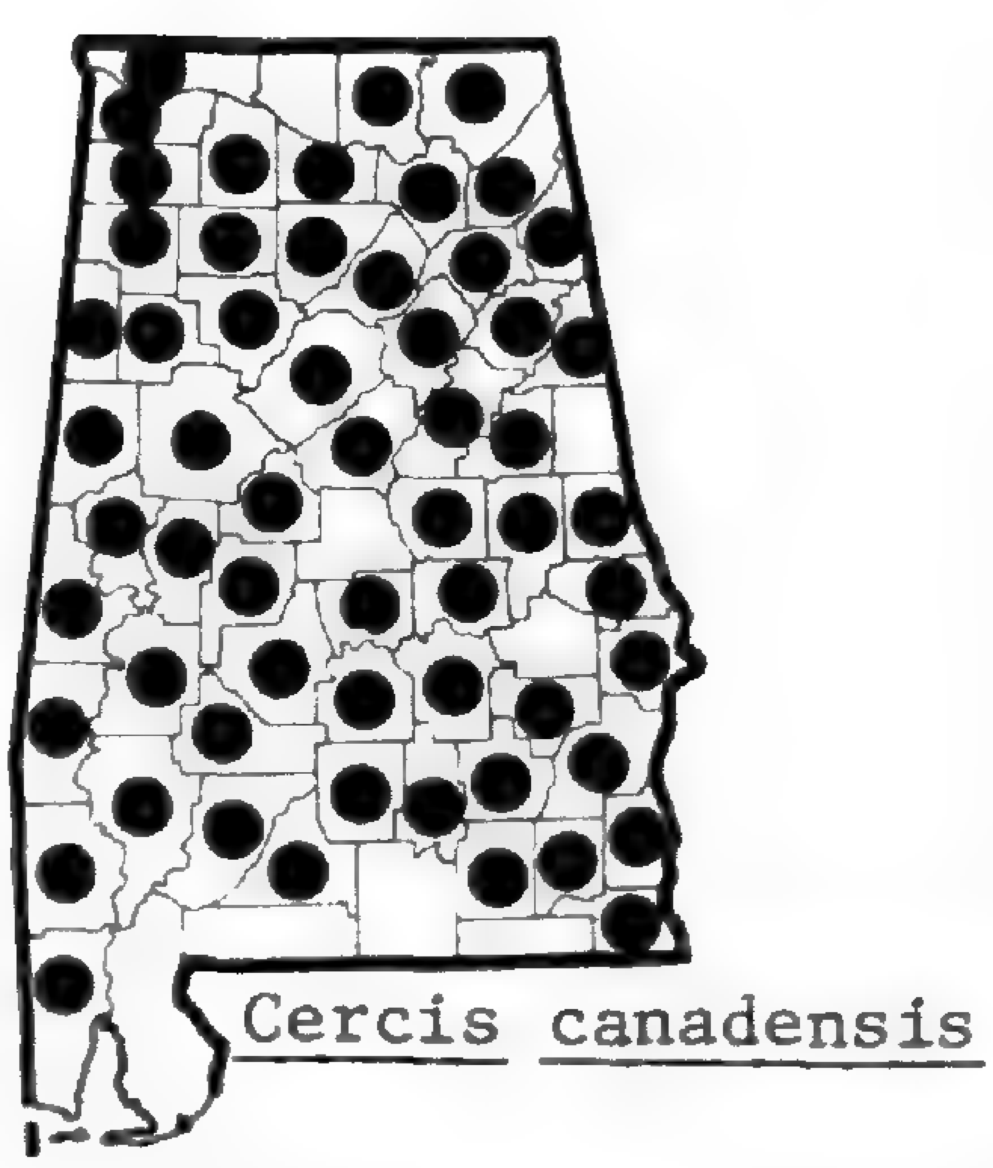
Albizia julibrissin



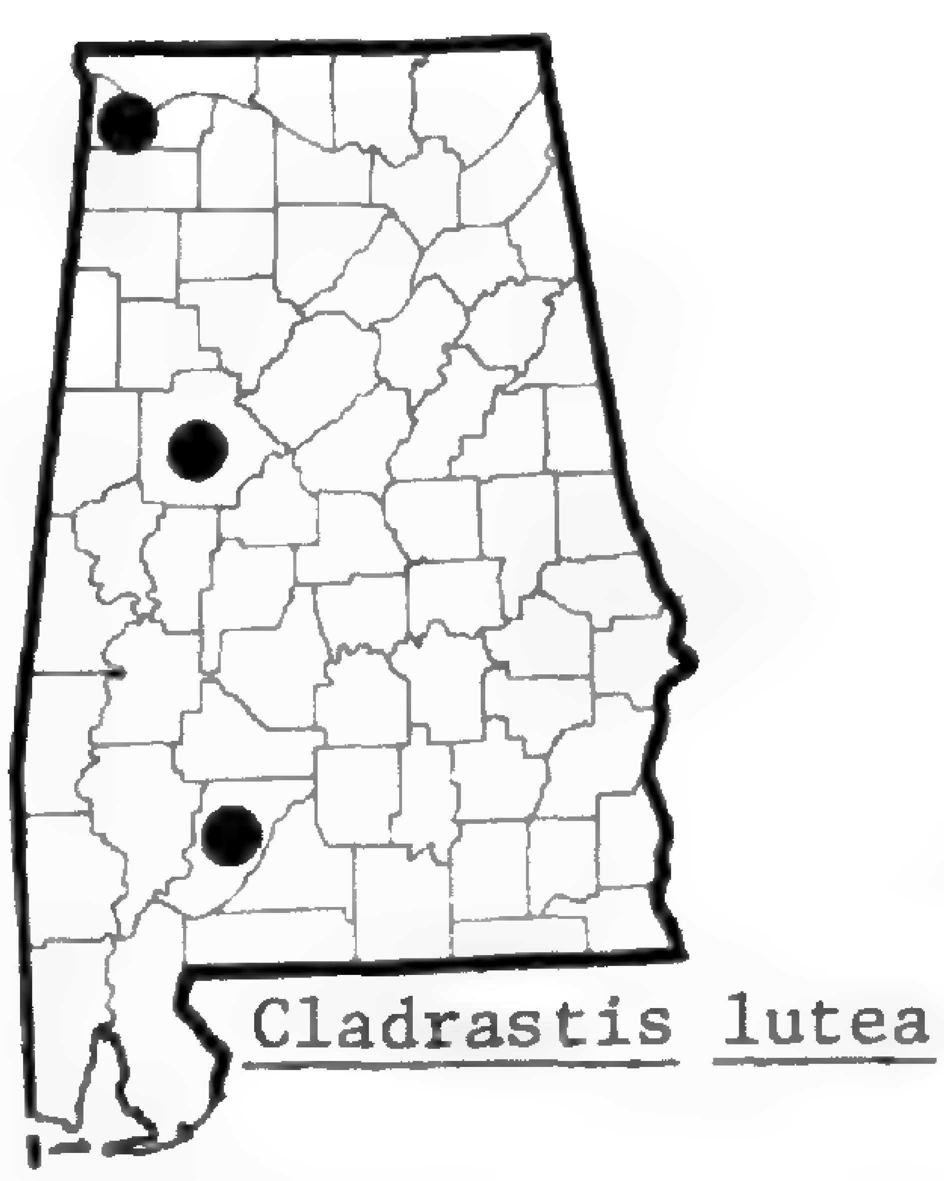
Amorpha fruticosa

Amorpha glabra

Amorpha schwerini



Cercis canadensis



Cladrastis lutea

Cytisus scoparius

30. FABACEAE

1. Leaves simple ... 3. *Cercis*
1. Leaves compound ... 2
  2. Leaves decompound ... 3
    3. Inflorescence capitate; stamens more than 10, united ... 4
      4. Stipular thorns present ... 12. *Vachellia*
      4. Stipular thorns absent ... 1. *Albizia*
    3. Inflorescence racemose or paniculate; stamens 10, free ... 5
      5. Leaflet margins crenulate; seed less than 0.5 cm thick ... 6. *Gleditsia*
      5. Leaflet margins entire; seed more than 1 cm thick ... 7. *Gymnocladus*
  2. Leaves once compound ... 6
    6. Leaf rachises winged ... 9. *Parkinsonia*
    6. Leaf rachises not winged ... 7
      7. Plant a trailing or twining vine ... 8
        8. Leaves 3-foliolate ... 10. *Pueraria*
        8. Leaves, at least most, 5- or more-foliolate ... 13. *Wisteria*
      7. Plant a shrub or tree ... 9
        9. Leaves 3-foliolate ... 8. *Lespedeza*
        9. Leaves predominantly 5- or more-foliolate ... 10
          10. Leaves even-pinnately compound; fruit 4-winged ... 5. *Daubentonia*
          10. Leaves odd-pinnately compound; fruit wingless ... 11
            11. Petal 1; calyces and fruit glandular-punctate ... 2. *Amorpha*
            11. Petals 5; calyces and fruit not glandular-punctate ... 12
              12. Inflorescence racemose; stamens monadelphous ... 11. *Robinia*
              12. Inflorescence paniculate; stamens distinct ... 4. *Cladrastis*

1. *Albizia* Durazzini.

1. *A. julibrissin* Durazzini, SILK TREE, MIMOSA. Late spring–summer; summer–fall. Commonly naturalized, usually in fencerows, rights-of-way, mesic woods; throughout.

2. *Amorpha* L.

1. Calyx lobes, at least some, 1.5 mm long or longer; calyx pilose ... 3. *A. schwerini*
1. Calyx lobes 1 mm or less long; calyx puberulent, strigillose or glabrous ... 2
  2. Calyx lobes more than 0.5 mm long ... 1. *A. fructicosa*
  2. Calyx lobes less than 0.5 mm long ... 2. *A. glabra*

1. *A. fruticosa* L. Spring–early summer; summer–fall. Stream-banks, open woods; throughout. *A. tennesseensis* Shuttlw.—S.

2. *A. glabra* Poiret. Spring–early summer; summer–fall. Reported by Mohr (1901) and later writers.

3. *A. schwerini* Schneider. Spring; summer–fall. Rocky woods, local; AM. *A. virgata* Sm. in part?—M, H.

3. *Cercis* L., JUDAS-TREE, REDBUD

1. *C. canadensis* L. Spring; summer–fall. Mesic woods; throughout.

4. *Cladrastis* Rafinesque, YELLOW-WOOD

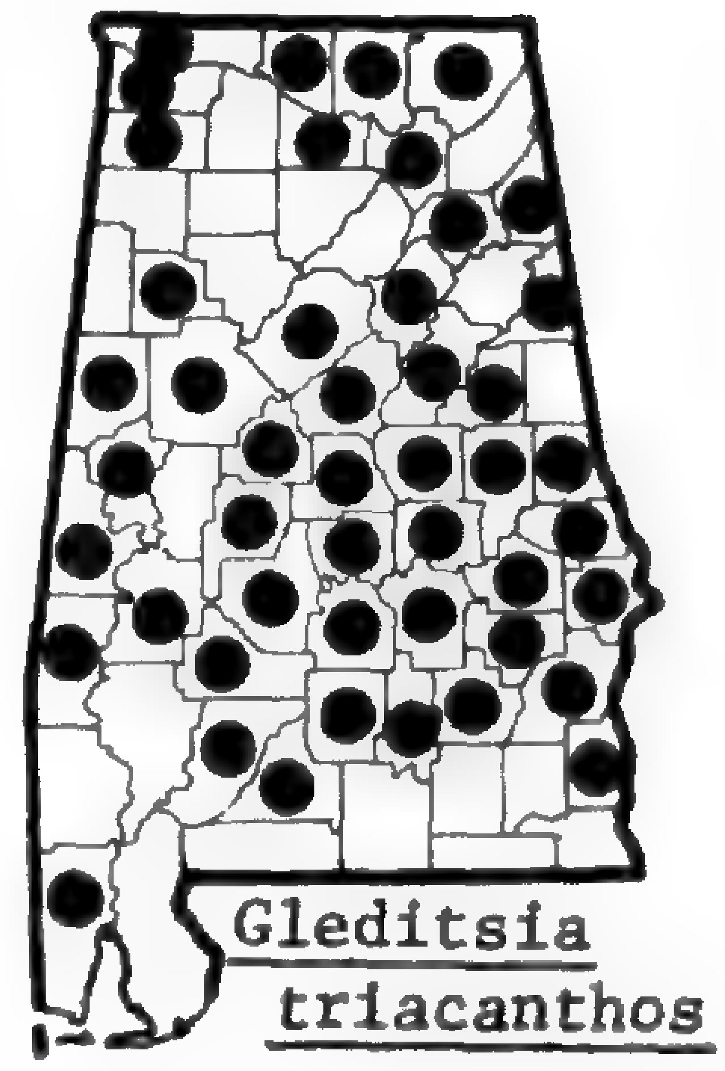
1. *C. lutea* (Michaux f.) K. Koch. Spring; summer. Rich woods, rare; CP, CuP, HR.

5. *Daubentonia* DC.

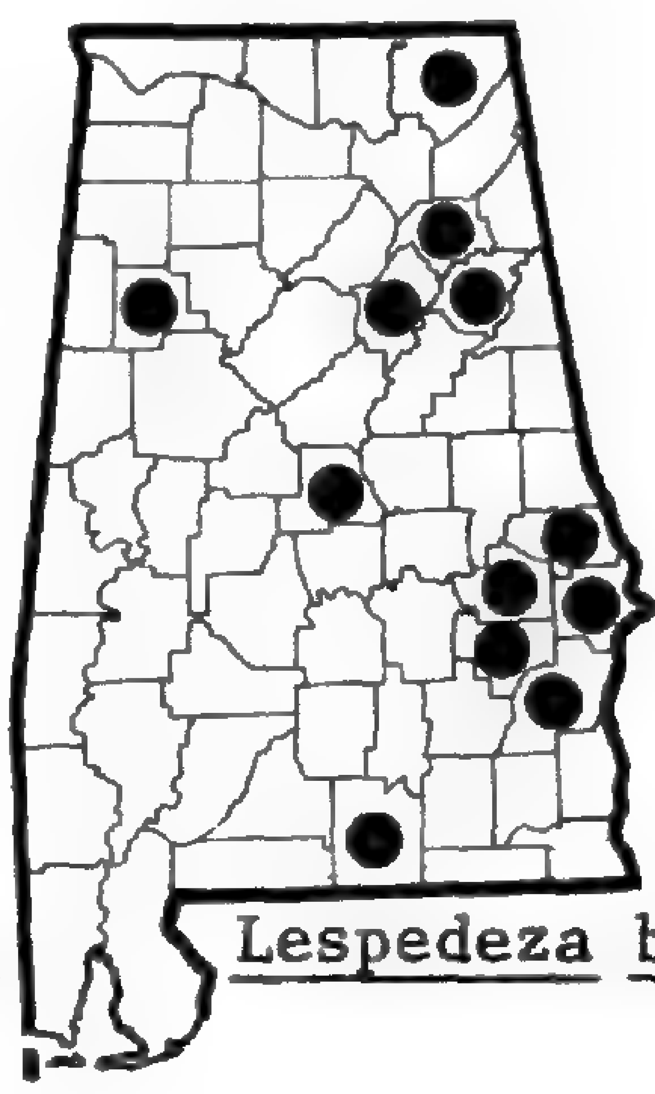
1. *D. punicea* (Cavanilles) DC. Summer; summer–fall. Ditches, low ground; OCP.


Daubentonia punicea

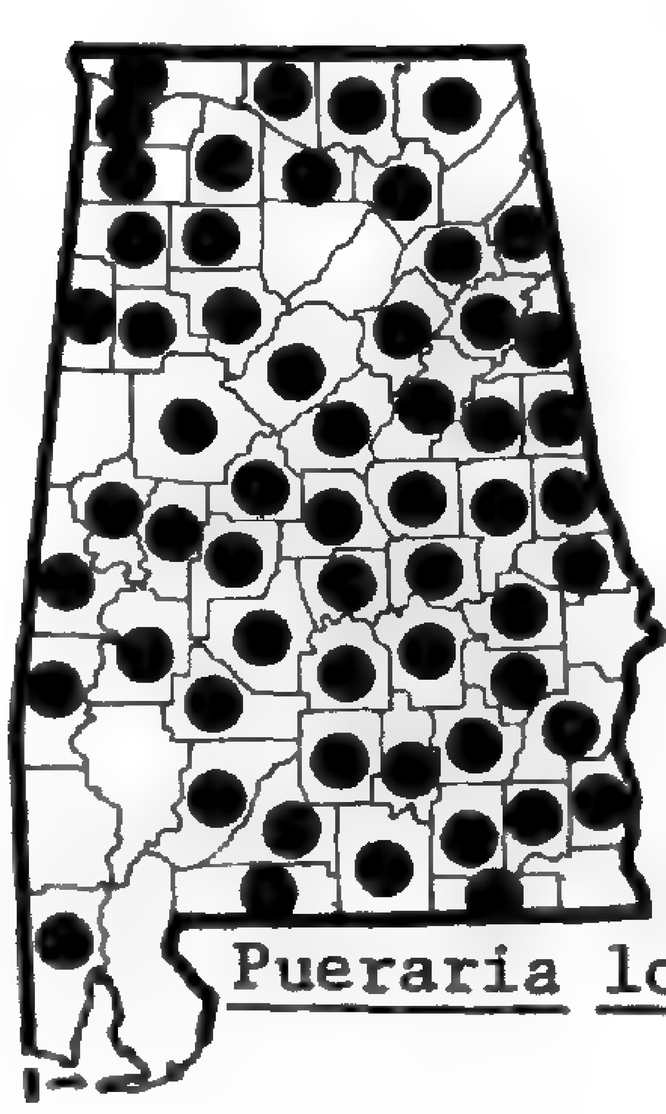

Gleditsia aquatica


Gleditsia triacanthos

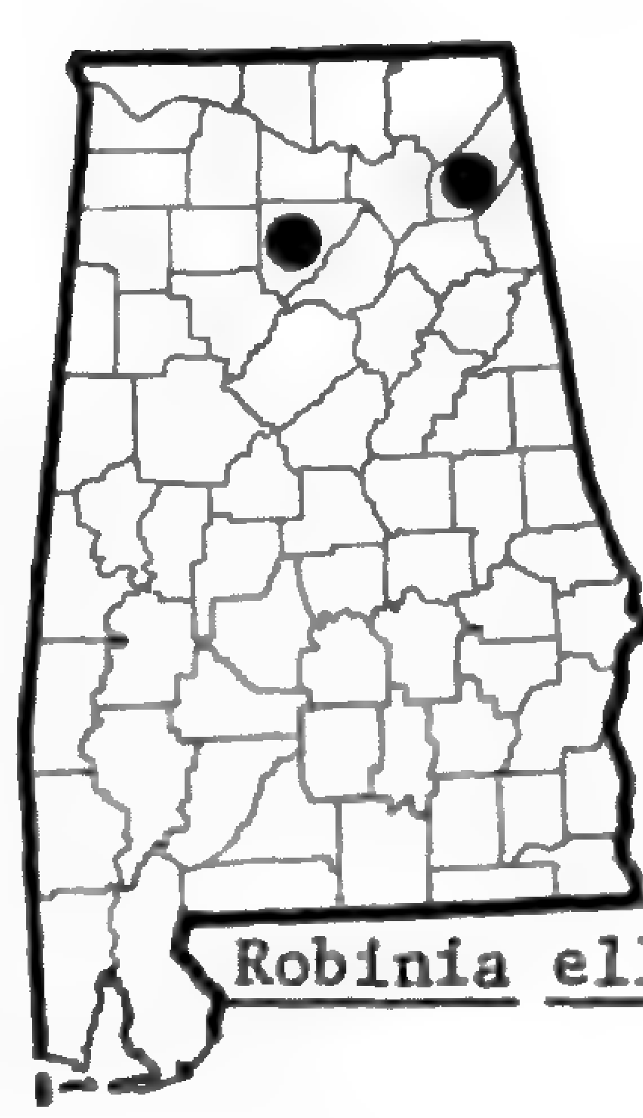

Gymnocladus dioica


Lespedeza bicolor


Parkinsonia aculeata


Pueraria lobata


Robinia boyntonii


Robinia elliottii

6. *Gleditsia* L.

1. *G. triacanthos* L., HONEY LOCUST. Spring; summer–fall. Low and upland woods, thickets, fencerows; throughout, but more common eastward and infrequent in southern CP.

Gleditsia aquatica Marshall (WATER LOCUST) has been reported by Wilbur in Radford, Ahles and Bell (1968), but no specimens have been seen by the writer.

7. *Gymnocladus* Lamarck, KENTUCKY COFFEE-TREE

1. *G. dioica* (L.) K. Koch. Spring; summer–winter. Persistent and weakly spreading from root or stump sprouts, rare; CuP, HR. No native individuals have been discovered.

8. *Lespedeza* Turzc.

1. *L. bicolor* Turzc. Summer; summer–fall. Roadsides, fencerows, rights-of-way, becoming naturalized from plantings, infrequent; CP, P, AM, CuP, VR.

9. *Parkinsonia* L.

1. *P. aculeata* L. Summer; fall. Waste ground, rare; OCP.

10. *Pueraria* DC.

1. *P. lobata* (Willd.) Ohwi, KUDZU. Summer–fall; fall. Rights-of-way, woods, fields; throughout.—Originally planted by the Soil Conservation Service for erosion control; now a serious pest.

11. *Robinia* L., LOCUST

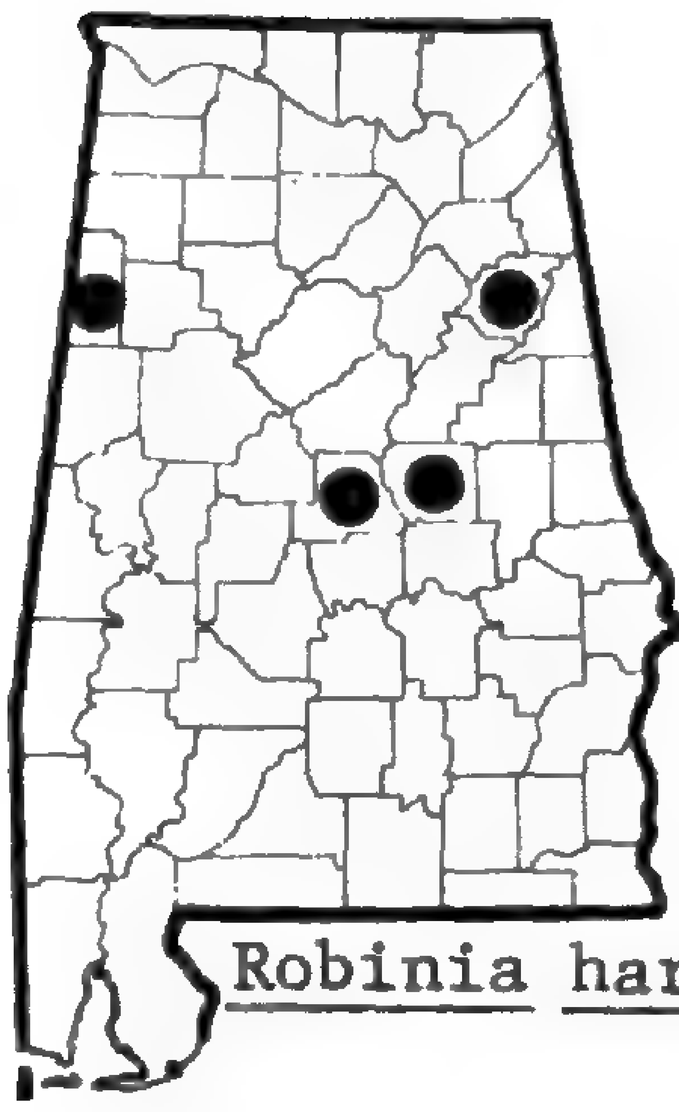
1. Lower 3 calyx lobes less than 2.5 mm long; fruit glabrous; petals white .... 5. *R. pseudo-acacia*
1. Lower 3 calyx lobes more than 2.5 mm long; fruit hispid; petals purplish to pink, rarely white 2
    2. Bracts more than 3 mm wide, longer than calyx; glandular pubescence of branches stout 3
        3. Branches and peduncles with sessile or subsessile, viscid glands .... 6. *R. viscosa*
        3. Branches and peduncles with stout, short-stalked glands .... 3. *R. hartwigii*
    2. Bracts less than 2 mm wide, equal to or shorter than calyx; glandular pubescence of branches slender 4
        4. Indurate trichomes more than 3 mm long present on last season's growth .... 4. *R. hispida*
        4. Indurate trichomes absent on last season's growth 5
            5. Pedicels glandular-hispid .... 1. *R. boyntonii*
            5. Pedicels not glandular-hispid .... 2. *R. elliottii*

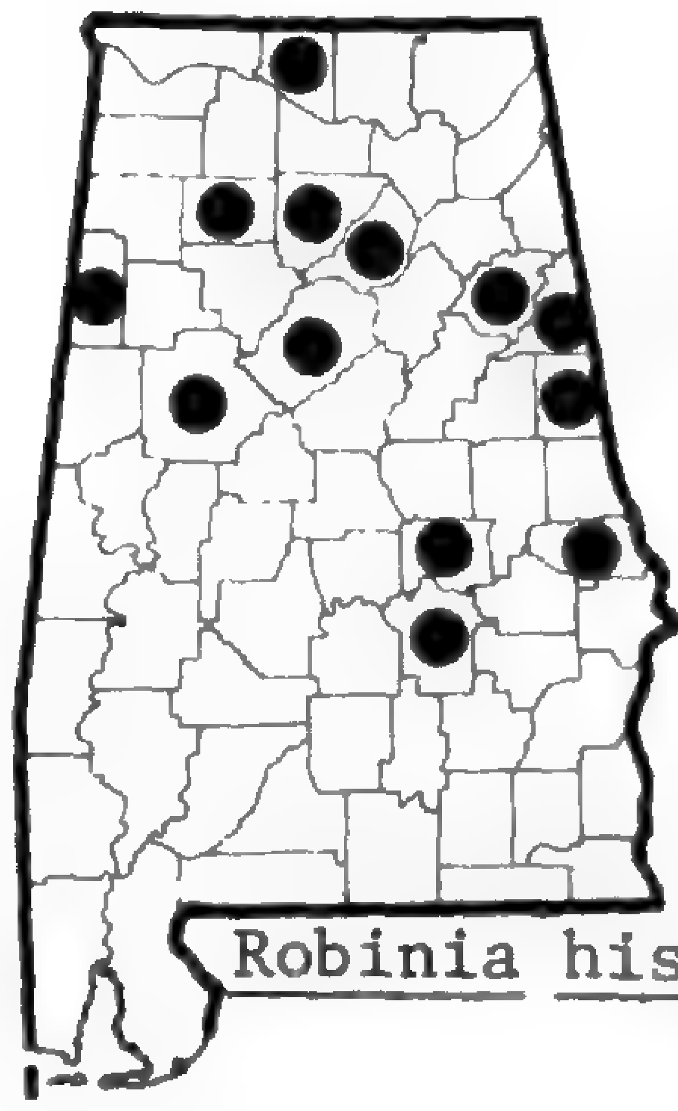
1. *R. boyntonii* Ashe. Spring; fruit not seen. Rocky woods, rare, reported from CuP by Wilbur in Radford, Ahles and Bell (1968).

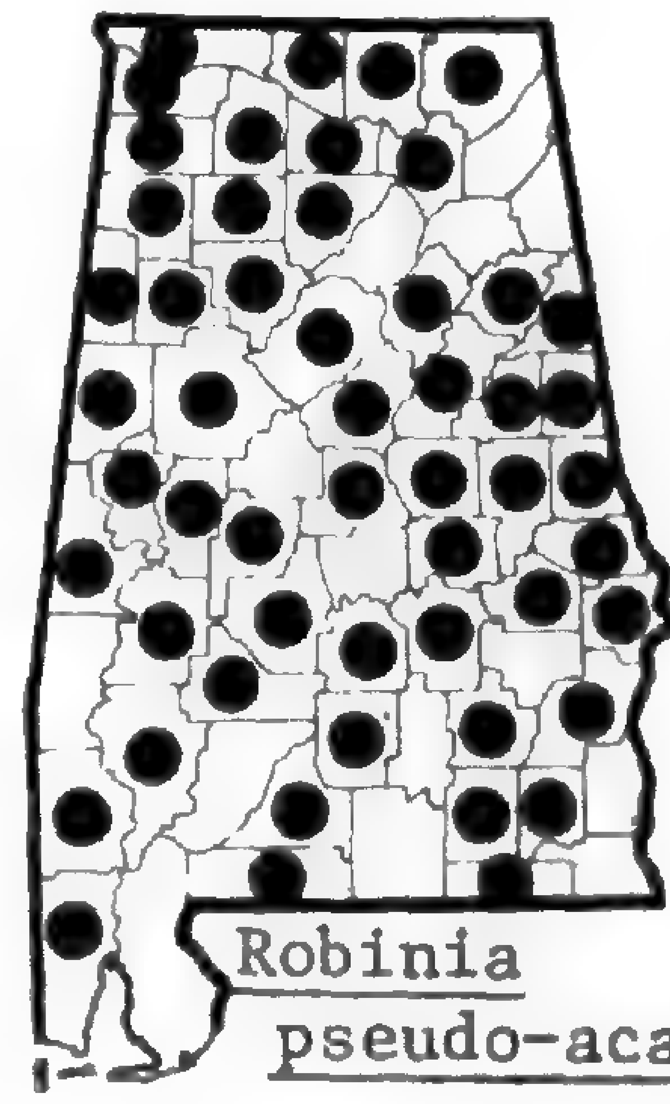
2. *R. elliottii* (Chapman) Ashe *ex* Small. Spring; summer–fall. Open woods, rare; CuP.

3. *R. hartwigii* Koehne. Spring; summer–fall. Rocky woods, infrequent, and occasionally persistent or escaping from cultivation; AM, CuP.

4. *R. hispida* L. Spring; summer–fall. Rocky woods, infrequent; P, AM, CuP, VR. *R. grandiflora* Ashe—S.


Robinia hartwigii

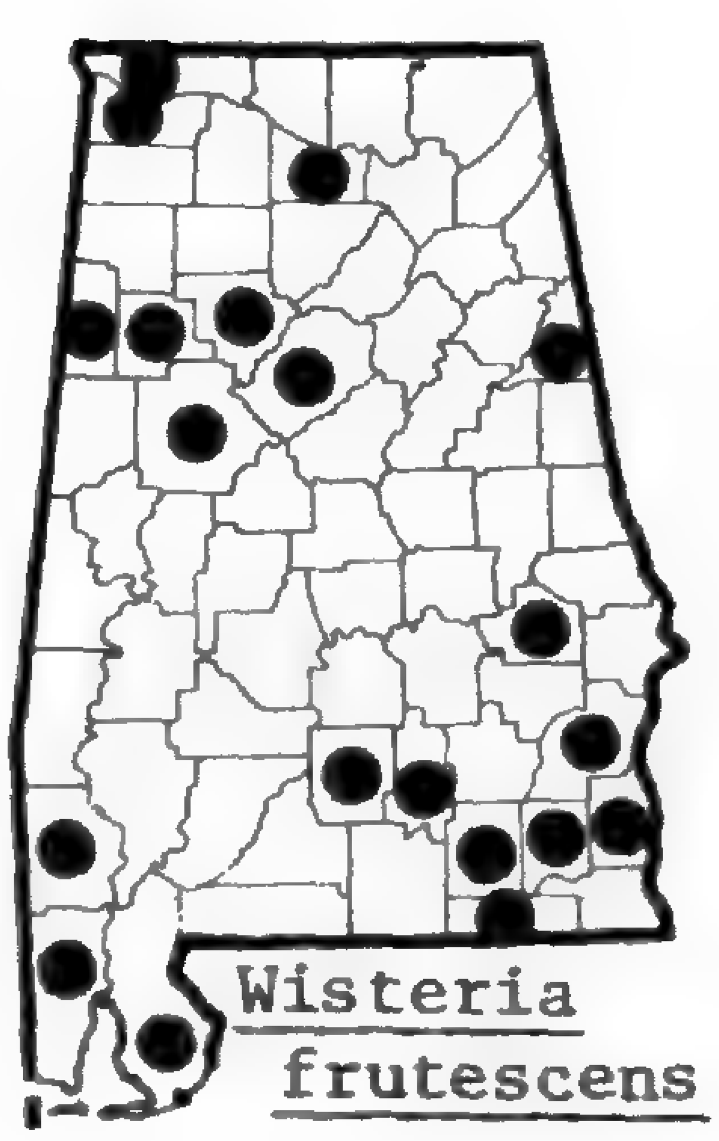

Robinia hispida

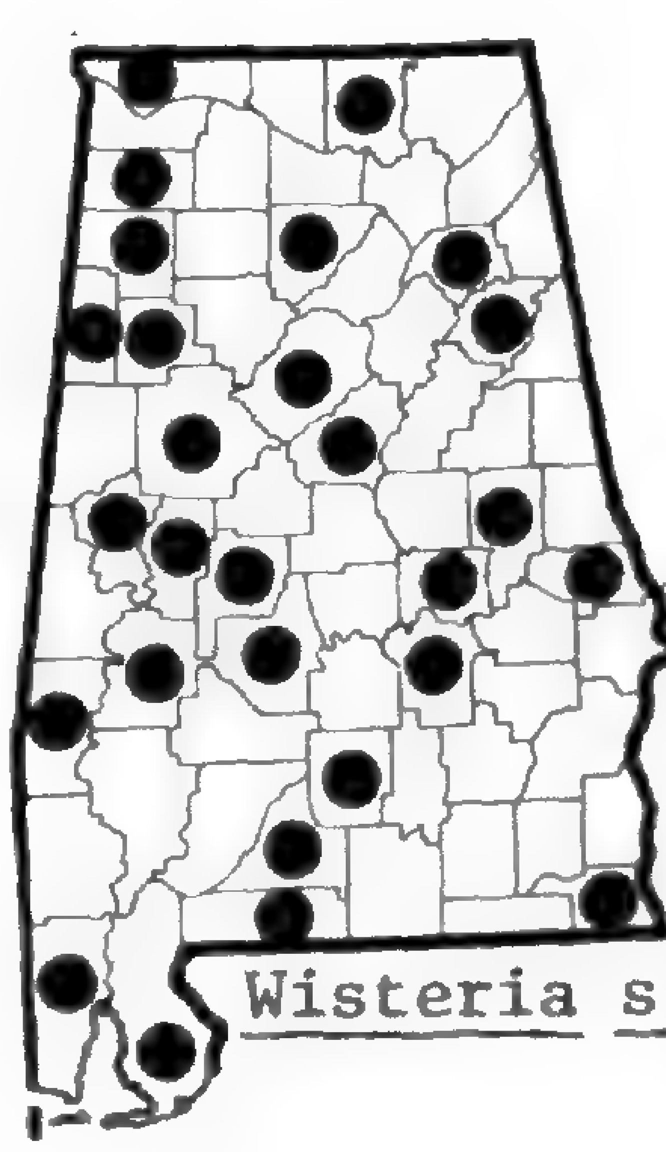

Robinia pseudo-acacia


Robinia viscosa

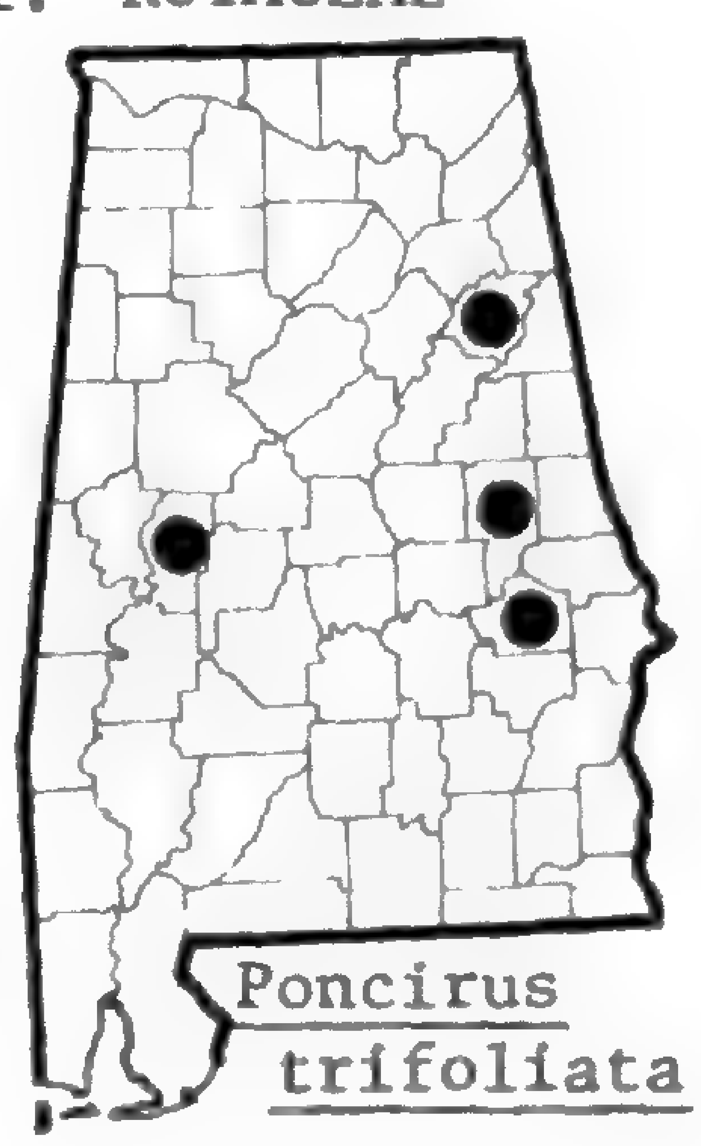

Vachellia farnesiana


Wisteria floribunda


Wisteria frutescens


Wisteria sinensis

31. RUTACEAE


Poncirus trifoliata

5. *R. pseudo-acacia* L., BLACK L. Spring; summer–fall. Deciduous woods, and spreading from cultivation into various habitats; throughout.

6. *R. viscosa* Vent. Spring; summer–fall. Reported by several writers, including Wilbur in Radford, Ahles and Bell (1968); no specimens seen by the writer.

12. *Vachellia* Wight & Arnott

1. *V. farnesiana* (L.) Wight & Arnott. Winter–spring. Waste ground, rare; OCP.

13. *Wisteria* Nuttall, WISTERIA

1. Ovary and fruit glabrous .... 2. *W. frutescens*
1. Ovary and fruit densely pubescent 2
   2. Leaflets 7–13; flowers more than 2 cm long .... 3. *W. sinensis*
   2. Leaflets 13–19; flowers 2 cm long or shorter .... 1. *W. floribunda*

1. *W. floribunda* (Willd.) DC. Spring–summer; summer–fall. Reported by Wilbur in Radford, Ahles and Bell (1968). *Kraunhia floribunda* (Willd.) Taub.—S.

2. *W. frutescens* (L.) Poiret. Spring; spring–fall. Low forest margins, thickets, infrequent; CP, AM, HR. *Kraunhia frutescens* (L.) Britt.—S; *K. frutescens* (L.) Greene—M.

3. *W. sinensis* (Sims) Sweet. Spring; summer–fall. Frequent escape to rights-of-way, open ground; throughout.

Cytisus scoparius (L.) Link (SCOTCH BROOM) has been cited as an escape in Alabama by Wilbur in Radford, Ahles and Bell (1968), but the present writer is unable to verify this.

31. RUTACEAE

1. Leaves 3-foliolate; leaflets entire 2
   2. Stem with thorns; petioles winged; fruit a berry .... 1. *Poncirus*
   2. Stem thornless; petioles wingless; fruit a samara .... 2. *Ptelea*
1. Leaves, at least most, 5- or more-foliolate; leaflets cuneate-serrate .... 3. *Zanthoxylum*

1. *Poncirus* Rafinesque, TRIFOLIATE ORANGE

1. *P. trifoliata* (L.) Rafinesque. Spring; fall. Escaped to alluvial woods, rare; CP, P, VR.

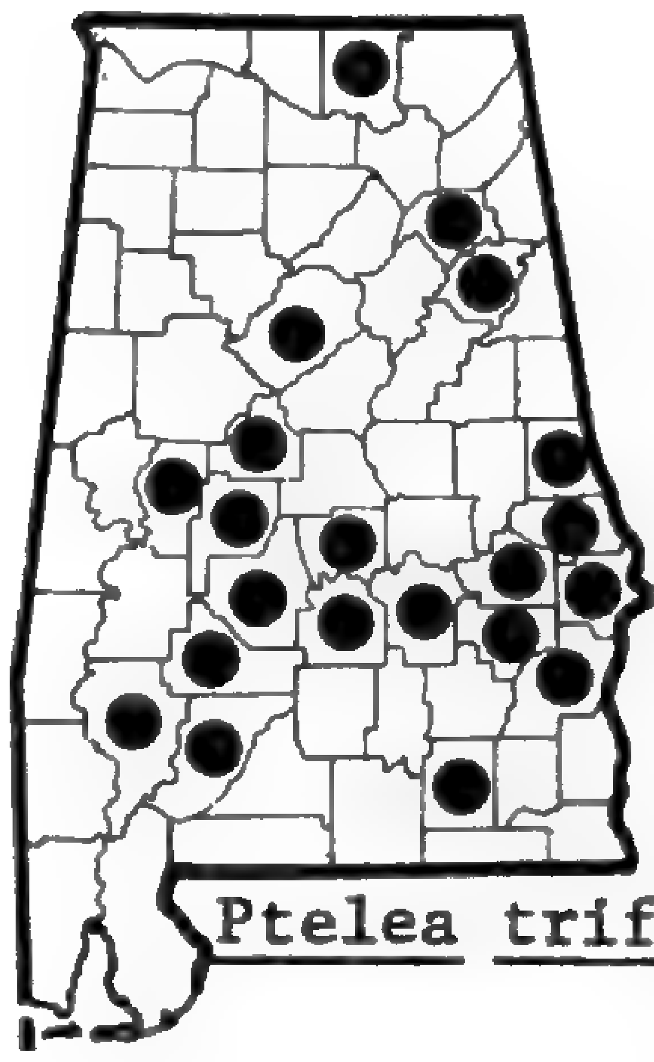
2. *Ptelea* L., WAFER-ASH

1. *P. trifoliata* L. Spring; summer. Dry or alluvial woods, infrequent; CP, CuP, VR. *P. microcarpa* Sm.—S.

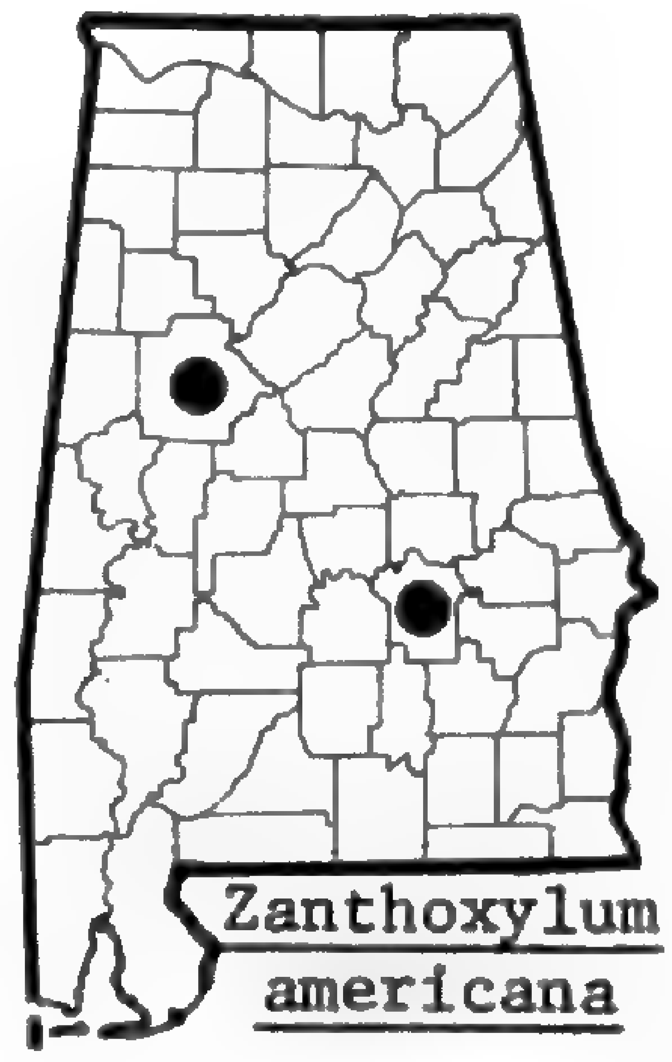
3. *Zanthoxylum* L., PRICKLY ASH, TOOTHACHE TREE

1. Inflorescences axillary; leaflets pubescent beneath .... 1. *Z. americana*
1. Inflorescence terminal; leaflets glabrous beneath .... 2. *Z. clava-herculis*

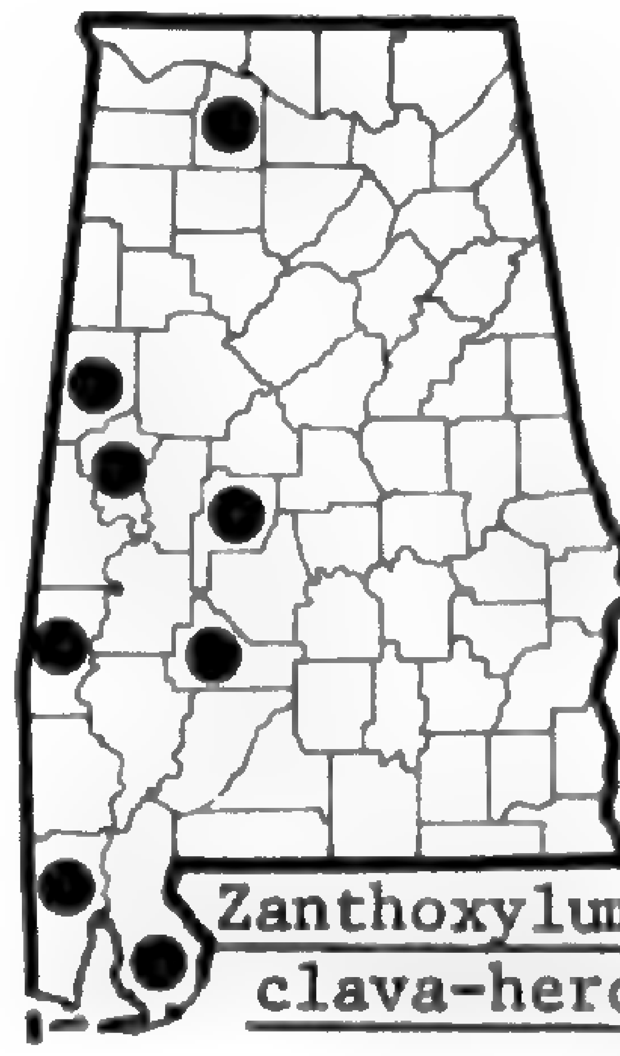
1. *Z. americana* Miller. Spring; summer. Rich, alluvial woods, very rare; CP, southern CuP.



Ptelea trifoliata

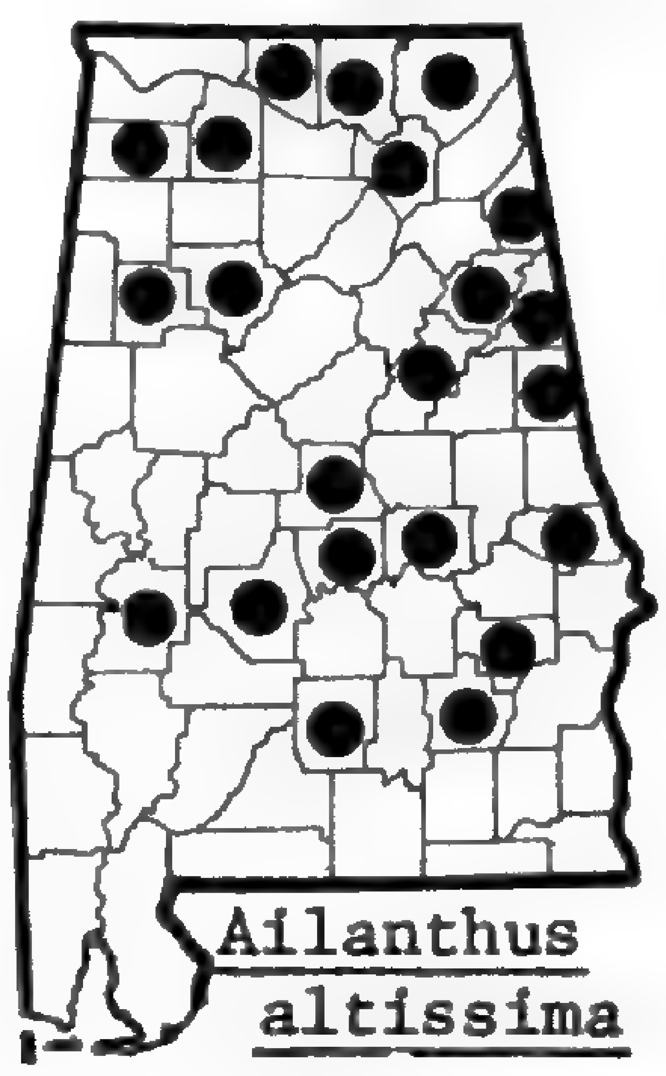


Zanthoxylum americana



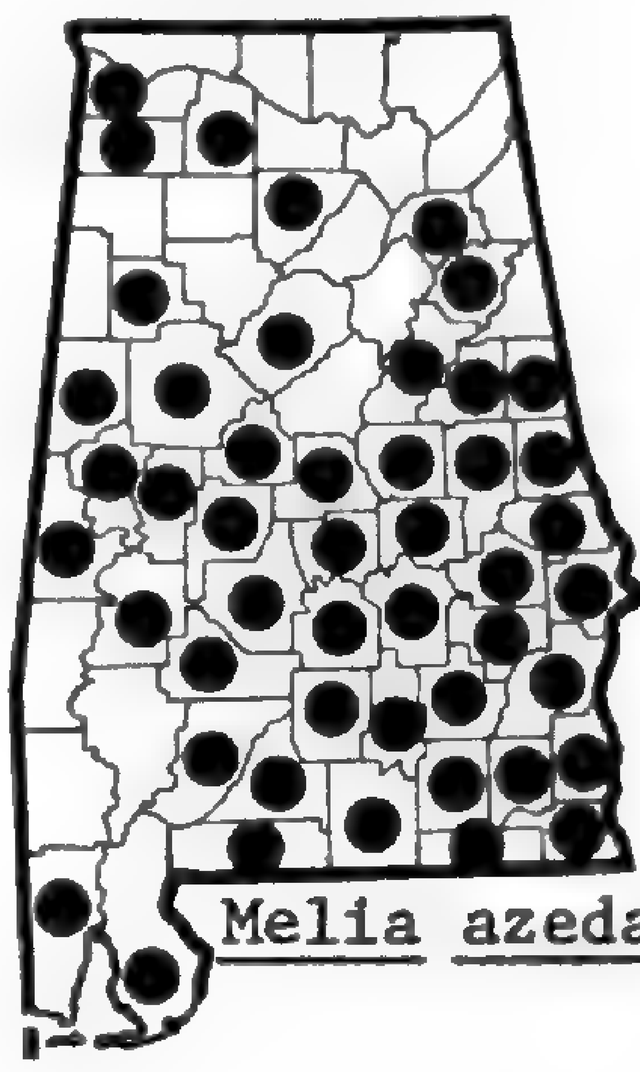
Zanthoxylum clava-herculis

32. SIMAROUBACEAE



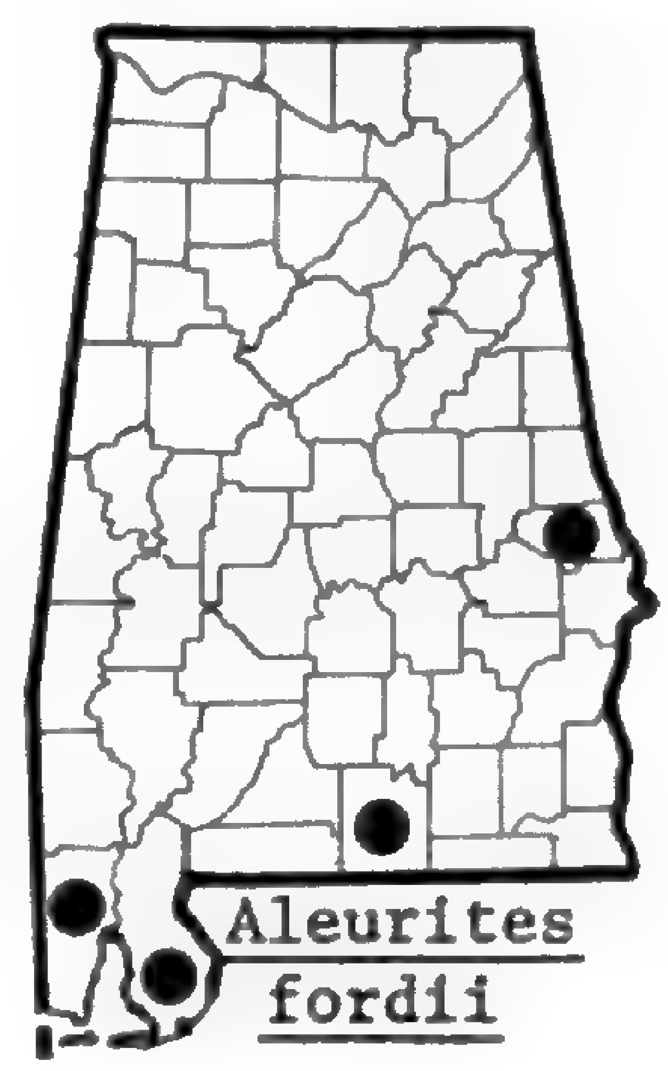
Ailanthus altissima

33. MELIACEAE

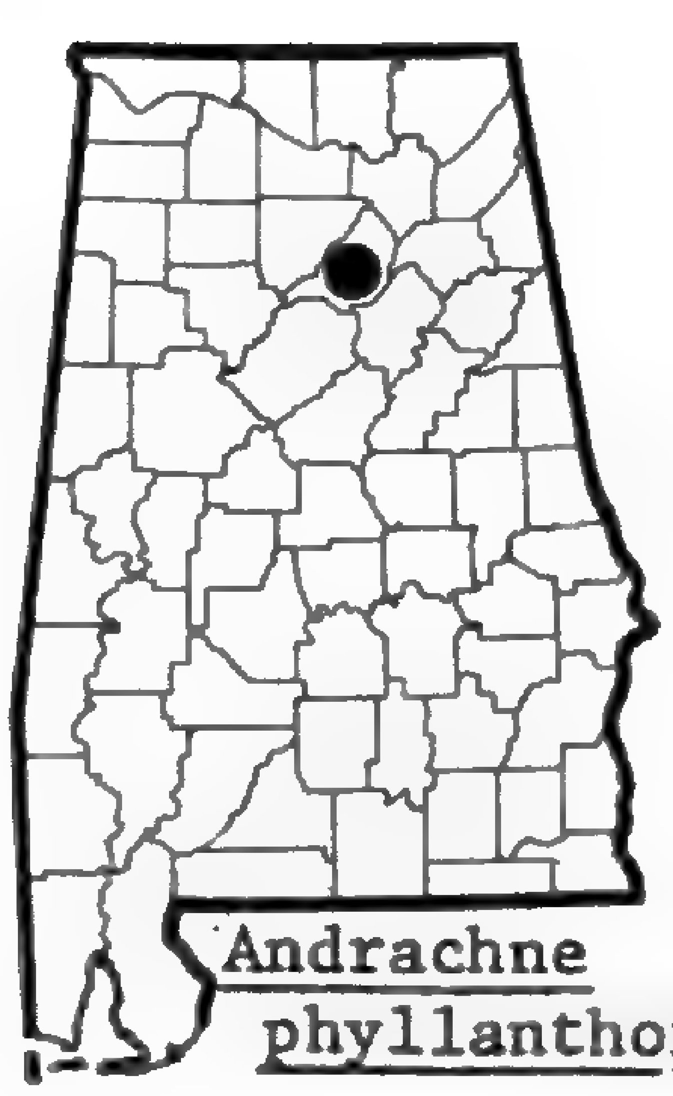


Melia azedarach

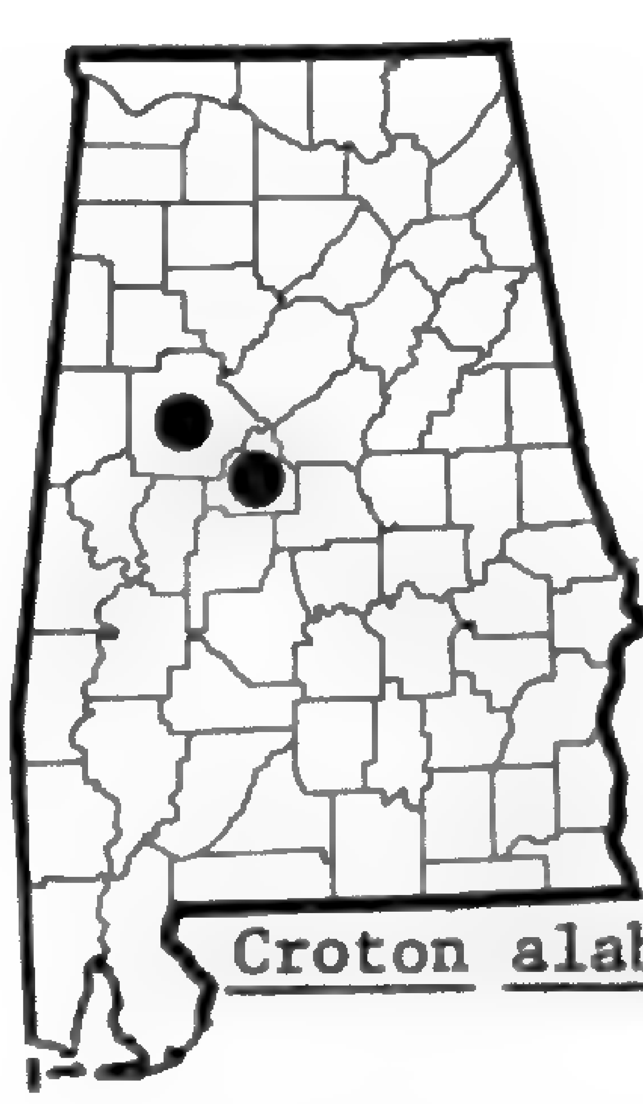
34. EUPHORBIACEAE



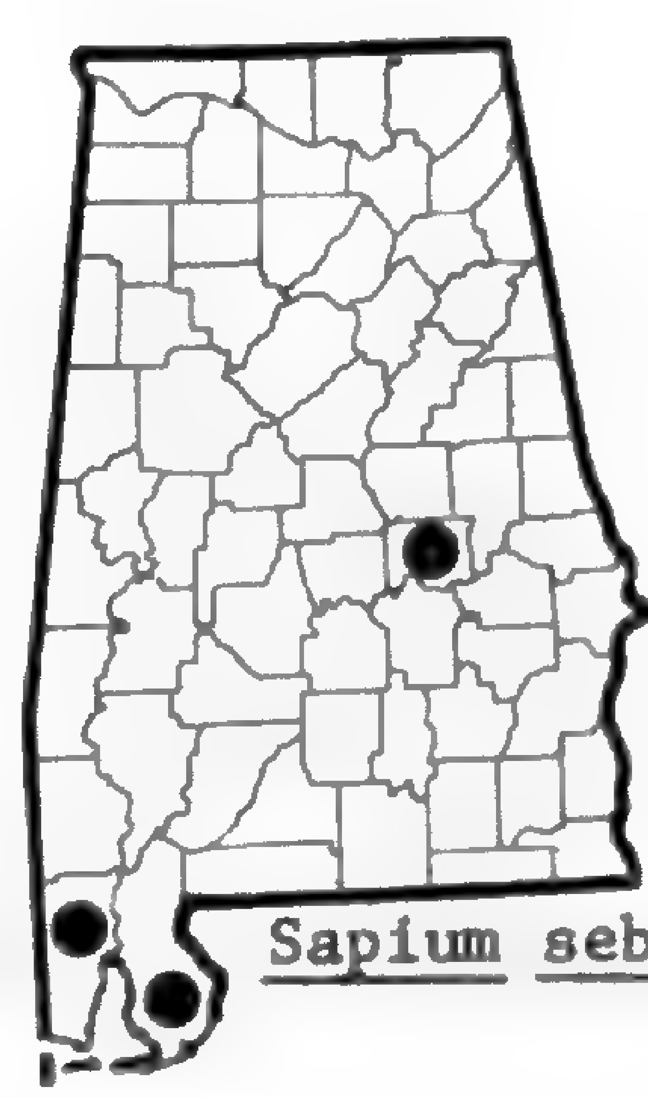
Aleurites fordii



Andrachne phyllanthoides



Croton alabamensis



Sapium sebiferum

2. *Z. clava-herculis* L. Spring; summer–fall. Thickets, alluvial woods, rare; CP, HR.

32. SIMAROUBACEAE

1. *Ailanthus* Desf., TREE OF HEAVEN

1. *A. altissima* (Miller) Swingle. Spring; summer–fall. Mesic woods, rights-of-way, waste places; throughout. *A. glandulosa* Desf.—M.

33. MELIACEAE

1. *Melia* L., CHINA-BERRY

1. *M. azedarach* L. Spring; late summer–winter. Fencerows, roadsides, waste places; throughout.

34. EUPHORBIACEAE

1. Leaves serrate .... 6. *Stillingia*
1. Leaves entire 2
    2. Twigs, inflorescences and lower surfaces of leaves covered with silvery, peltate scales .... 3. *Croton*
    2. Twigs, inflorescences and lower surfaces of leaves lacking peltate scales, not silvery 3
        3. Leaves cordate .... 1. *Aleurites*
        3. Leaves truncate to cuneate 4
            4. Inflorescences terminal 5
                5. Petioles 1 cm or less long; leaves lanceolate to elliptic .... 5. *Sebastiania*
                5. Petioles more than 2 cm long; leaves rhombic .... 4. *Sapium*
            4. Inflorescences of axillary-solitary flowers .... 2. *Andrachne*

1. *Aleurites* Forst.

1. *A. fordii* Hemsl., TUNG OIL TREE. Flowers not seen; summer. Fencerows, rights-of-way, rare; OCP.

2. *Andrachne* L.

1. *A. phyllanthoides* (Nuttall) Mueller. Summer–fall. Sand bar, extremely rare; CuP.—This is the only population of this plant known from east of Arkansas (Clark, 1967).

3. *Croton* L.

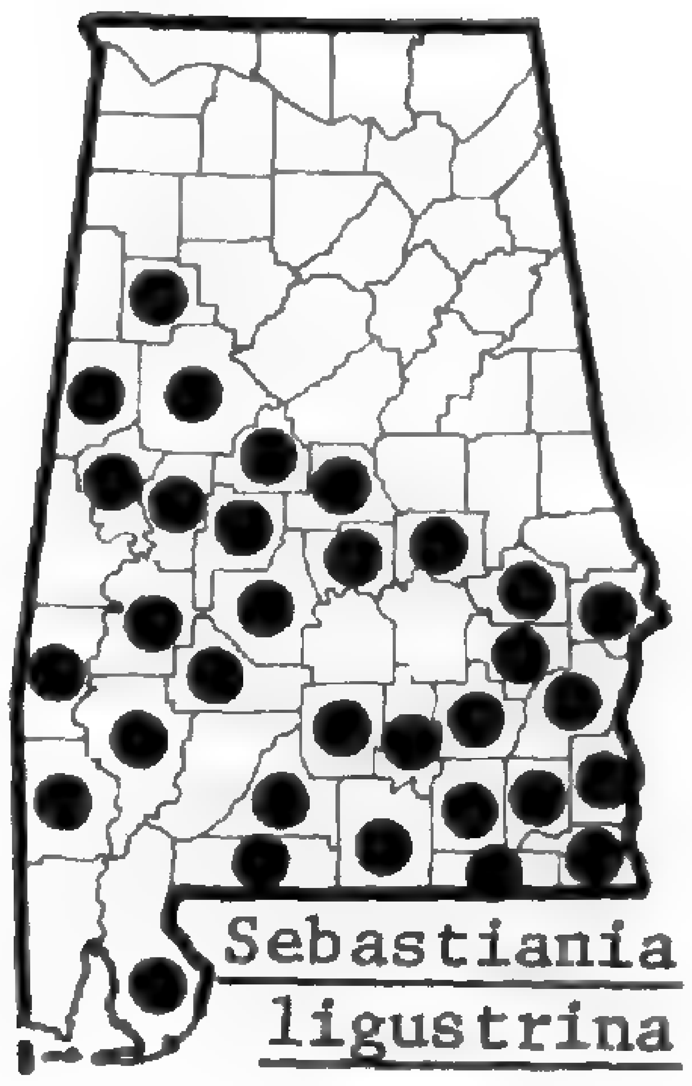
1. *C. alabamensis* Smith. Spring. Rocky slopes, rare and local; southern CuP.—A single population of this species in southern Tennessee is the only known population outside Alabama.

4. *Sapium* Browne

1. *S. sebiferum* (L.) Roxburgh. Spring–early summer; summer–fall. Low thickets, rights-of-way; OCP and a single locality inland. *Triadica sebifera* (L.) Sm.—S; *S. sebiferum* Roxb.—M.

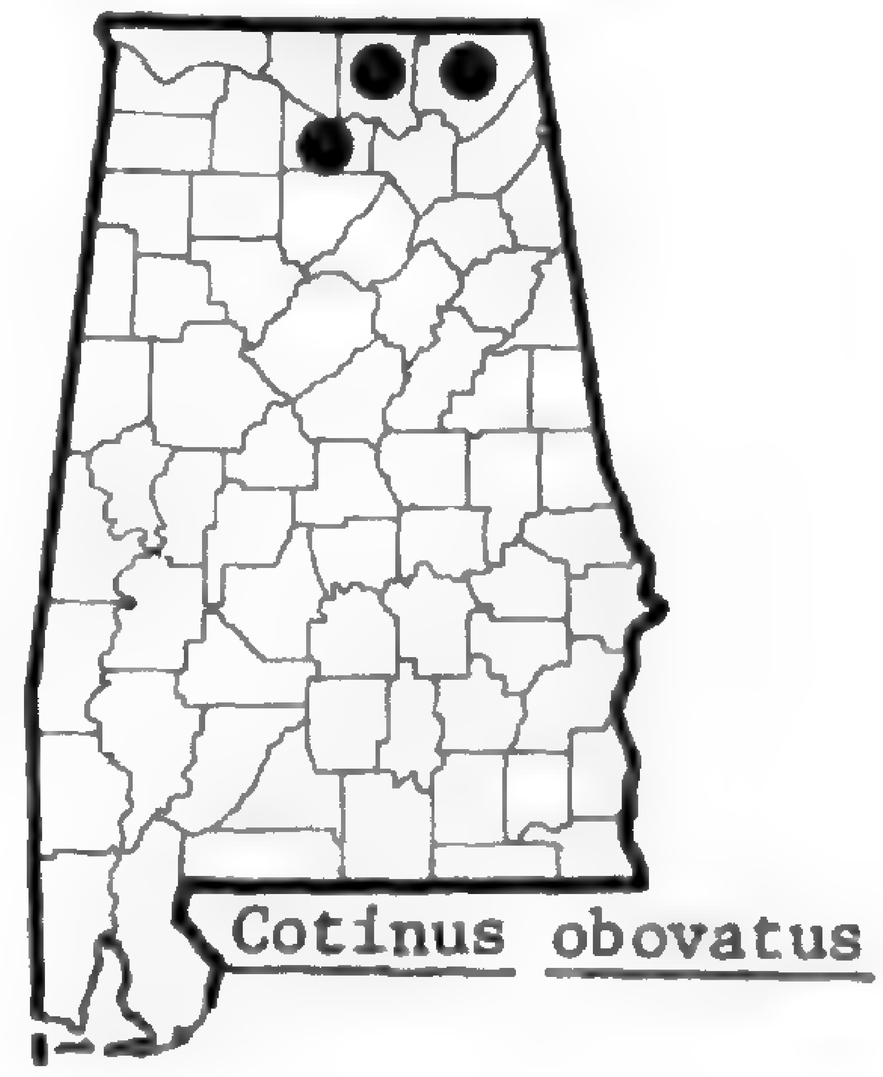
5. *Sebastiania* Sprengel

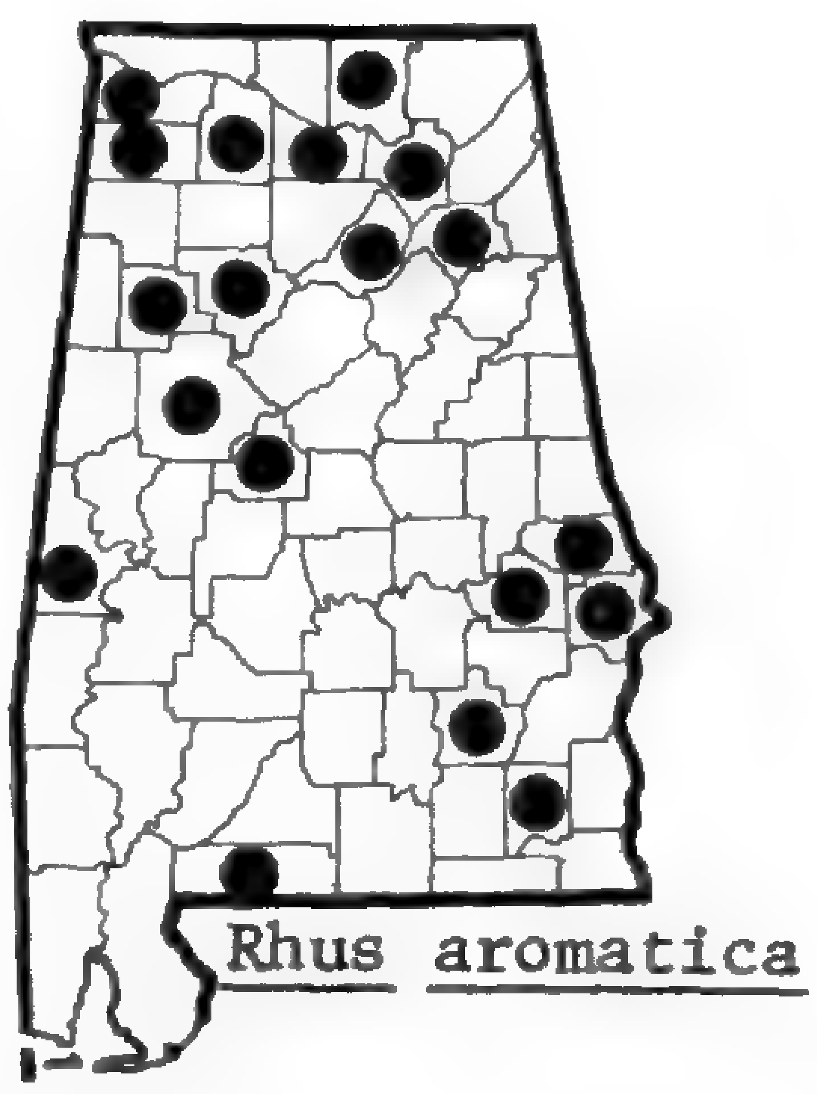
1. *S. ligustrina* (Michaux) Muell.-Arg. Spring; summer. Swamp forests, alluvial woods; CP. *Sebastiana ligustrina* (Michx.) Muell.-Arg.—S.

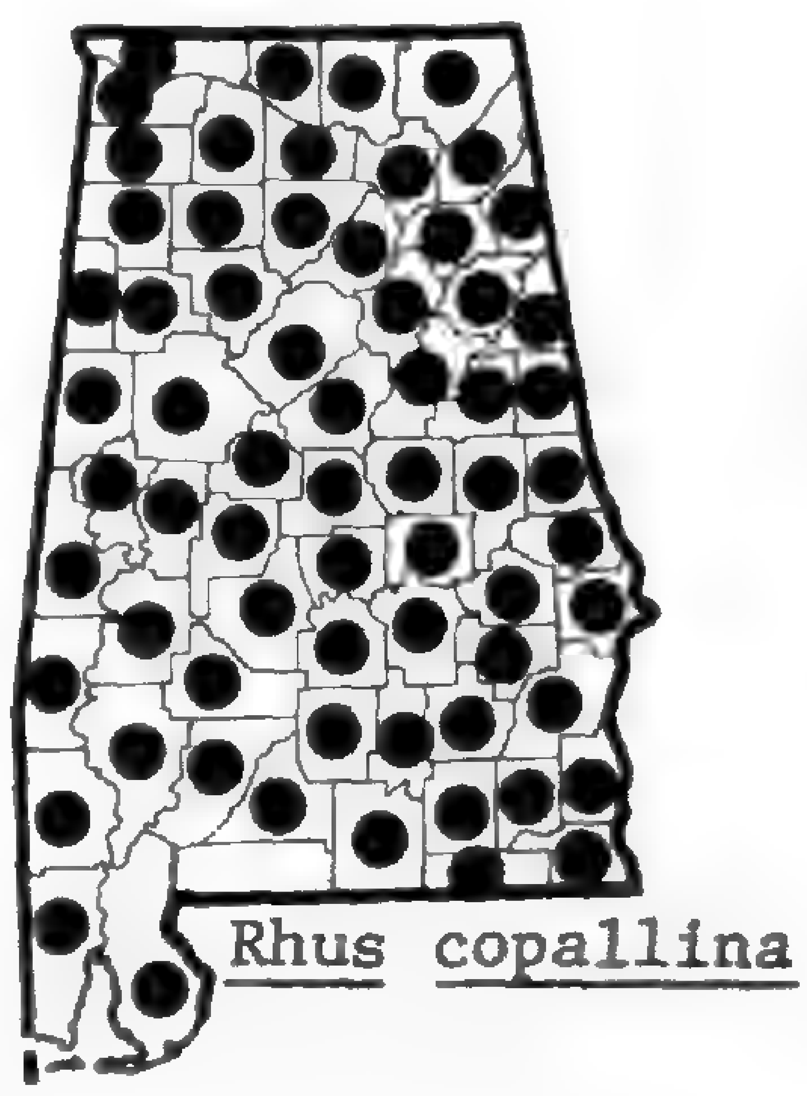

Sebastiania ligustrina

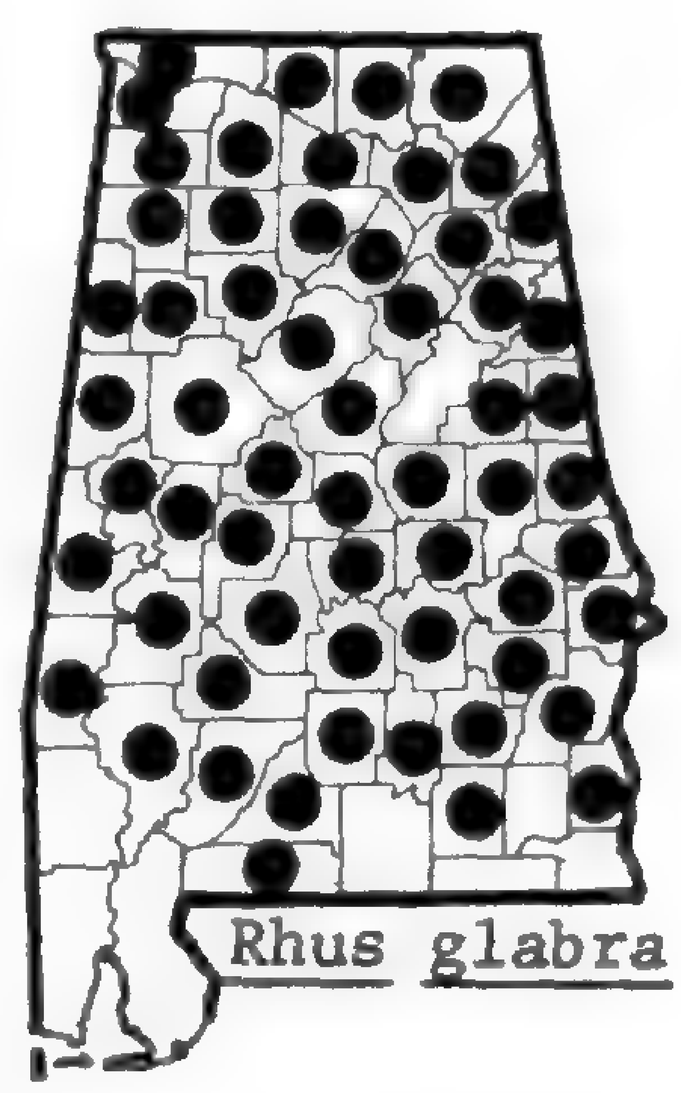

Stillingia aquatica

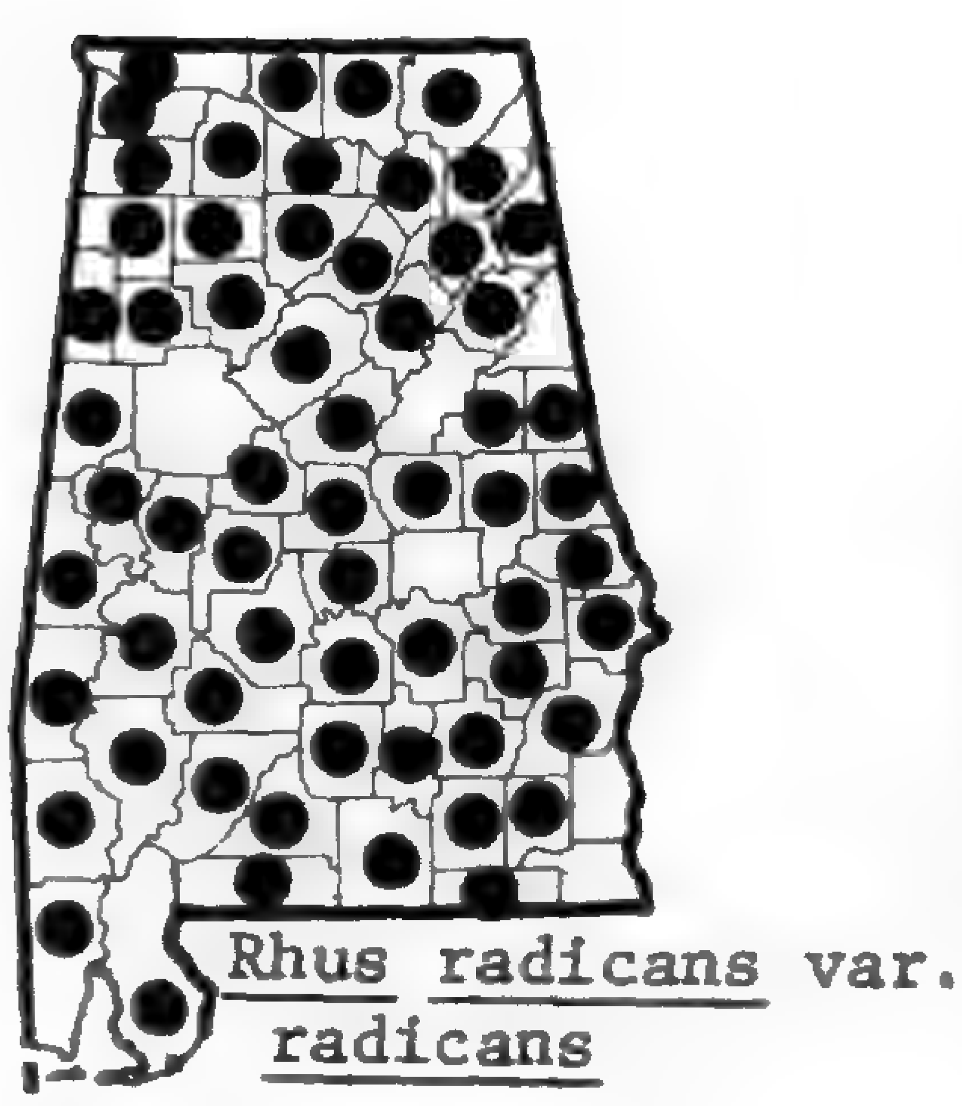
35. ANACARDIACEAE

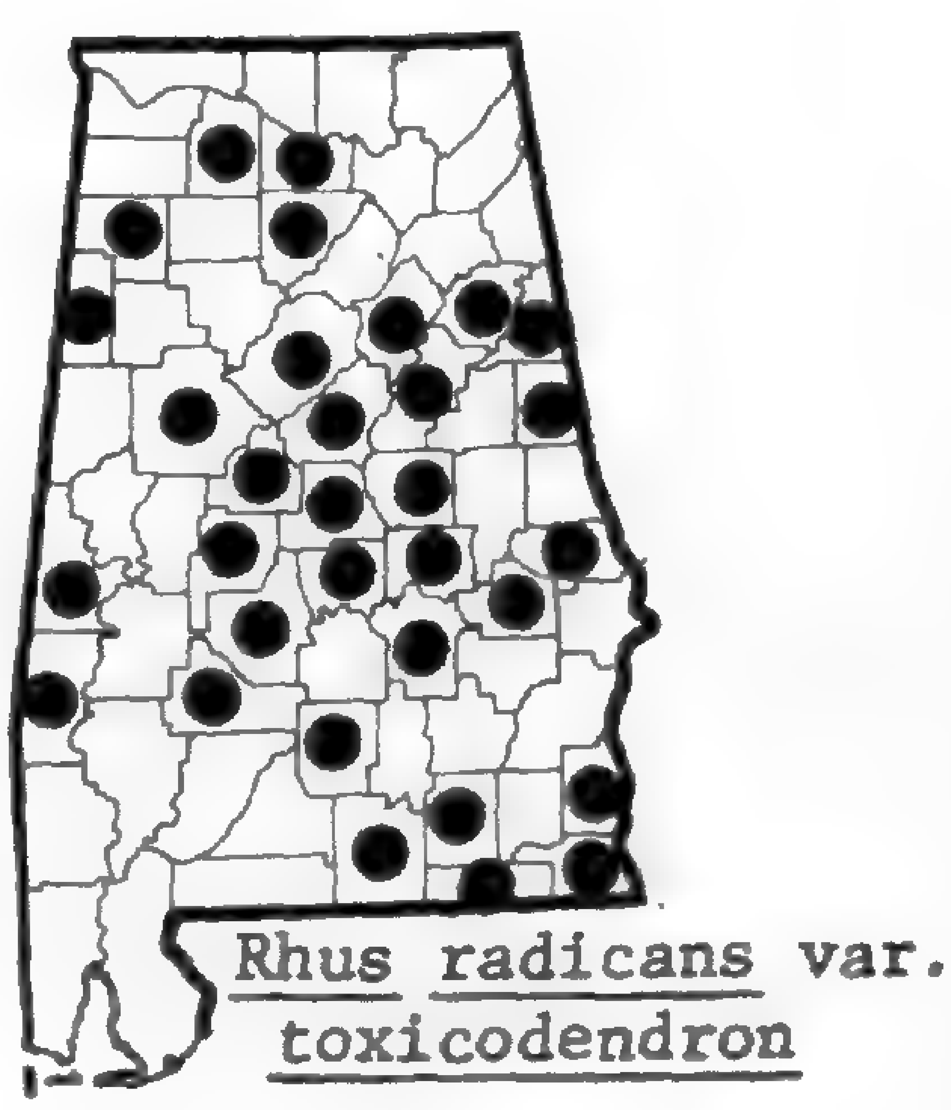

Cotinus obovatus


Rhus aromatica


Rhus copallina


Rhus glabra


Rhus radicans var. radicans


Rhus radicans var. toxicodendron


Rhus typhina

6. *Stillingia* Garden

1. *S. aquatica* Chapman. Spring–fall. Ponds, rare; OCP.

35. ANACARDIACEAE

1. Leaves simple	1. *Cotinus*
1. Leaves compound	2. *Rhus*

1. *Cotinus* Adanson, CHITTAM-WOOD, SMOKE-TREE

1. *C. obovatus* Rafinesque. Spring; spring–summer. Rocky woods, local; border of CuP and HR. *C. cotinoides* (Nutt.) Britt.—M; *C. americanus* Nutt.—H, S.

2. *Rhus* L.

1. Leaflets 3, or leaves absent at anthesis	2
2. Leaves absent at anthesis	1. *R. aromatica*
2. Leaves present	3
3. Inflorescence terminal	1. *R. aromatica*
3. Inflorescence axillary	4. *R. radicans*
1. Leaflets 5 or more	4
4. Inflorescence axillary	6. *R. vernix*
4. Inflorescence terminal	5
5. Leaf rachises winged, at least distally	2. *R. copallina*
5. Leaf rachises not winged	6
6. Twigs glabrous	3. *R. glabra*
6. Twigs densely pubescent	5. *R. typhina*

1. *R. aromatica* Aiton, FRAGRANT SUMAC. Winter–spring; summer–fall. Dry or rocky woods; CP (rare), CuP, VR, HR. More common northwestward. *Schmaltzia aromatica* (Ait.) Sm.—H; *S. crenata* (Mill.) Greene—H, S.

2. *R. copallina* L., DWARF SUMAC, WINGED SUMAC. Summer; summer–fall. Fields, fencerows, right-of-way, thickets; throughout.

3. *R. glabra* L., SMOOTH SUMAC. Spring–summer; summer–fall. Fields, fencerows, right-of-way, thickets; throughout.

4. *R. radicans* L. Spring; summer–fall.

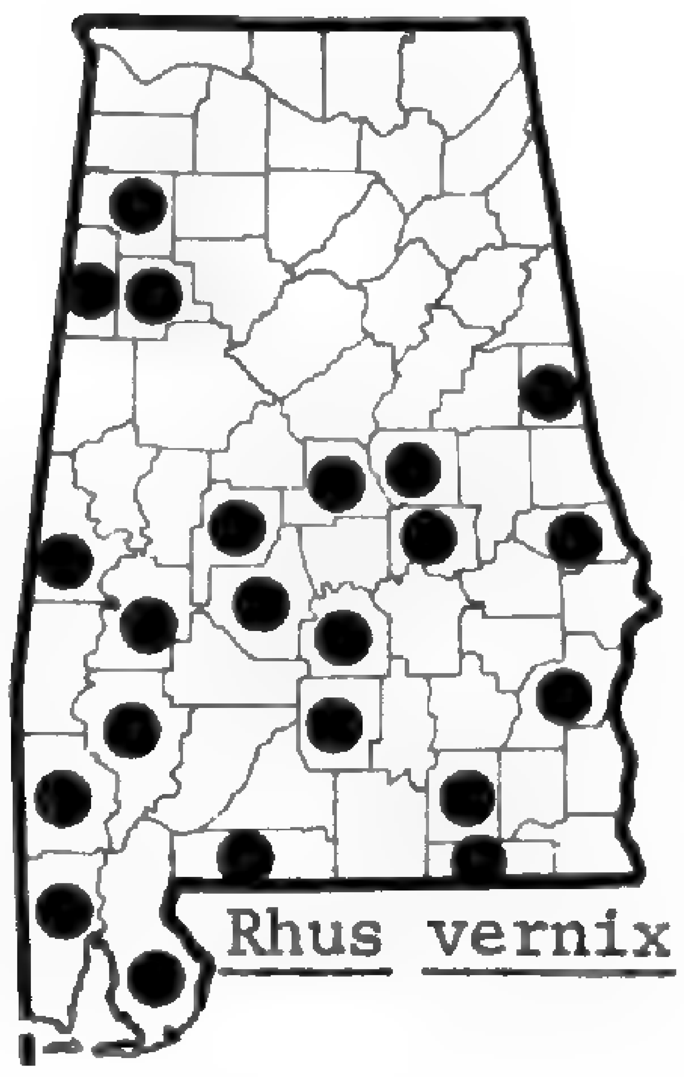
1. Fruit glabrous; stems climbing or trailing	*R. radicans* var. *radicans*
1. Fruit pubescent; stems not climbing or trailing	*R. radicans* var. *toxicodendron*

R. radicans L. var. *radicans*, POISON IVY. Fields, thickets, woods; throughout. *Toxicodendron radicans* (L.) Kuntze—S; *T. goniocarpum* Greene—H.—One of Alabama's commonest woody plants.

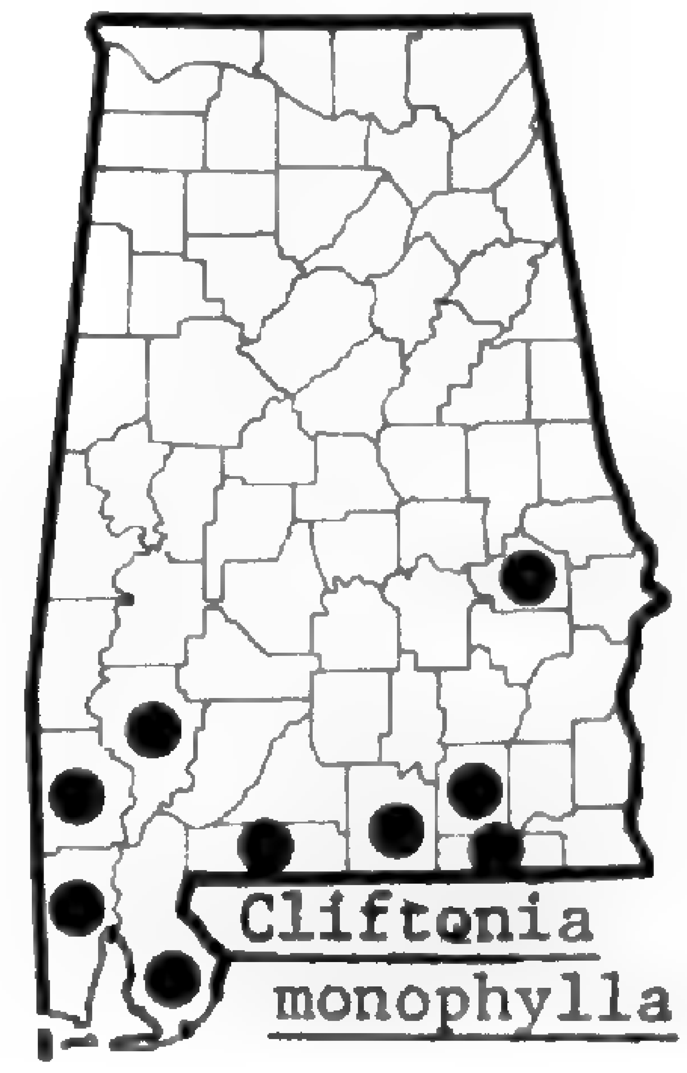
R. radicans L. var. *toxicodendron* (L.) Persoon, POISON OAK. Fields, thickets, upland woods, more infrequent than the typical variety; throughout. *R. toxicodendron* L.—M, RAB; *Toxicodendron toxicodendron* (L.) Britt.—S; *T. quercifolium* (Steud.) Greene—H.

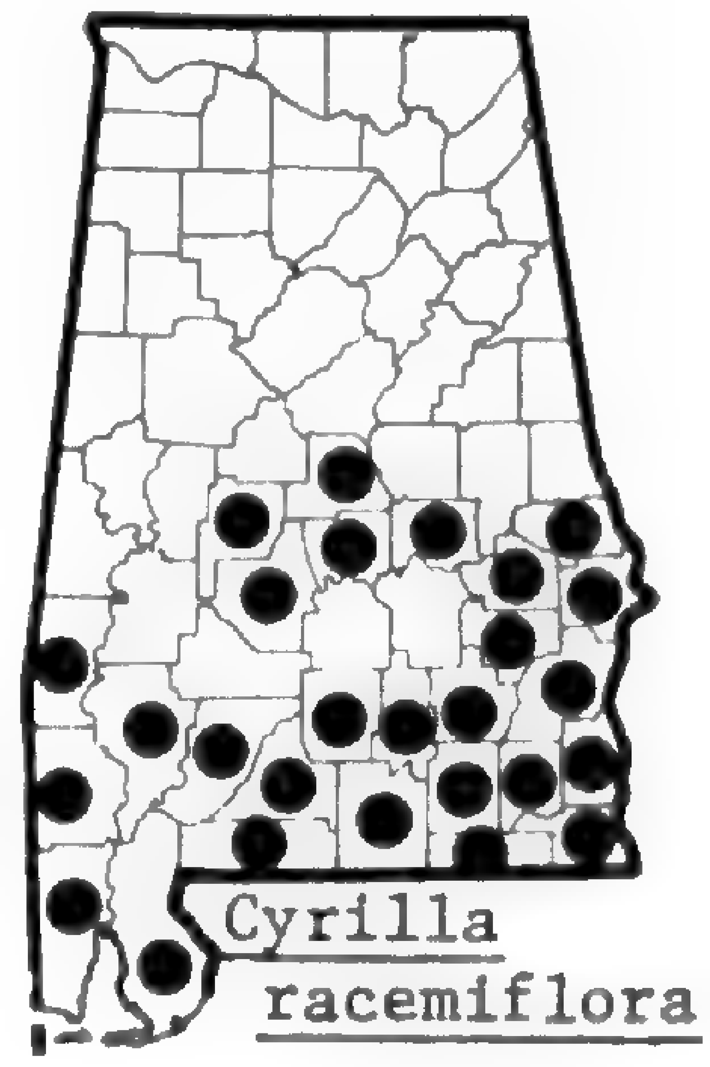
5. *R. typhina* L., STAGHORN SUMAC. Spring; summer. Margin of rich woods, very rare; HR. *R. hirta* (L.) Sudw.—S.—Only a single, small population is presently known.

6. *R. vernix* L., POISON SUMAC, THUNDERWOOD. Spring; summer; Seepages, ditches, swamp ecotones; CP, AM. *Toxicodendron pinnatum* Mill.—H; *T. vernix* (L.) Kuntze—S.

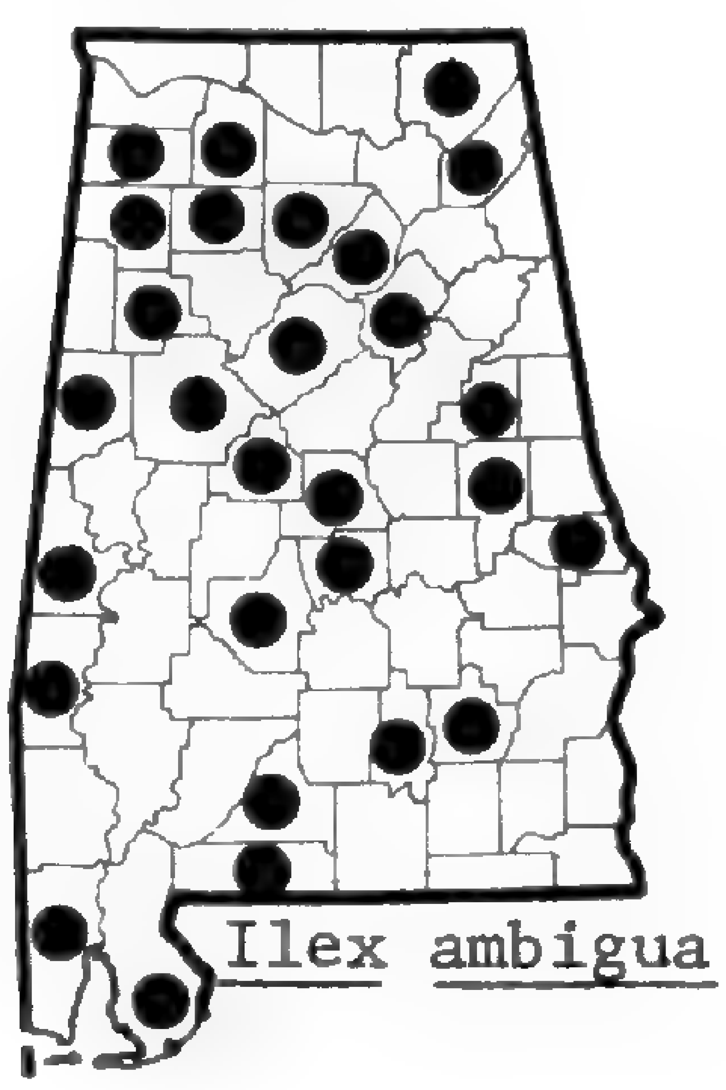

Rhus vernix

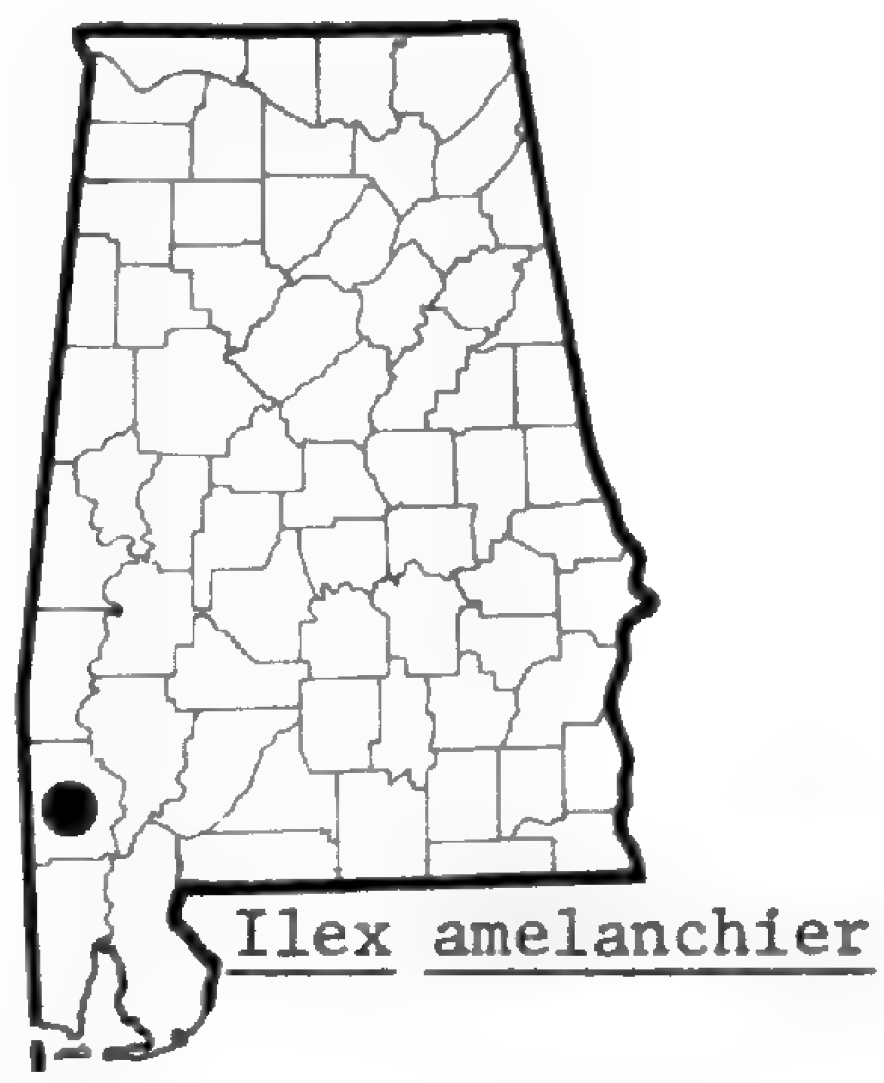
36. CYRILLACEAE

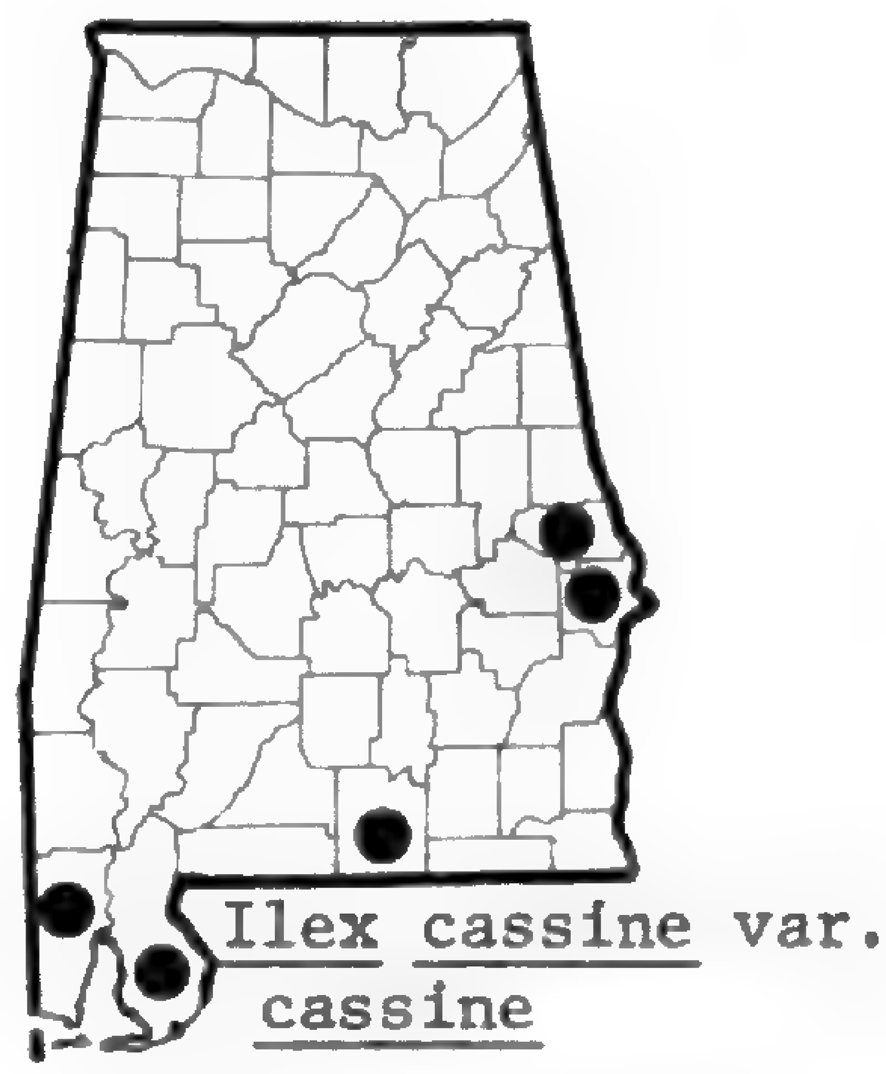

Cliftonia monophylla

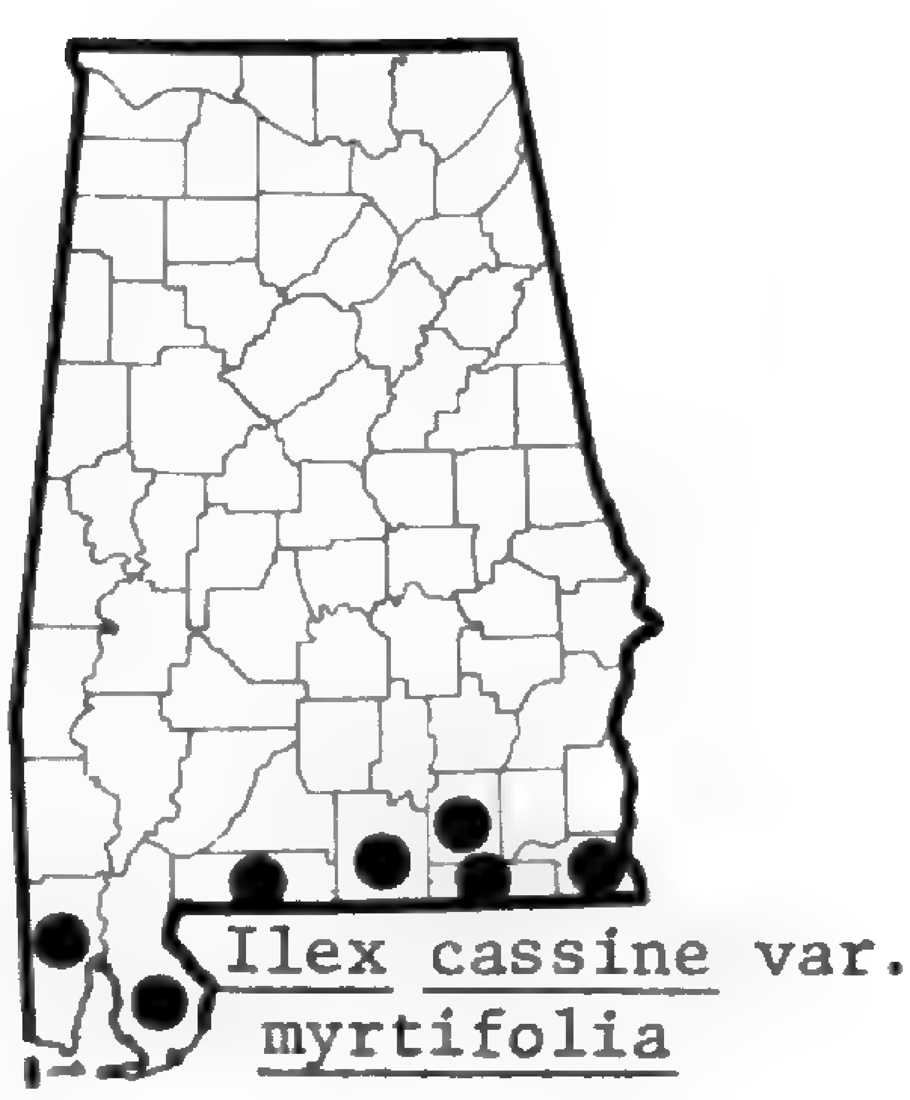

Cyrilla racemiflora

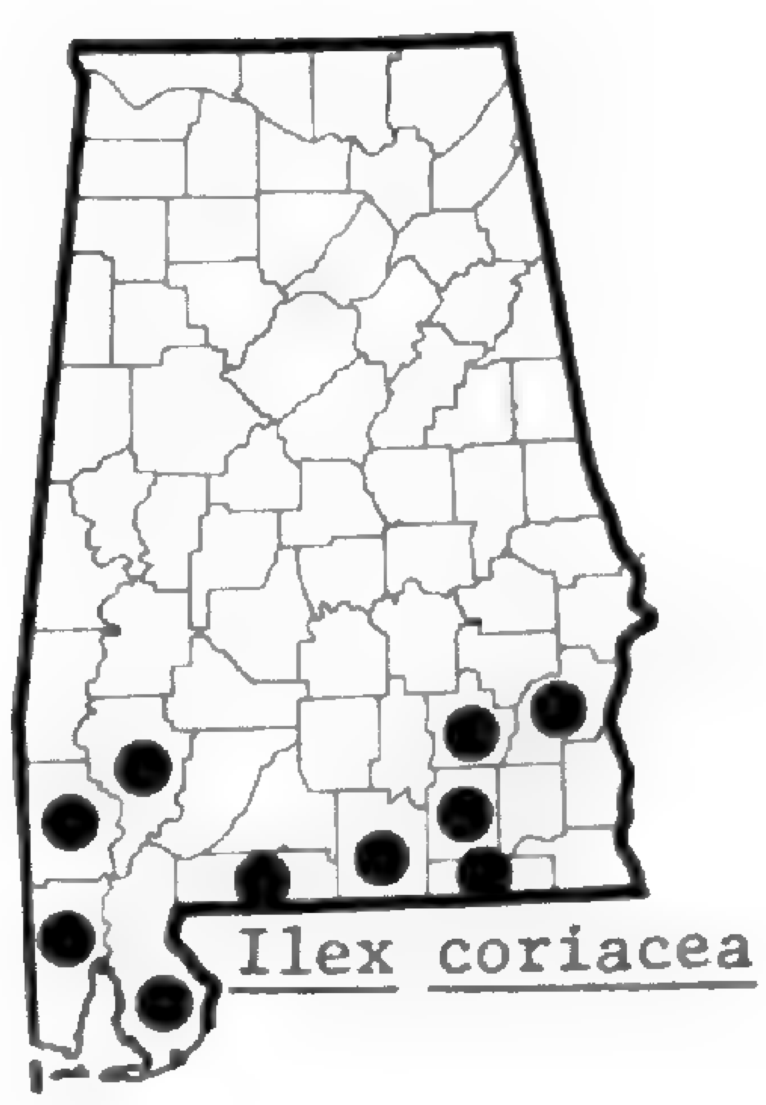
37. AQUIFOLIACEAE

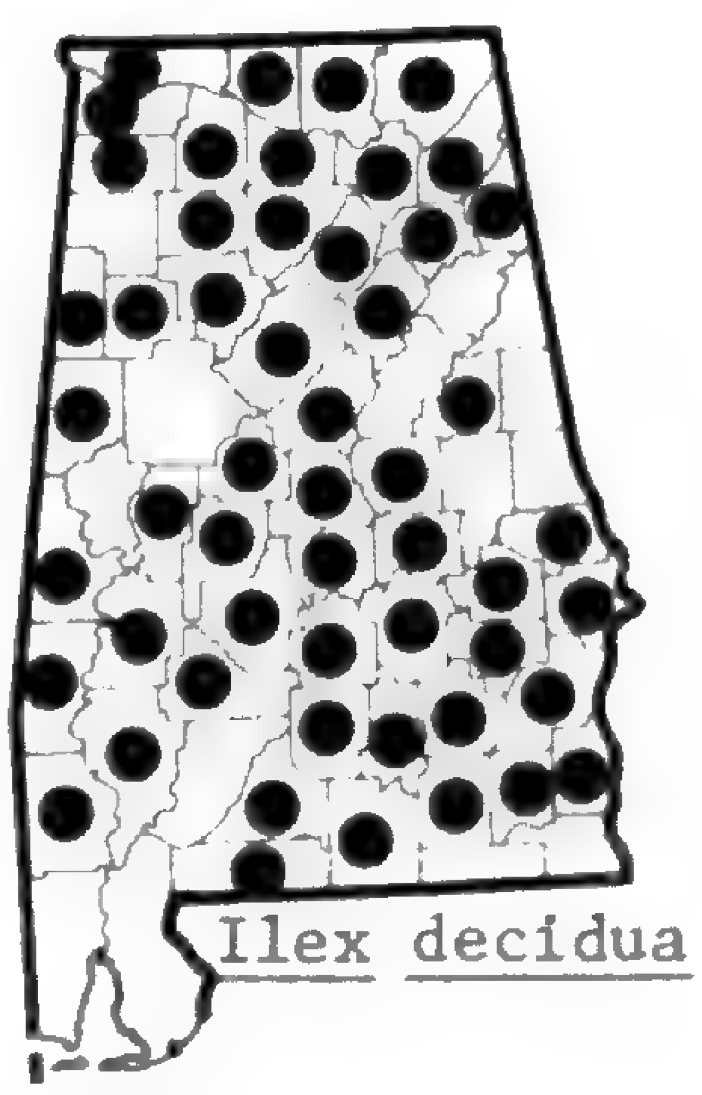

Ilex ambigua


Ilex amelanchier


Ilex cassine var. *cassine*


Ilex cassine var. *myrtifolia*


Ilex coriacea


Ilex decidua

36. CYRILLACEAE

1. Stamens 10; fruit winged .... 1. *Cliftonia*
1. Stamens 5; fruit wingless .... 2. *Cyrilla*

1. *Cliftonia* Banks *ex* Gaertner, TITI

1. *C. monophylla* (Lamarck) Sargent. Spring–early summer; summer–fall. Ditches, creek swamps; OCP.—The validity of a single specimen from Macon County should be questioned.

2. *Cyrilla* L., TITI

1. *C. racemiflora* L. Spring–summer; summer–fall. Creek swamps, ditches, swamp ecotones, alluvial woods; chiefly CP.

37. AQUIFOLIACEAE

1. *Ilex* L., HOLLY

1. Leaves evergreen 2
  2. Leaves spinose-dentate, at least remotely so .... 7. *I. opaca*
  2. Leaves crenate, serrate or entire 3
    3. Leaves crenate throughout, not spinulose .... 9. *I. vomitoria*
    3. Leaves serrate, crenulate, or crenate apically only; often spinulose or entire 4
      4. Leaves remotely crenate apically, not spinulose .... 6. *I. glabra*
      4. Leaves spinulose-serrate or entire 5
        5. Leaves acute to emarginate, often 3 times or more as long as wide .... 3. *I. cassine*
        5. Leaves (at least most) abruptly acuminate, less than 3 times as long as wide .... 4. *I. coriacea*
1. Leaves deciduous 6
  6. Plant in fruit 7
    7. Pyrene smooth, lacking dorsal ribbing .... 8. *I. verticillata*
    7. Pyrene grooved or ribbed, at least dorsally 8
      8. Sepals eciliate 9
        9. Leaves narrowly cuneate, or margin distinctly crenate-serrate .... 5. *I. decidua*
        9. Leaves rounded to truncate, entire to serrate, not regularly crenate-serrate .... 2. *I. amelanchier*
      8. Sepals ciliate 10
        10. Pedicels less than 5 mm long .... 1. *I. ambigua*
        10. Pedicels more than 5 mm long .... 2. *I. amelanchier*
  6. Plant in flower 11
    11. Staminate flowers present 12
      12. Inflorescence a pedunculate cyme 13
        13. Sepals ciliate .... 8. *I. verticillata*
        13. Sepals eciliate .... 2. *I. amelanchier*
      12. Inflorescence not pedunculate; flowers pedicellate only 14
        14. Sepals, petals and stamens 4 .... 5. *I. decidua*
        14. Sepals, petals and stamens 5 or more .... 1. *I. ambigua*
    11. Pistillate flowers or immature fruit present 15
      15. Pedicels less than 5 mm long 16
        16. Sepals eciliate .... 5. *I. decidua*
        16. Sepals ciliate 17
          17. Petals ciliate .... 1. *I. ambigua*
          17. Petals eciliate .... 8. *I. verticillata*
      15. Pedicels more than 5 mm long 18
        18. Leaves narrowly cuneate, or margin distinctly crenate-serrate .... 5. *I. decidua*
        18. Leaves rounded to truncate, entire to serrate, not regularly crenate-serrate .... 2. *I. amelanchier*

1. *I. ambigua* (Michaux) Torrey. Spring; summer–fall. Mesic woods, infrequent; throughout. *I. monticola* Gray—M, S; *I. monticola mollis* (Gray) Britt., *I. caroliniana* Walt.—M.—*Ilex ambigua* var. *montana* (T. & G.) Ahles is a recognizable entity east and north of Alabama, but the writer has not seen any Alabama plants to which this name should be applied.

2. *I. amelanchier* Curtis. Spring; fall. Low woods, very rare; CP.

3. *I. cassine* L. Spring; fall–spring.

1. Leaves, at least some, ovate to obovate .... *I. cassine* var. *cassine*
1. Leaves lanceolate to narrowly elliptic .... I. *cassine* var. *myrtifolia*

I. cassine L. var. *cassine*, Cassena, Dahoon. Low ground, rare; CP.

I. cassine L. var. *myrtifolia* (Walter) Sargent, Yaupon. Ponds; OCP. *I. myrtifolia* Walt.—M, H, S.

4. *I. coriacea* (Pursh) Chapman, Gallberry. Spring; fall–spring. Low woods, seepages, swamp ecotones; OCP.

5. *I. decidua* Walter. Spring; late summer–fall. Upland and low woods, thickets, most common in circumneutral situations; CP, AM, CuP, VR, HR. *I. longipes* Chapm.—M, H, S; *I. decidua* var. *longipes* (Chapm.) Ahles—RAB.—This taxon is extremely polymorphic west and south of the Appalachians. *Ilex longipes* Chapm. has often been applied to plants with relatively long pedicels, but this character is not discontinuous and has been used too subjectively. *Ilex collina* Alexander has been applied to plants with relatively large leaves. This complex needs intensive study.

6. *I. glabra* (L.) Gray, Gallberry. Spring; fall–spring. Low woods, thickets, seepages, swamp ecotones; CP.

7. *I. opaca* Aiton, Common H. Spring; fall–spring. Low and upland woods; throughout.

8. *I. verticillata* (L.) Gray. Spring; fall. Seepages, bogs, streambanks, infrequent; throughout.

9. *I. vomitoria* Aiton, Yaupon. Spring; fall–spring. Sandy woods and thickets; CP, CuP (very rare).

38. Celastraceae

1. Leaves alternate; plant a twining vine .... 1. *Celastrus*
1. Leaves opposite; plant shrubby .... 2. *Euonymus*

1. *Celastrus* L., Bittersweet

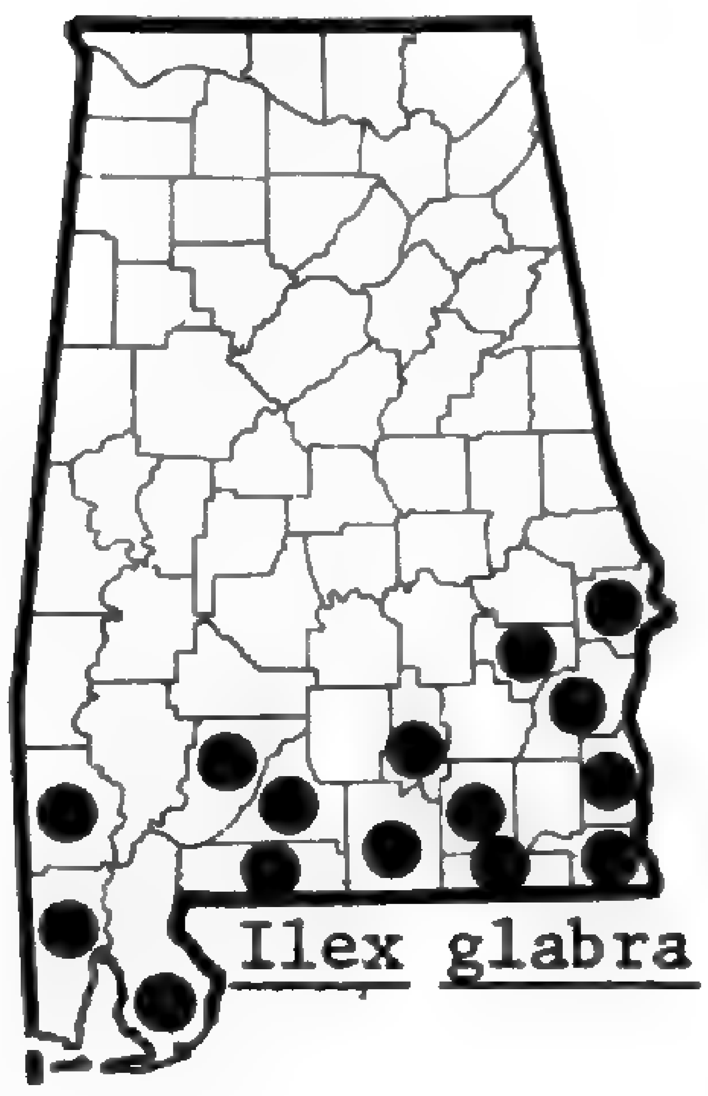
1. *C. scandens* L. Spring; summer–fall. Rocky woods, rare; CuP, HR.

2. *Euonymus* L.

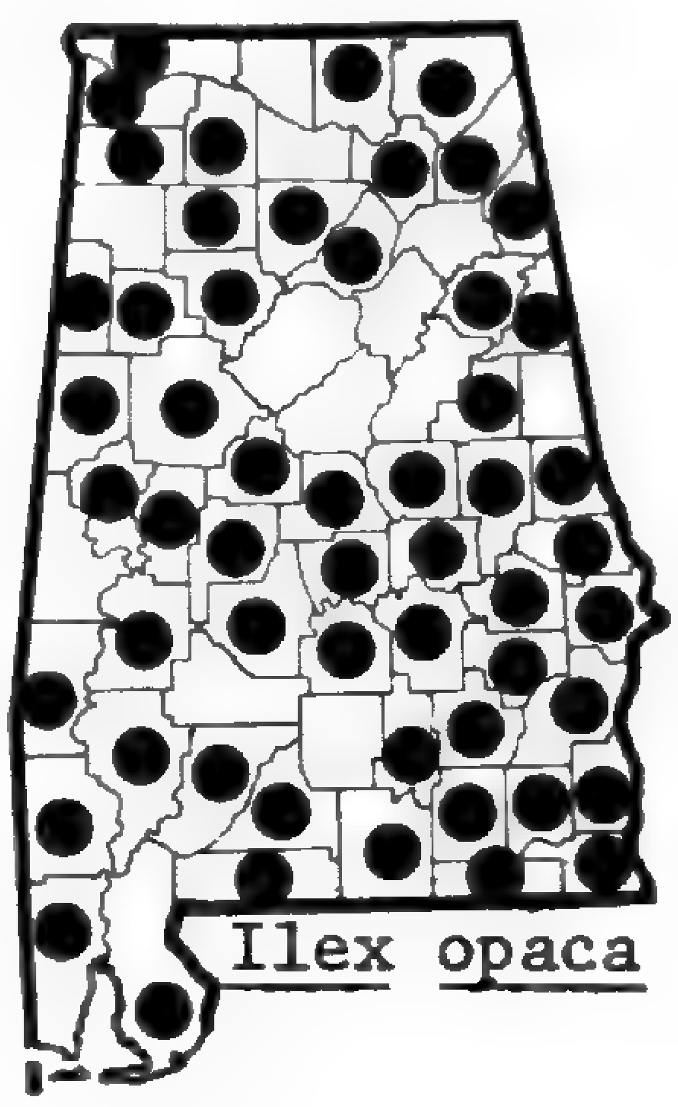
1. Leaves variegated, of two contrasting colors .... 3. *E. fortunei* var. *radicans*
1. Leaves not variegated 2
   2. Flowers 4-merous; fruit smooth .... 2. *E. atropurpureus*
   2. Flowers 5-merous; fruit tuberculate .... 1. *E. americanus*

1. *E. americanus* L., Strawberry Bush. Spring; late summer–fall. Rich and low woods, fencerows and thickets; throughout.

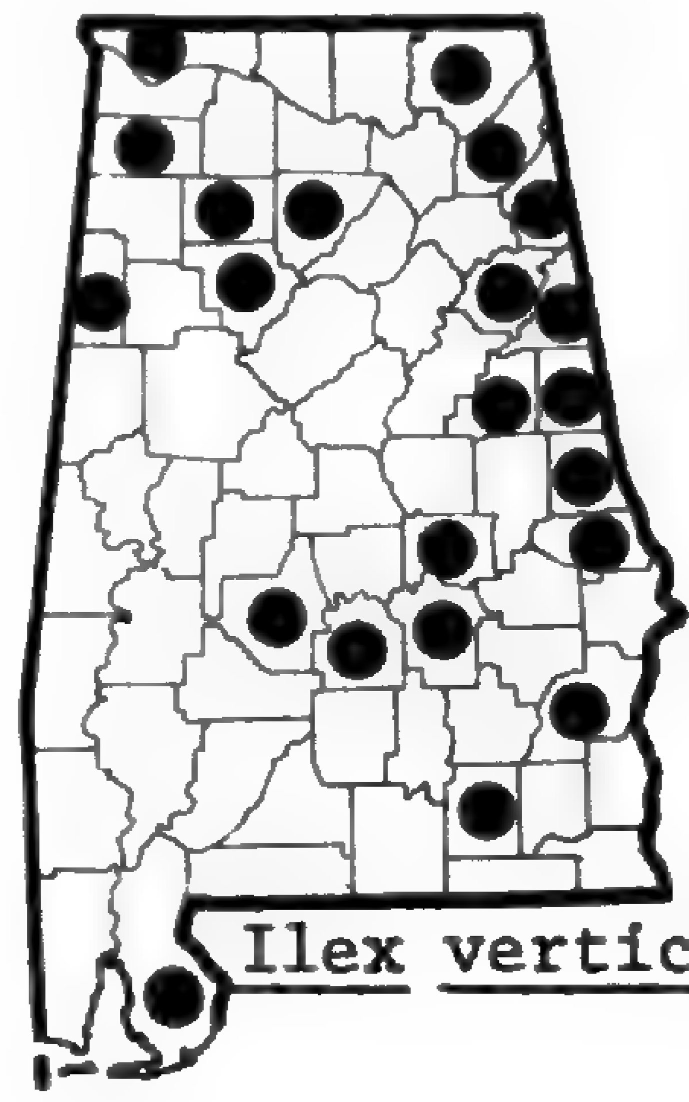
2. *E. atropurpureus* Jacquin, Wahoo. Spring; late summer–fall. Rich woods over calcareous substrata, rare; CP, CuP, HR.



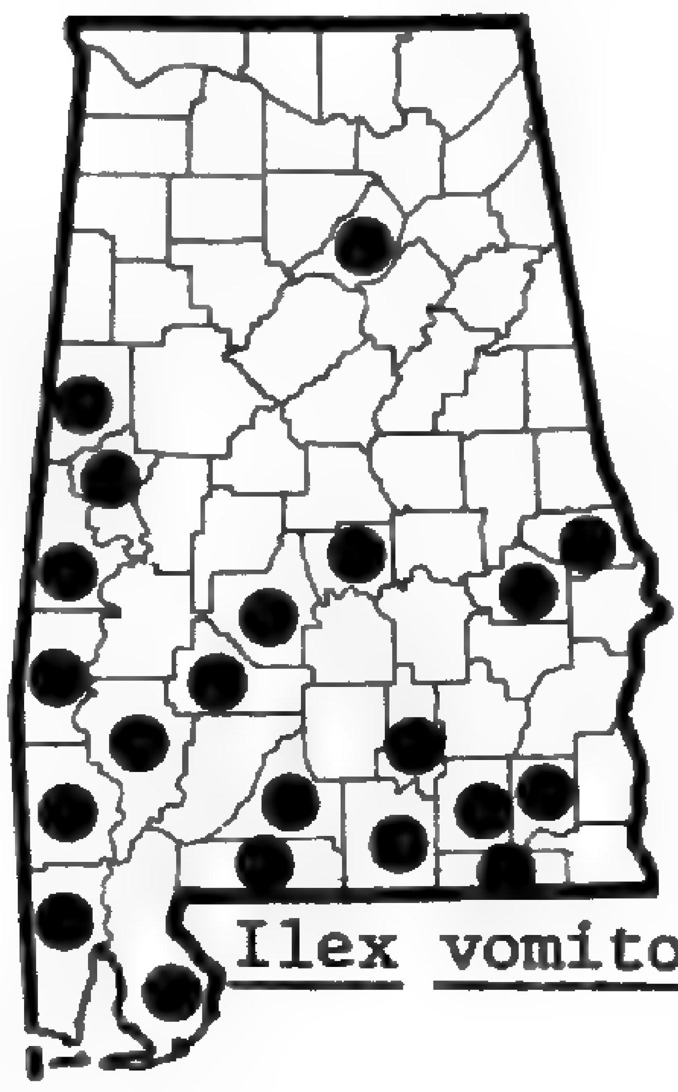
Ilex glabra



Ilex opaca



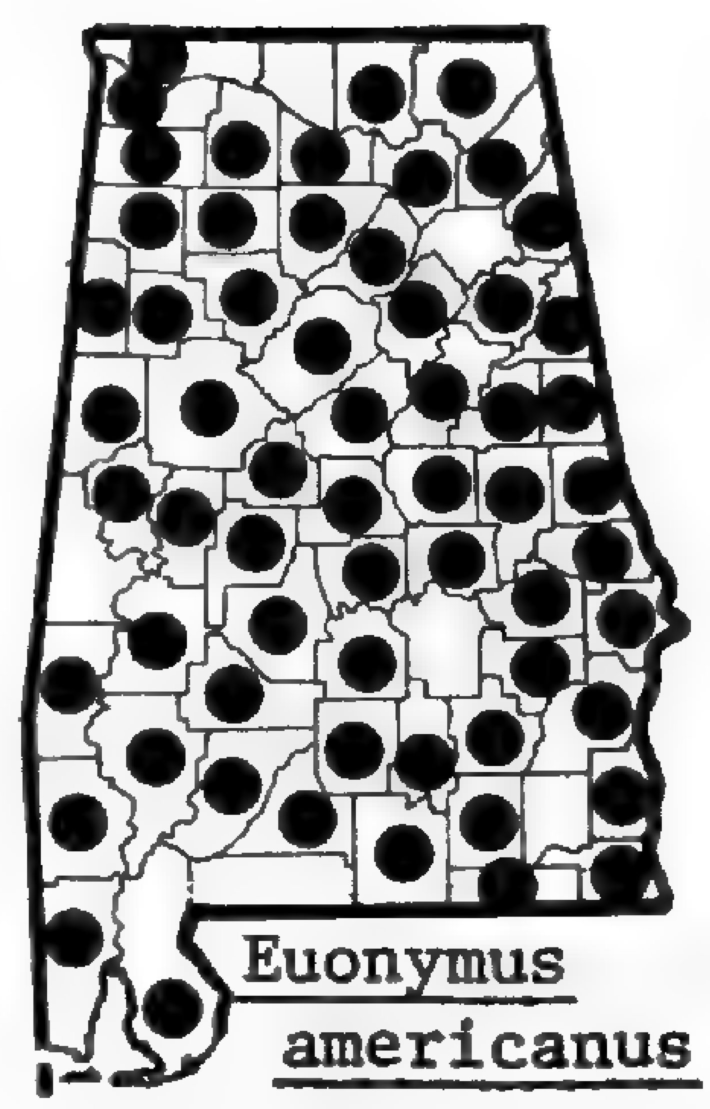
Ilex verticillata



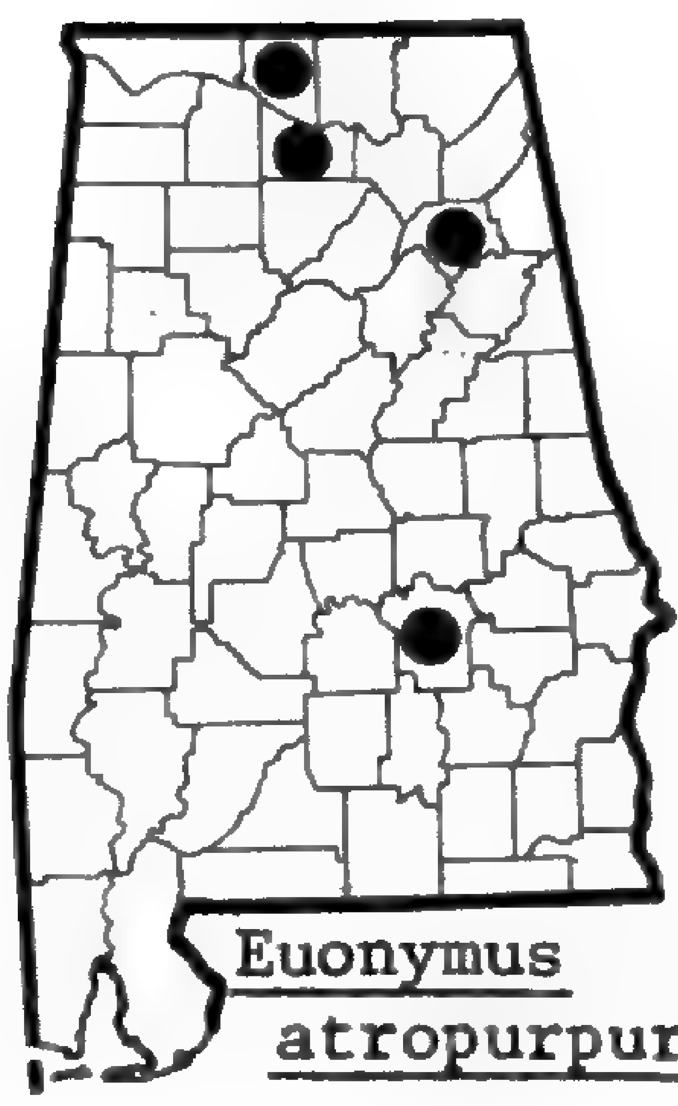
Ilex vomitoria

38. CELASTRACEAE

Celastrus scandens



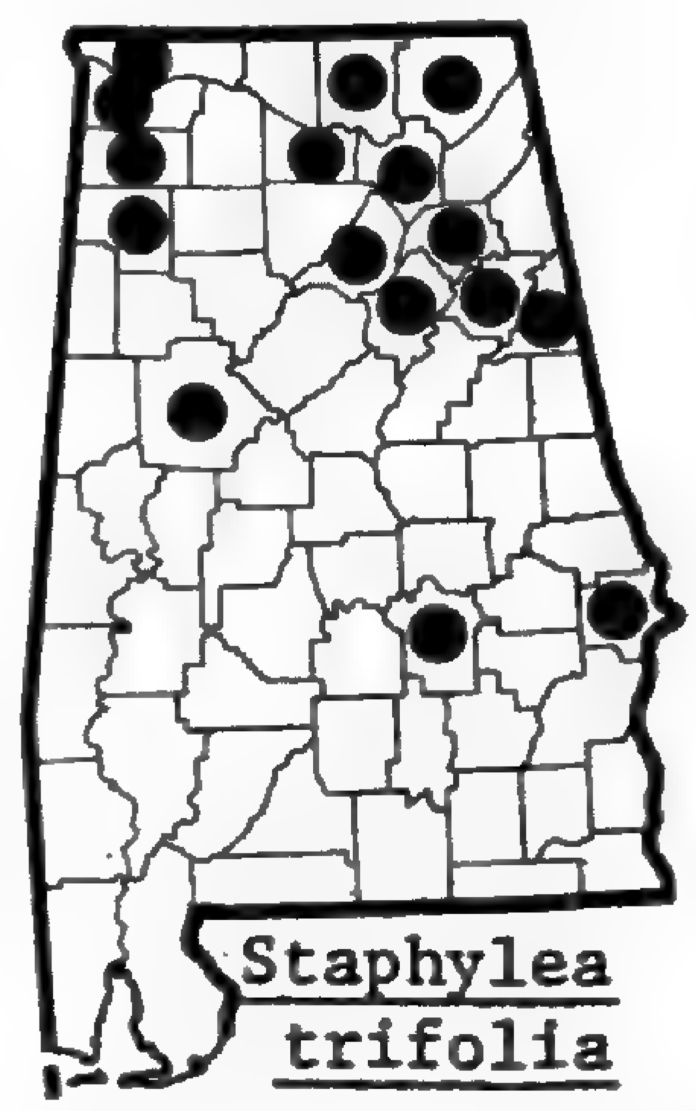
Euonymus americanus



Euonymus atropurpureus

Euonymus fortunei var. radicans

39. STAPHYLEACEAE



Staphylea trifolia

3. *E. fortunei* Hand.-Mazz. var. *radicans* Rehder. Flowers, fruit not seen. Occasionally persistent and rarely spreading; HR.

39. Staphyleaceae

1. *Staphylea* L., Bladdernut

1. *S. trifolia* L. Spring; summer–fall. Alluvial and rich woods; CP (rare), AM, CuP, VR, HR.

40. Aceraceae

1. *Acer* L., Maple

1. Leaves compound .... 1. *A. negundo*
1. Leaves simple, or absent at anthesis 2
   2. Inflorescence terminal .... 4. *A. saccharum*
   2. Inflorescence axillary 3
      3. Petals similar to sepals; fruit 2.5 cm or less long; pedicel longer than fruit, often more than twice as long .... 2. *A. rubrum*
      3. Petals absent; fruit 4 cm or more long; pedicel shorter than fruit ... 3. *A. saccharinum*

1. *A. negundo* L., Box-Elder. Spring; spring–fall. Ditches, low woods; throughout, infrequent to rare in OCP. *Negundo negundo* (L.) Karst.—S.

2. *A. rubrum* L., Red M. Winter–spring; spring–fall.

1. Leaves glabrous beneath, or pubescent only near the principal veins .. *A. rubrum* var. *rubrum*
1. Leaves pubescent beneath .... *A. rubrum* var. *drummondii*

A. rubrum L. var. *rubrum*. Low or upland woods; throughout. *Rufacer rubrum* (L.) Sm., *R. carolinianum* (Walt.) Sm.—S.

A. rubrum L. var. *drummondii* (Hooker & Arnold) Sargent. Low or upland woods, infrequent; throughout. *Rufacer drummondii* (Hook. & Arn.) Sm.—S.

3. *A. saccharinum* L., Silver M. Winter–spring; spring–summer. Low woods, streambanks, infrequent; CP, P, VR, HR.

4. *A. saccharum* Marshall, Sugar M.

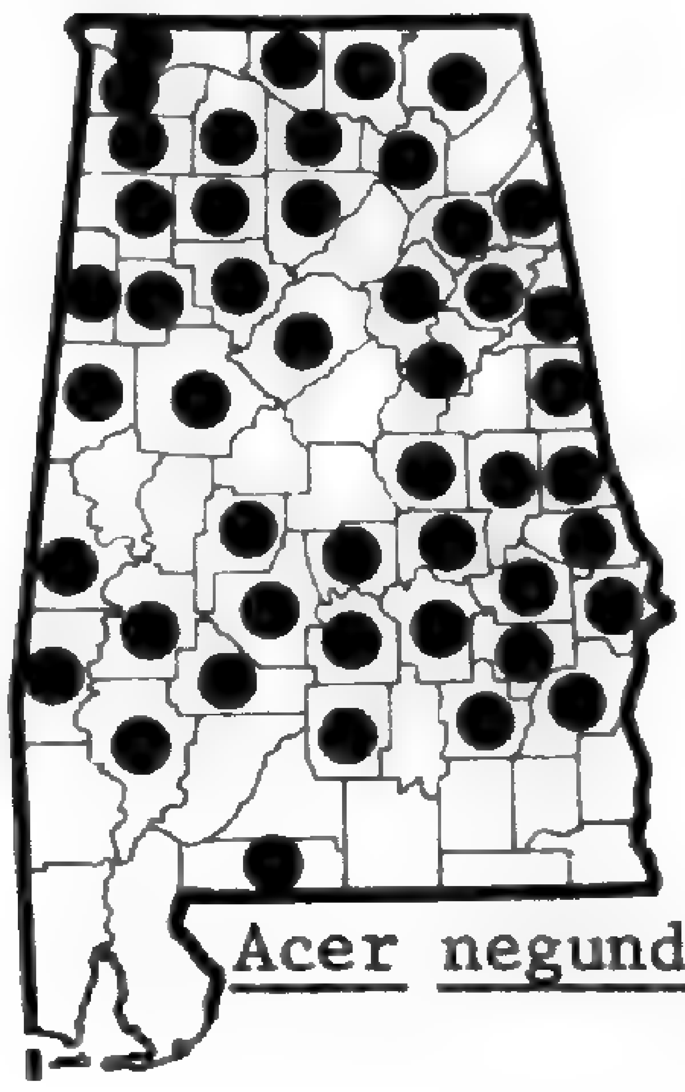
1. Leaves either essentially glabrous or strongly glaucous beneath 2
   2. Leaves essentially glabrous beneath, pubescence when present, confined to larger veins .... *A. saccharum* subsp. *saccharum*
   2. Leaves pubescent beneath, the pubescence not confined to the veins or veinlets .... *A. saccharum* subsp. *floridanum*
1. Leaves pubescent and greenish beneath 3
   3. Leaves averaging more than 10 cm long; bark dark, roughened .... *A. saccharum* subsp. *nigrum*
   3. Leaves averaging less than 10 cm long; bark whitish, smooth or tardily cracking .... *A. saccharum* subsp. *leucoderme*

A. saccharum Marshall subsp. *saccharum*, Rock M., Hard M. Spring; summer. Rich woods, rare southward; throughout. *Saccharodendron barbatum* (Michx.) Niewl.—S.

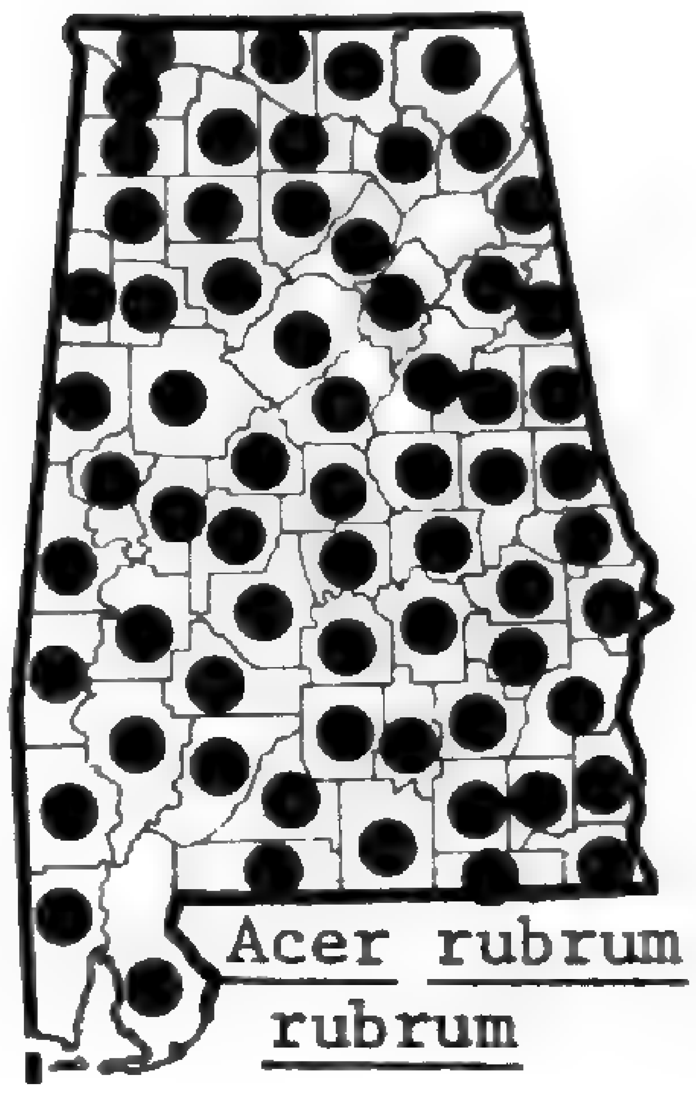
A. saccharum Marshall subsp. *floridanum* (Chapm.) Desmarais, Southern Sugar M. Spring; spring–fall. Upland and mesic woods; CP, P, AM, CuP, VR. *Saccharodendron floridanum* (Chapm.) Niewl.—S; *A. floridanum* (Chapm.) Pax —M, H.

A. saccharum Marshall subsp. *leucoderme* (Small) Desmarais, Chalk-Bark

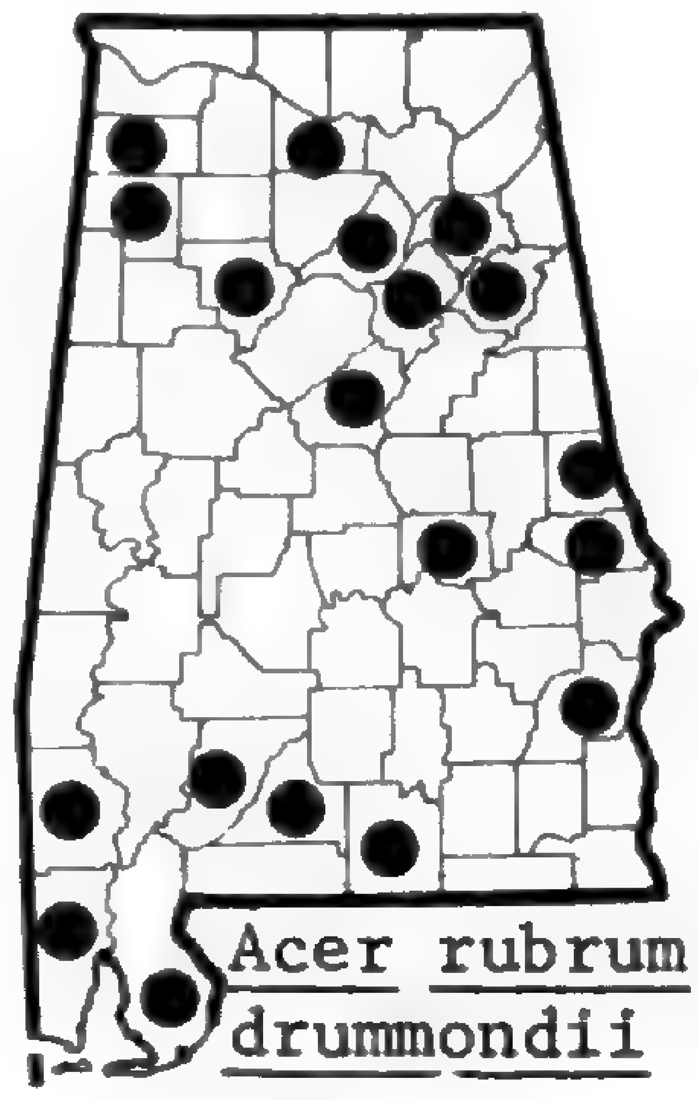
40. ACERACEAE



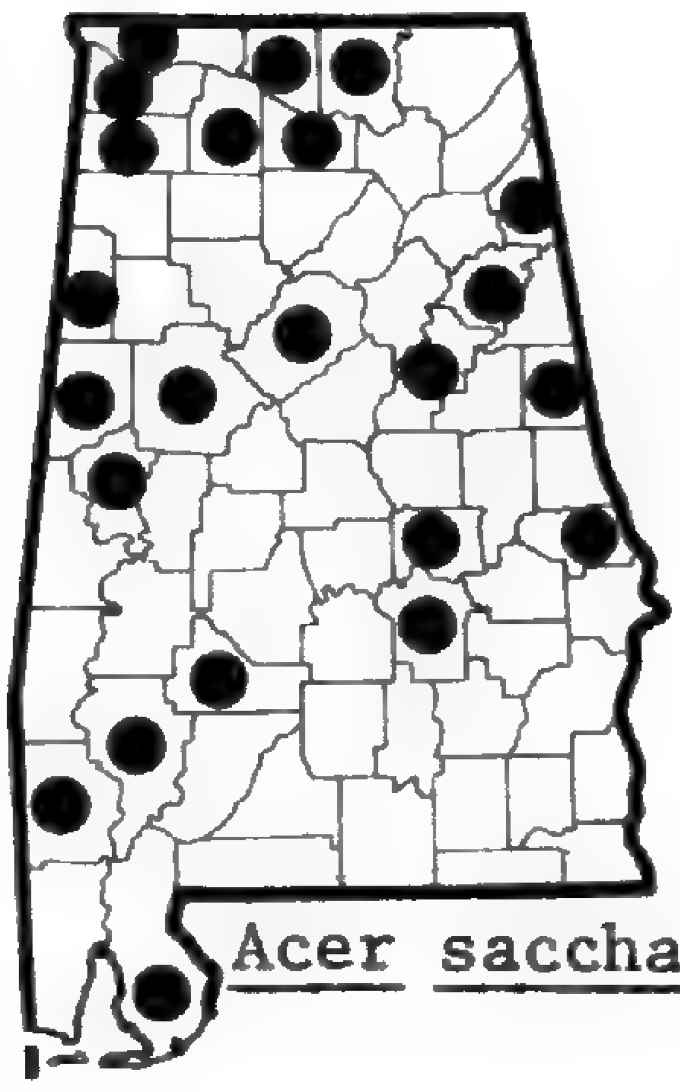
Acer negundo



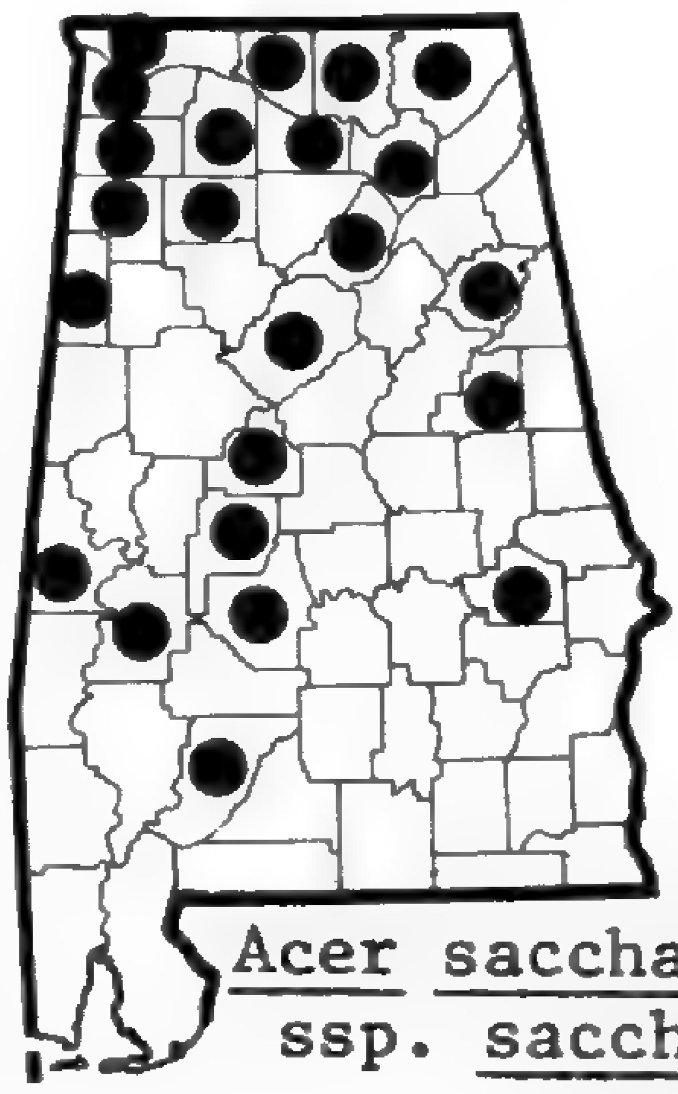
Acer rubrum var. rubrum



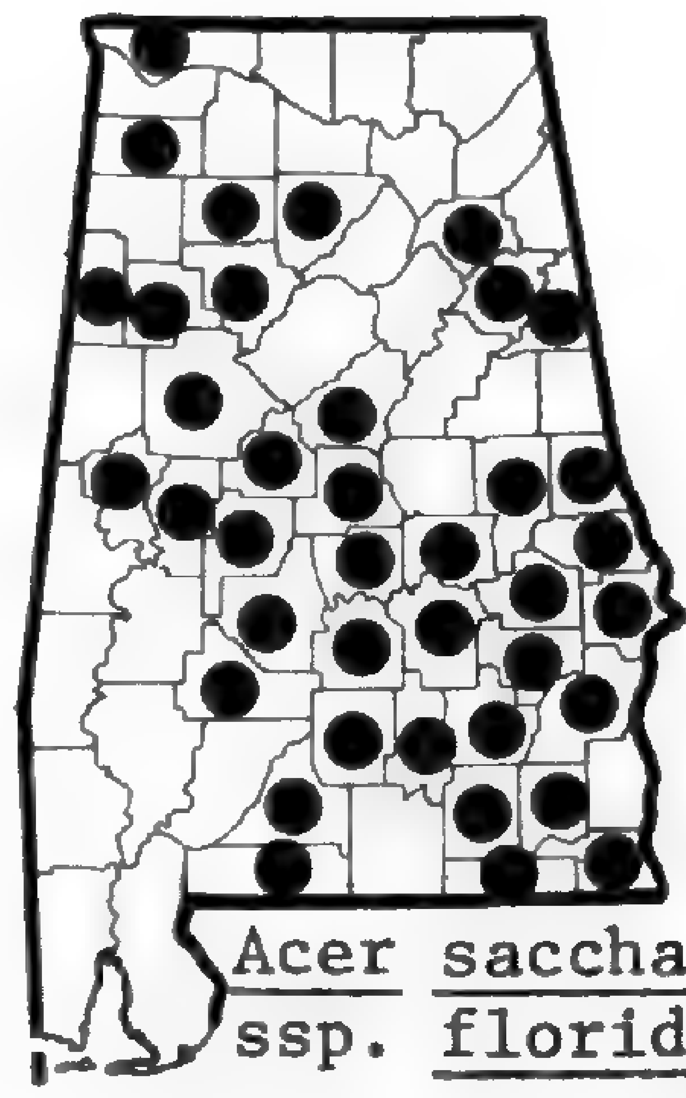
Acer rubrum var. drummondii



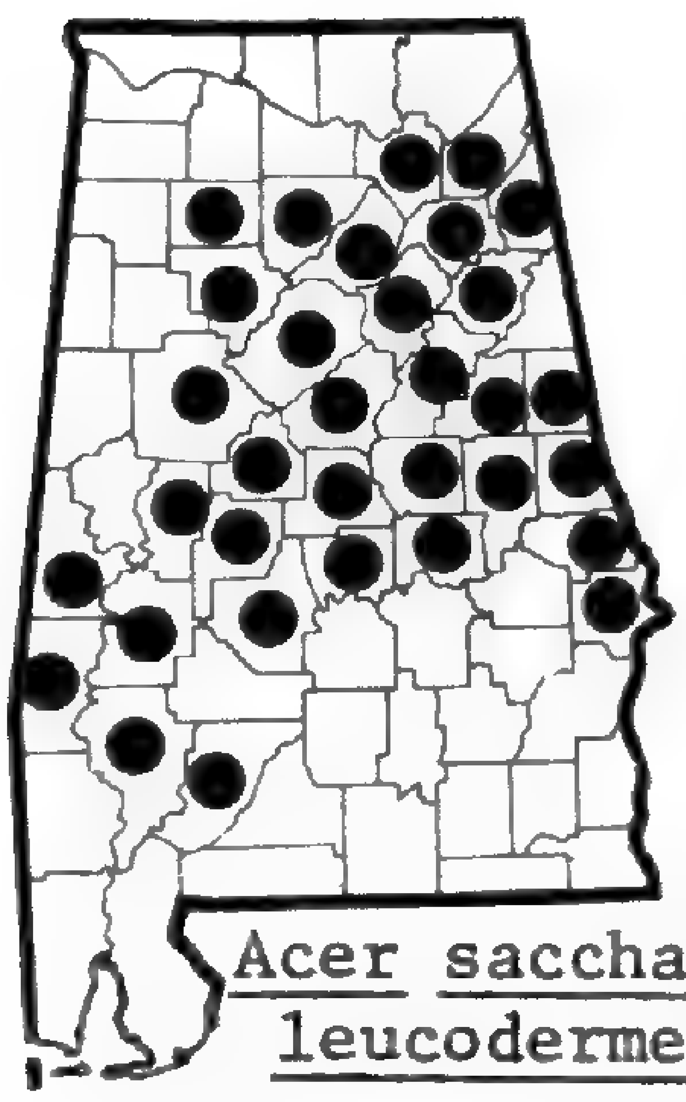
Acer saccharinum



Acer saccharum ssp. saccharum



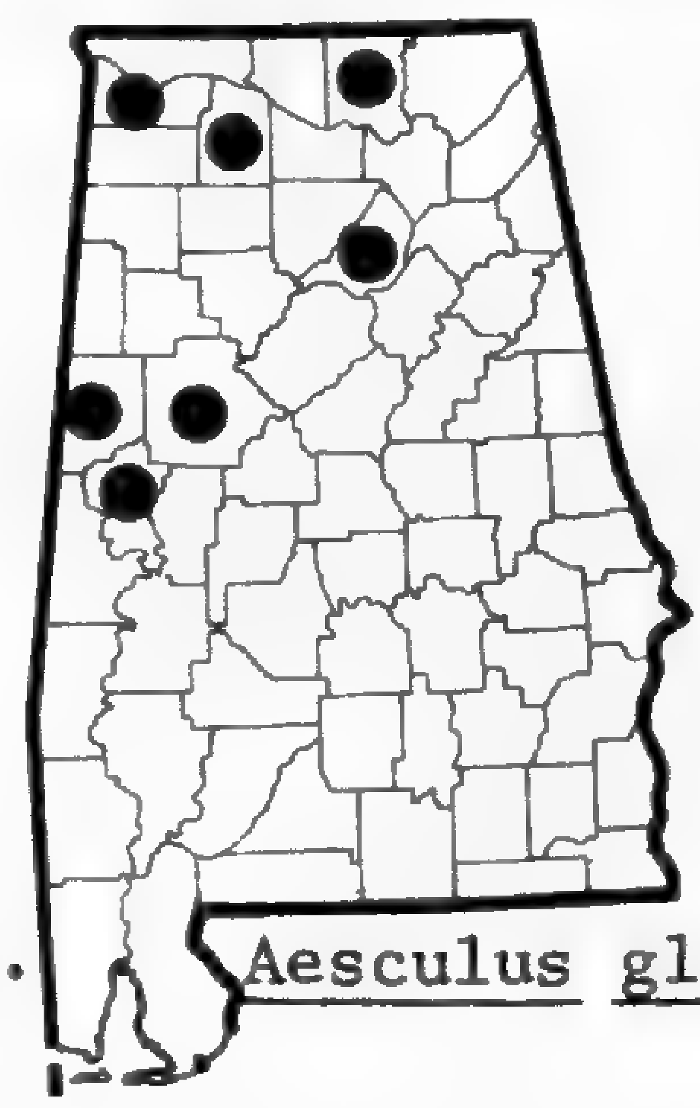
Acer saccharum ssp. floridanum



Acer saccharum ssp. leucoderme

Acer saccharum ssp. nigrum

41. HIPPOCASTANACEAE



Aesculus glabra

M. Spring; spring–fall. Upland woods, river bluffs, local; CP, P, AM, VR, CuP. Apparently absent from southeastern CP. *A. leucoderme* Sm.—M, H; *Saccharodendron leucoderme* (Sm.) Niewl.—S.

A. saccharum Marshall subsp. *nigrum* (Michaux f.) Desmarais. Rich woods, rare; CuP, HR. *Saccharodendron nigrum* (Michx.) Sm.—S.

41. Hippocastanaceae

1. *Aesculus* L., Buckeye

1. Flowers white; stamens 3–4 times as long as petals; inflorescence 2–3 dm long .... 3. *A. parviflora*
1. Flowers yellow to red; stamens 2 or less times as long as petals; inflorescence usually less than 2 dm long 2
    2. Petals subequal; flowers pale yellow to greenish-yellow .... 1. *A. glabra*
    2. Petals of two distinct lengths; flowers yellow to red 3
        3. Margins of lateral petals eglandular; stamens included within lateral petals 4
            4. Pedicels stipitate-glandular .... 2. *A. octandra*
            4. Pedicels eglandular .... 5. *A. sylvatica*
        3. Margins of lateral petals glandular; stamens exerted beyond lateral petals .... 4. *A. pavia*

1. *A. glabra* Willd. Spring; summer. Rich woods, rare; CP, CuP, HR.

2. *A. octandra* Marshall. Spring; summer. Rich woods, rare; northeastern CuP.

3. *A. parviflora* Bartram, Bottlebrush B. Late spring–summer; late summer–fall. Rich woods, usually in circumneutral soil, local; CP, P, AM, VR, CuP.

4. *A. pavia* L., Red B. Spring; summer. Deciduous woodland borders and openings; throughout.

5. *A. sylvatica* Bartram. Spring; summer. Mesic or low woods, infrequent; CP (rare), AM, CuP. *A. octandra* Marsh.—S, in part.

42. Sapindaceae

1. *Sapindus* L., Soap-Berry

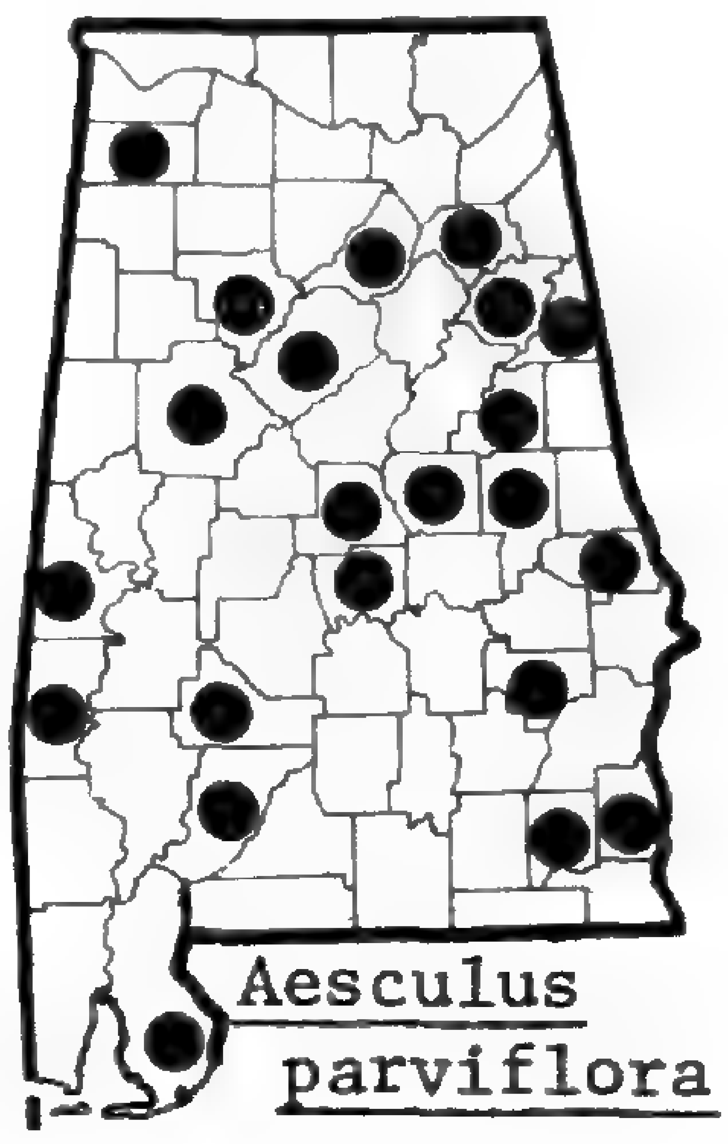
1. *S. marginatus* Willd. Spring; fall. Reported (Dean, 1961) as a rare escape; OCP. No specimens have been seen by the writer.

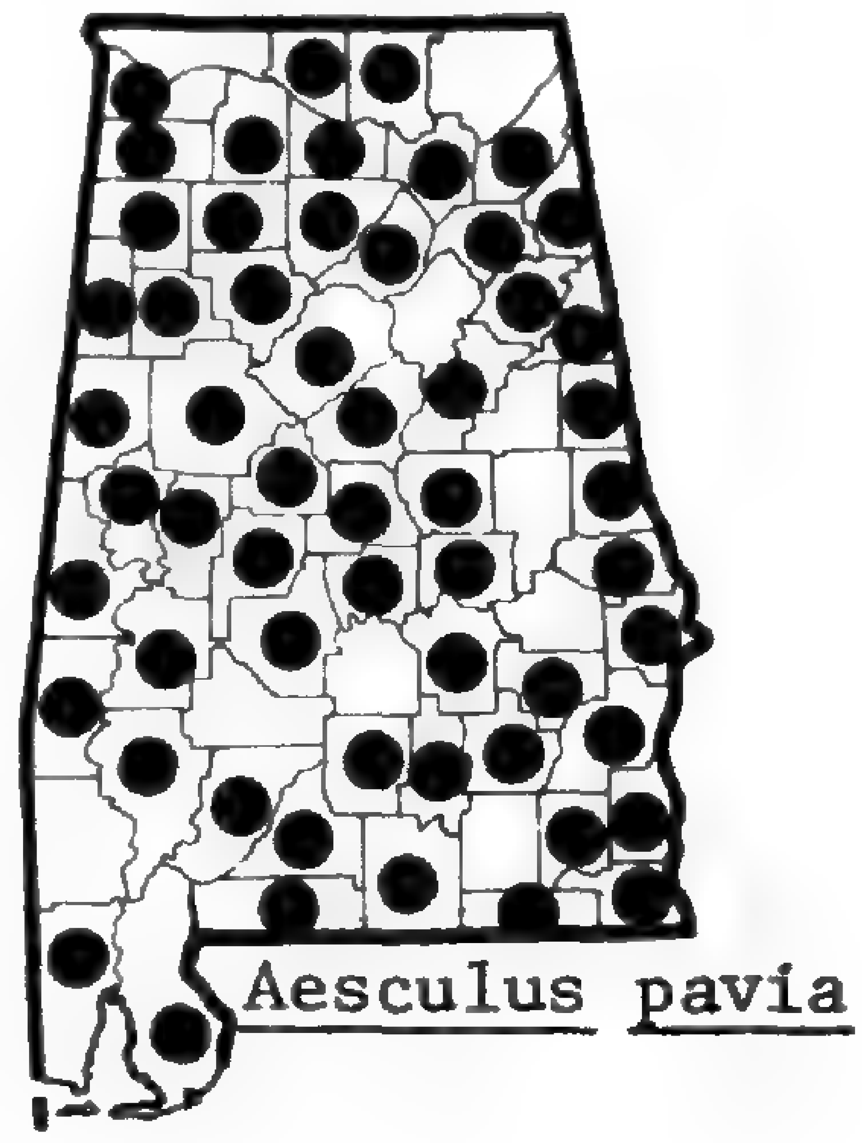
43. Rhamnaceae

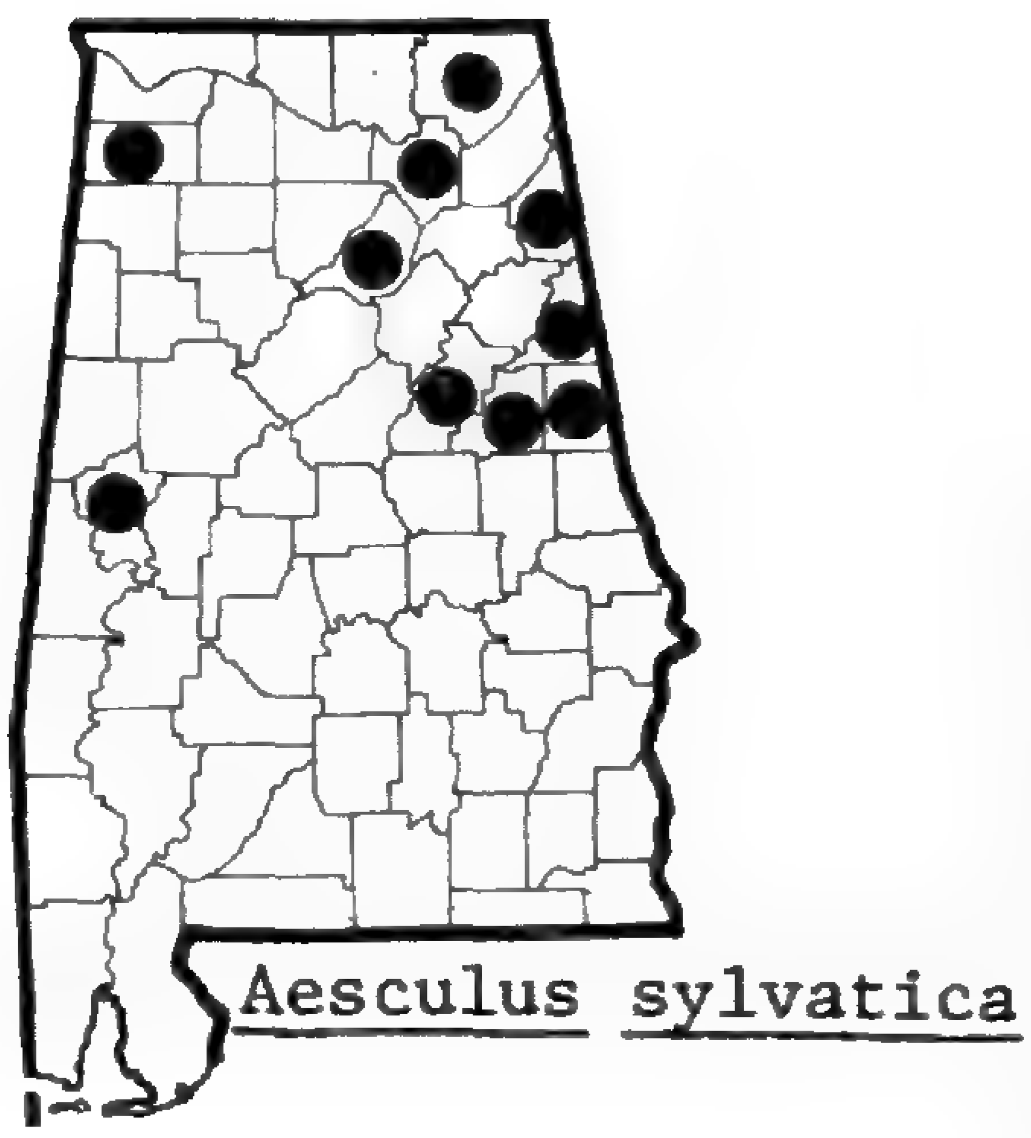
1. Leaves opposite .... 4. *Sageretia*
1. Leaves alternate 2
    2. Plant a vine, climbing by twining .... 1. *Berchemia*
    2. Plant a shrub or tree 3
        3. Inflorescences terminal .... 2. *Ceanothus*
        3. Inflorescences axillary 4
            4. Stem spiny; sepals shorter than petals; fruit more than 2 cm long .... 5. *Zizyphus*
            4. Stem unarmed; sepals longer than petals or petals absent; fruit less than 2 cm long .... 3. *Rhamnus*

1. *Berchemia* Necker, Rattan Vine

1. *B. scandens* (Hill) K. Koch. Spring; summer–fall. Thickets, fencerows, low or upland woods; CP, P (rare), VR, CuP (rare), HR.

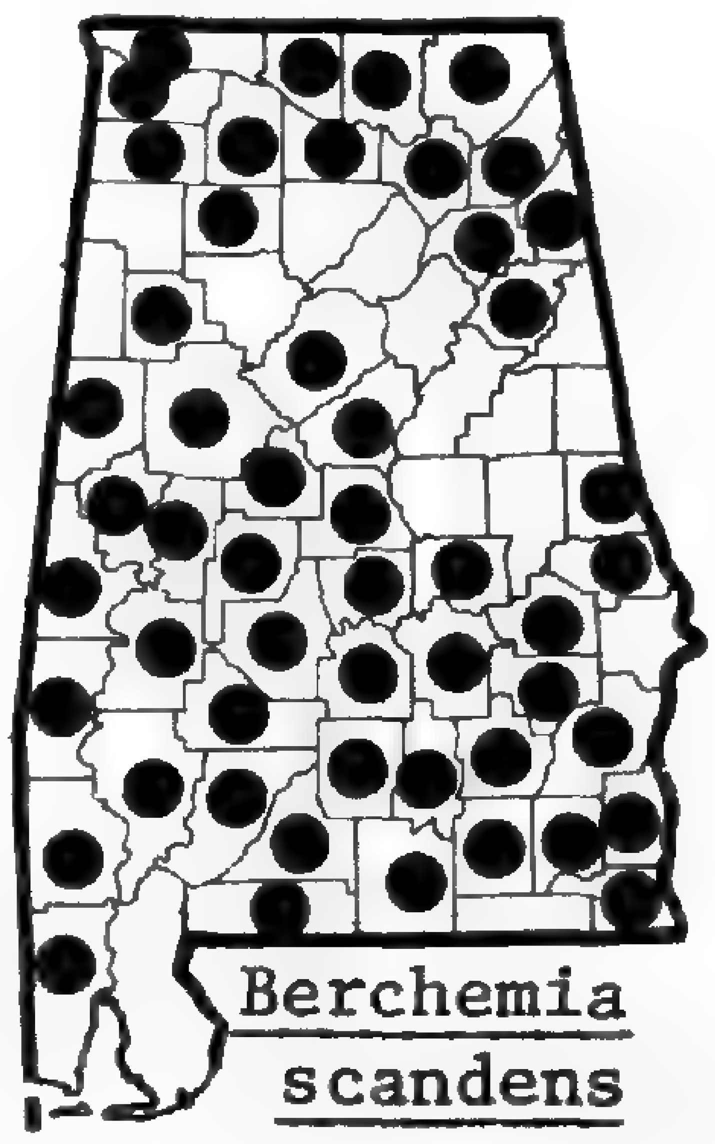


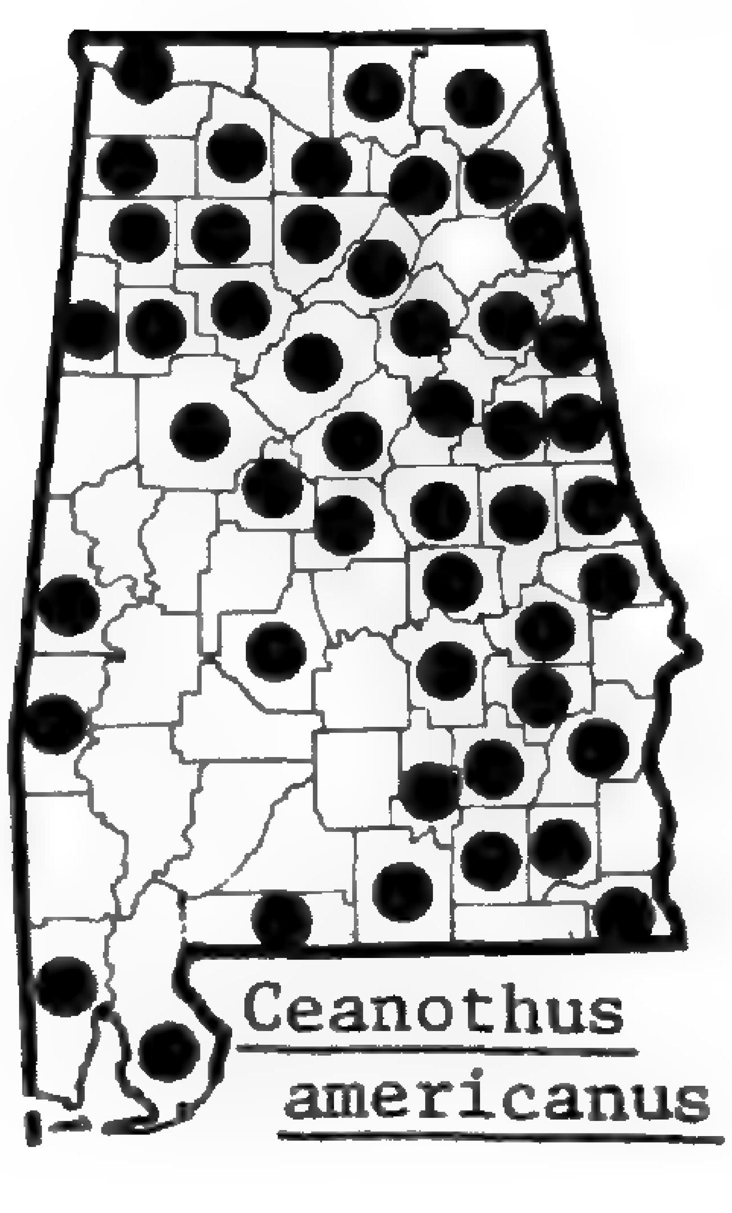


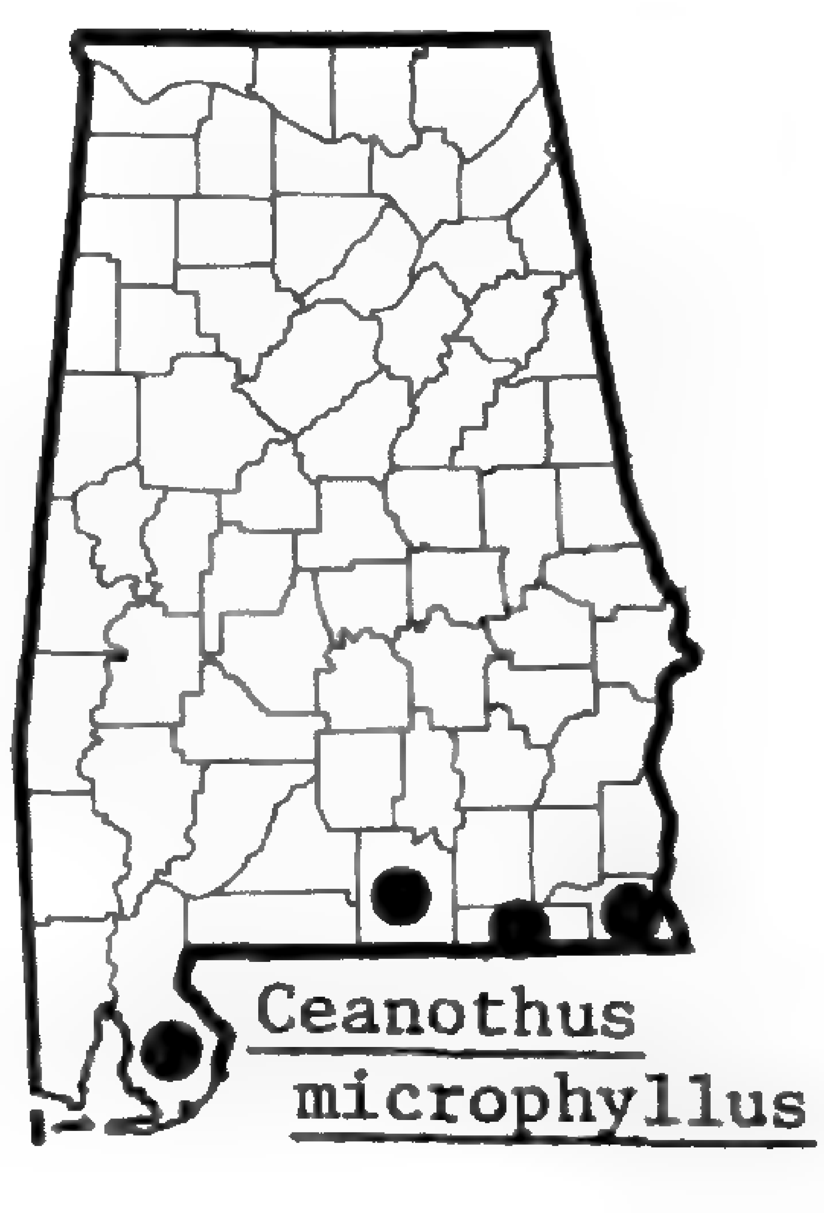


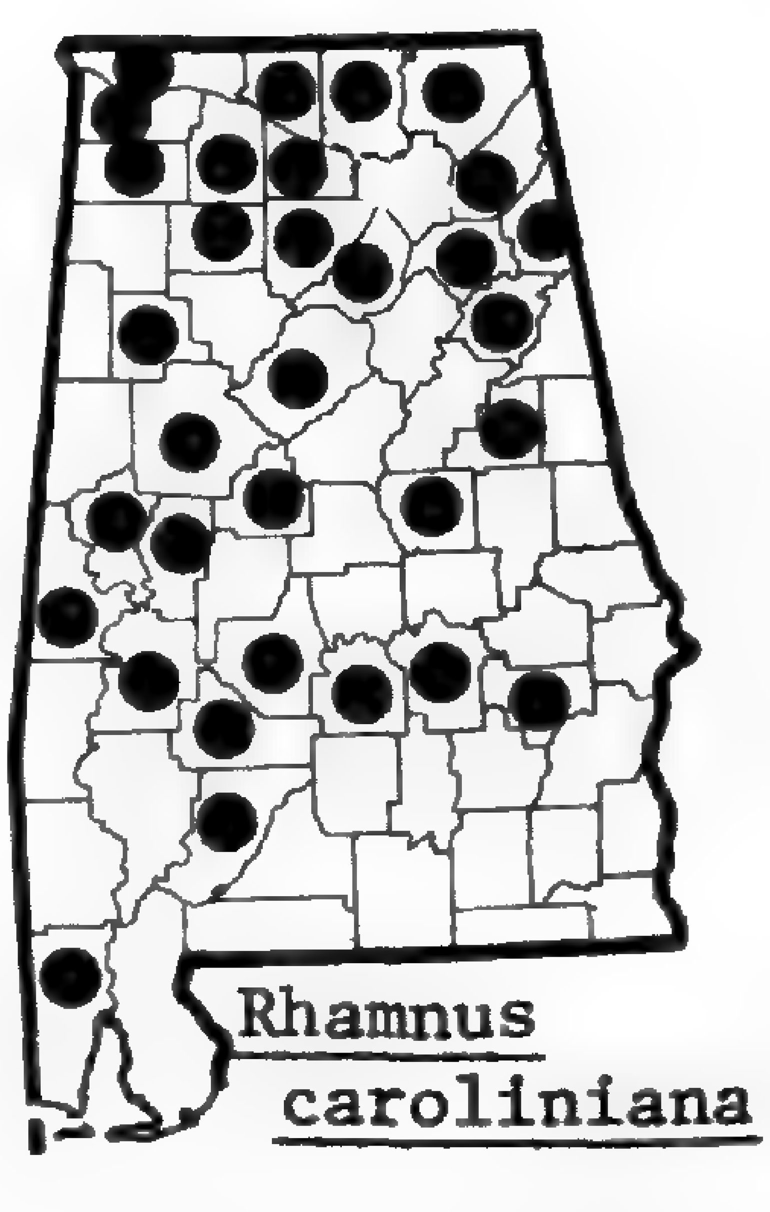
42. SAPINDACEAE

43. RHAMNACEAE









2. *Ceanothus* L.

1. Leaves crenate .... 1. *C. americanus*
1. Leaves entire, occasionally remotely toothed .... 2. *C. microphyllus*

1. *C. americanus* L., New Jersey Tea. Spring–early summer; summer. Upland woods, rights-of-way, clearings; throughout, but rare in southwestern CP. *C. americanus intermedius* (Pursh) T. & G.—M; *C. intermedius* Pursh, *C. pubescens* (T. & G.) Rydb.—S.

2. *C. microphyllus* Michaux. Sandy ground, rare; eastern OCP.

3. *Rhamnus* L., Buckthorn

1. Leaves crenate-serrulate; calyx lobes, petals and stamens 5 .... 1. *R. caroliniana*
1. Leaves regularly serrulate; calyx lobes, petals and stamens 4 .... 2. *R. lanceolata*

1. *R. caroliniana* Walter. Spring; late summer–fall. Rich woods, usually in circumneutral soil; throughout, but rare in southern CP.

2. *R. lanceolata* Pursh. Flowers, fruit not seen in Alabama. Rich woods, apparently in circumneutral soil, very rare; CP.

4. *Sagerretia* Brongniart

1. *S. minutiflora* (Michaux) Trelease. Flowers, mature fruit not seen. Beaches, rare; OCP.

5. *Zizyphus* Gaertner, Jujube

1. *Z. vulgaris* Lamarck. Flowers, fruit not seen. Reported as escaped by Mohr (1901); OCP.

44. Vitaceae

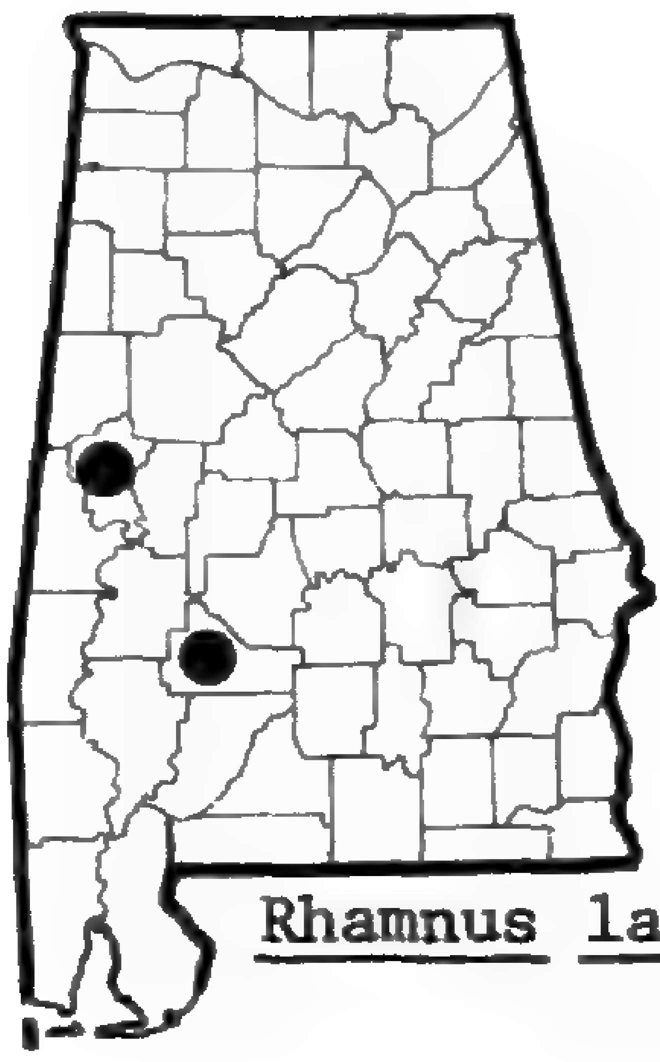
1. Leaves, at least some, compound, 2- or more-foliolate 2
   2. Leaflets 3 or less .... 2. *Cissus*
   2. Leaflets 5 or more 3
      3. Leaves palmately compound; tendrils with terminal adhesive discs .... 3. *Parthenocissus*
      3. Leaves pinnately or bipinnately compound; tendrils lacking adhesive discs .... 1. *Ampelopsis*
1. Leaves simple 4
   4. Pith of young branches interrupted at node .... 4. *Vitis*
   4. Pith of young branches continuous through node 5
      5. Tendrils simple; corolla deciduous as a unit; fruit 1 cm or more in diameter, yellow when immature, purplish-black at maturity .... 4. *Vitis*
      5. Tendrils branched; petals separate, deciduous singly; fruit less than 1 cm in diameter, white when immature, bright blue at maturity .... 1. *Ampelopsis*

1. *Ampelopsis* Michaux

1. Leaves decompound .... 1. *A. arborea*
1. Leaves simple .... 2. *A. cordata*

1. *A. arborea* (L.) Koehne. Spring–summer; summer–fall. Fencerows, ditches, low woods; CP, VR, HR. *A. arborea* (L.) Rusby—M, H, S.

2. *A. cordata* Michaux. Spring–summer; late summer. Fencerows, thickets, low woods, in circumneutral soil; CP, VR, CuP, HR.

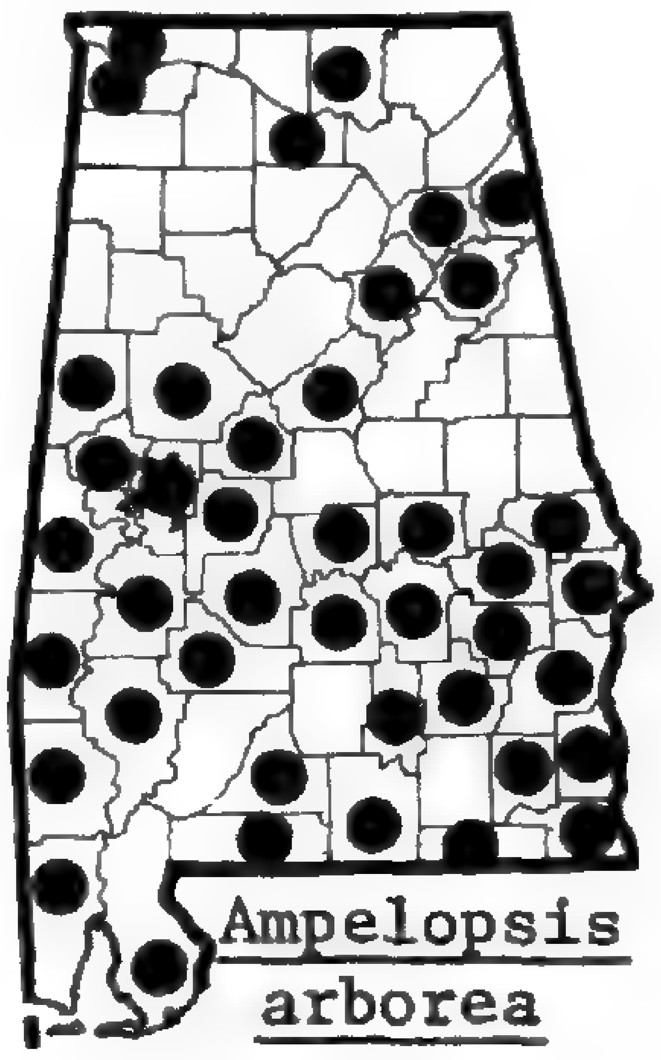


Rhamnus lanceolata

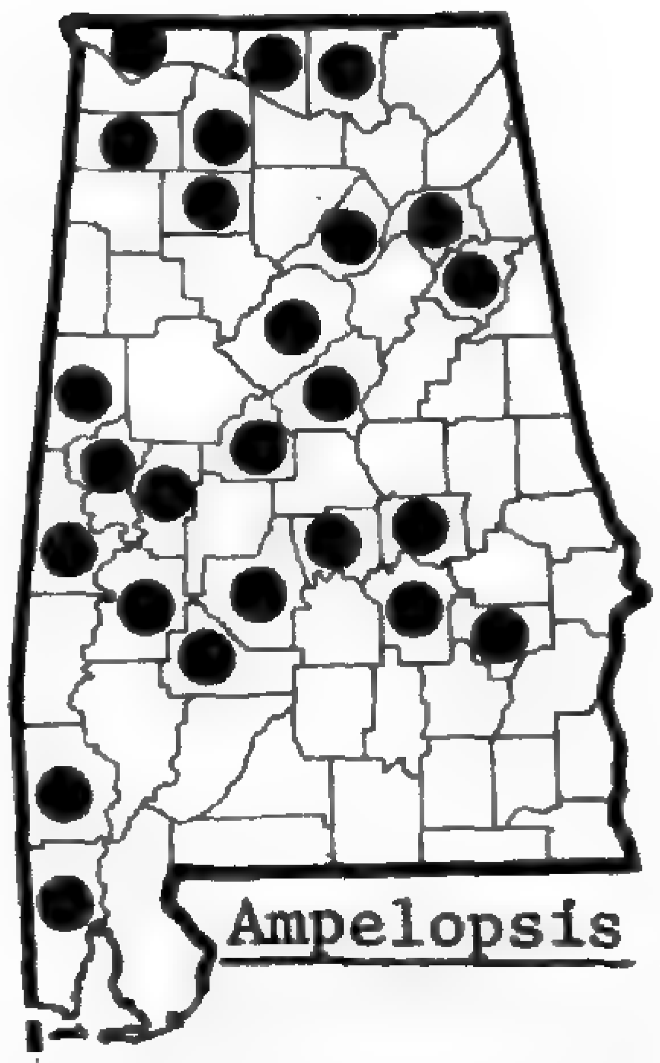
Sageretia minutiflora

Zizyphus vulgaris

44. VITACEAE

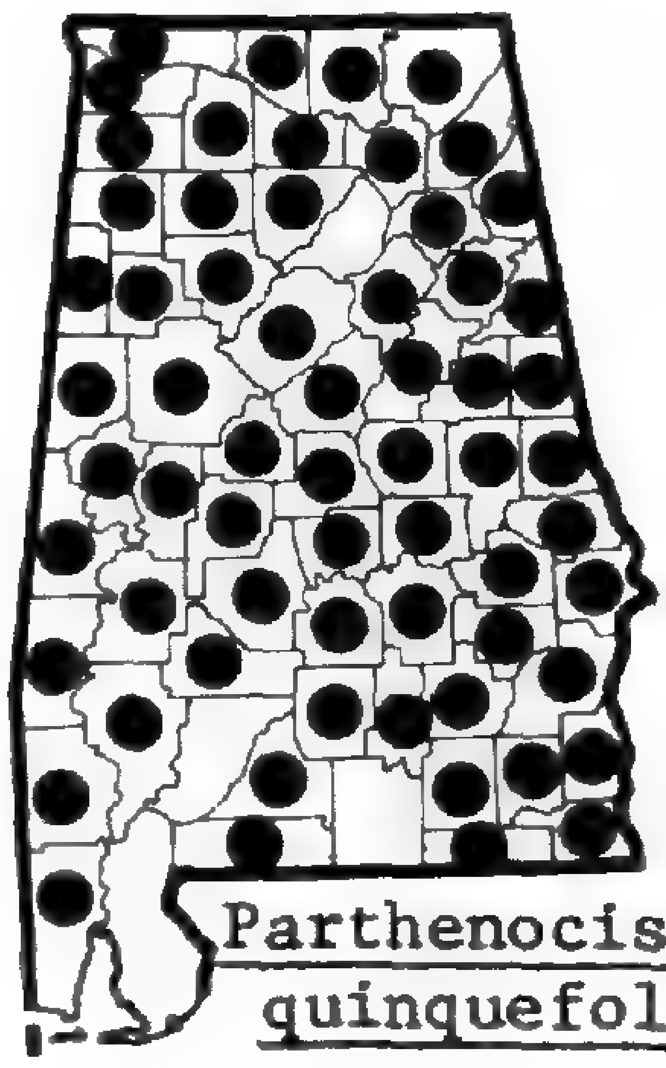


Ampelopsis arborea

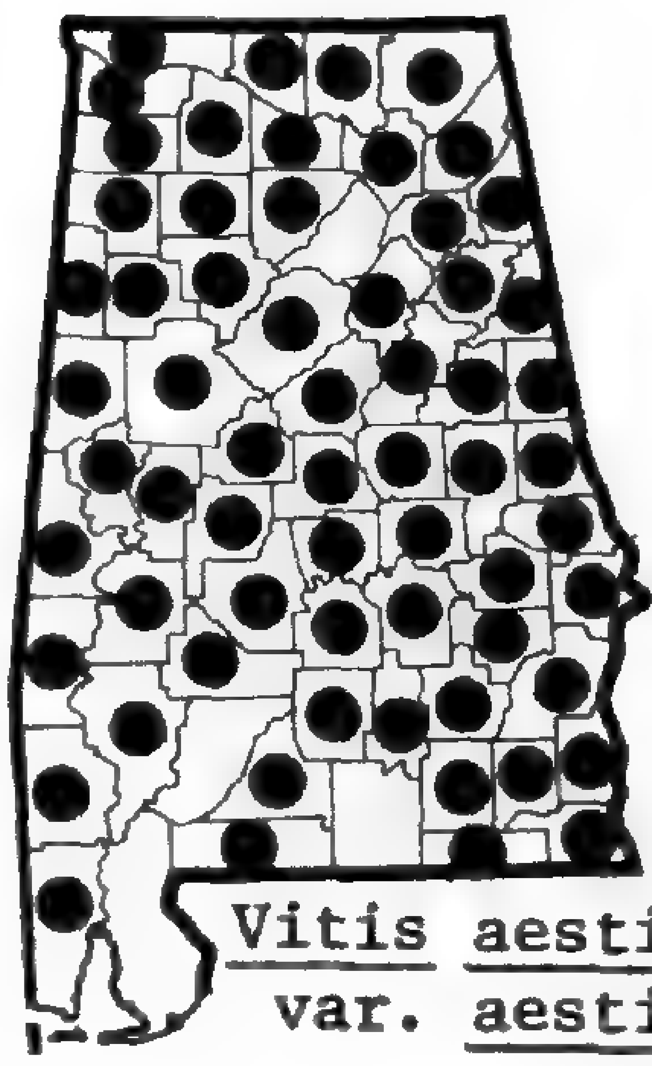


Ampelopsis cordata

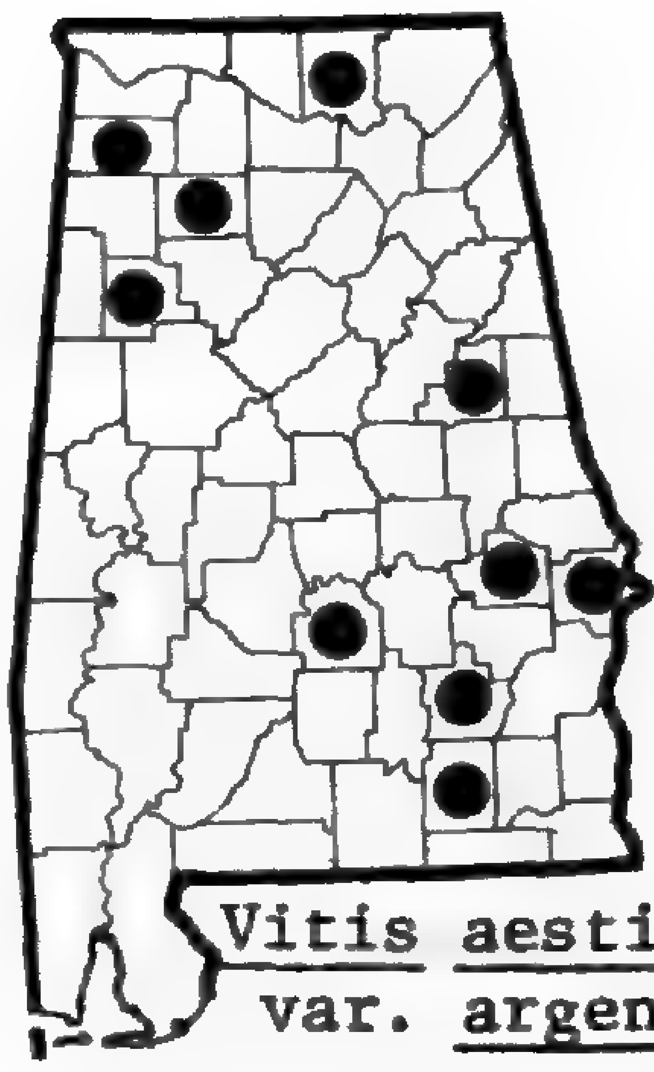
Cissus incisa



Parthenocissus quinquefolia



Vitis aestivalis var. aestivalis



Vitis aestivalis var. argentifolia

2. *Cissus* L.

1. *C. incisa* (Nuttall) Des Moulins. Flowers, fruit not seen in Alabama. Dunes, rare; OCP. *C. incisa* Desmoul.—S; *Ampelopsis incisa* (Nutt.) Desmoul.—M.

3. *Parthenocissus* Planchon, Virginia Creeper

1. *P. quinquefolia* (L.) Planchon. Spring–early summer; summer–fall. Fencerows, waste places, woods; throughout.

4. *Vitis* L., Grape

1. Pith of young branches continuous through the nodes .... 7. *V. rotundifolia*
1. Pith of young branches interrupted at the nodes 2
  2. Lower surfaces of leaves entirely obscured by dense pubescence 3
    3. Abaxial leaf pubescence distinctly rusty-tawny .... 3. *V. labrusca*
    3. Abaxial leaf pubescence not rusty-tawny .... 4. *V. mustangensis*
  2. Lower surfaces of leaves not entirely obscured by dense pubescence, or if obscured, then the pubescence floccose 4
    4. Young twigs angled .... 2. *V. cinerea*
    4. Young twigs terete or subterete 5
      5. Leaves not greenish beneath, but tomentose or floccose .... 1. *V. aestivalis*
      5. Leaves greenish, glabrous or glabrate beneath 6
        6. Leaves unlobed, or lateral lobes not prominent .... 8. *V. vulpina*
        6. Leaves obviously 3-lobed 7
          7. Mature twigs of current season green, gray or brown .... 6. *V. riparia*
          7. Mature twigs of current season red to purplish-red .... 5. *V. palmata*

1. *V. aestivalis* Michaux, Summer G. Spring; late summer–fall.

1. Leaves not strongly glaucous beneath .... *V. aestivalis* var. *aestivalis*
1. Leaves strongly glaucous beneath .... *V. aestivalis* var. *argentifolia*

V. aestivalis Michaux var. *aestivalis.* Mixed woods, often rocky; throughout.

V. aestivalis Michaux var. *argentifolia* (Munson) Fernald. Low or rocky woods, infrequent; CP, AM, CuP. *V. bicolor* LeConte—M, H, S.

2. *V. cinerea* Engelm. Late spring; fall. Low woods, local; CP, CuP, HR.

3. *V. labrusca* L., Fox G. Spring; late summer–fall. Upland fencerows, woods, very rare; P, AM, CuP.

4. *V. mustangensis* Buckley. Flowers, fruit not seen. Calcareous soil, very rare; CP.

5. *V. palmata* Vahl. Flowers, fruit not seen. Alluvial woods, rare; western CP.

6. *V. riparia* Michaux. Spring; late summer–fall. Roadsides, upland and low woods; throughout, but rare or absent in southern CP and very rare on CuP.

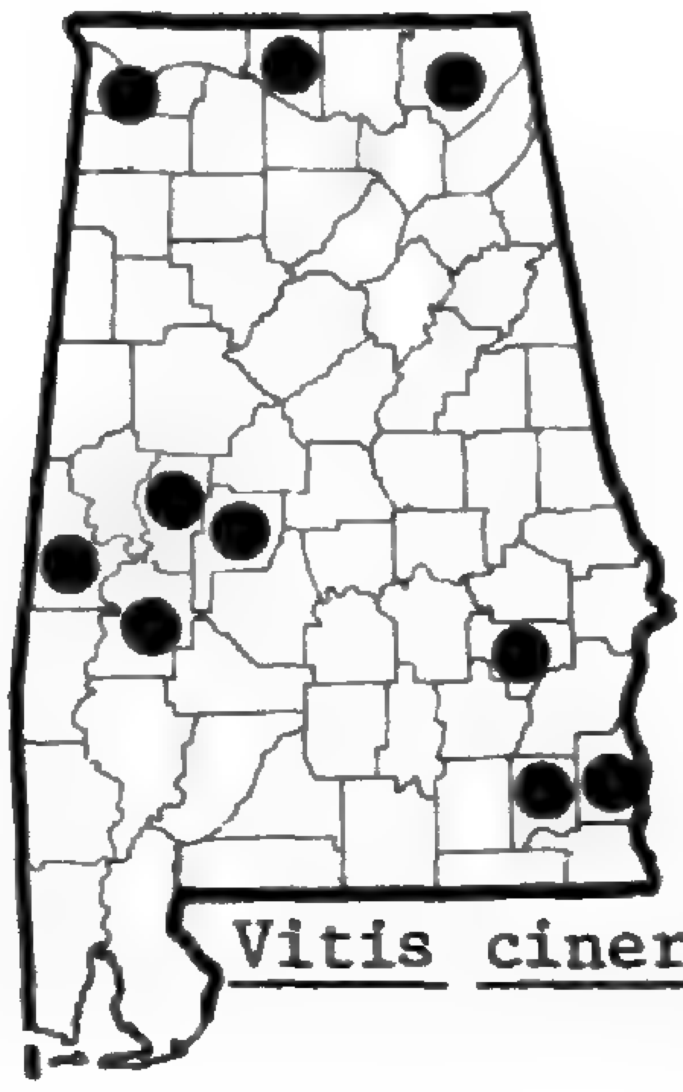
7. *V. rotundifolia* Michaux, Muscadine G. Spring; late summer–fall. Upland woods, thickets, fencerows, throughout. *Muscadina rotundifolia* (Michx.) Sm. —S.

8. *V. vulpina* L. Spring; late summer–fall. Low woods; throughout. *V. cordifolia* Lam.—M, H, S; *V. baileyana* Munson—S, RAB.

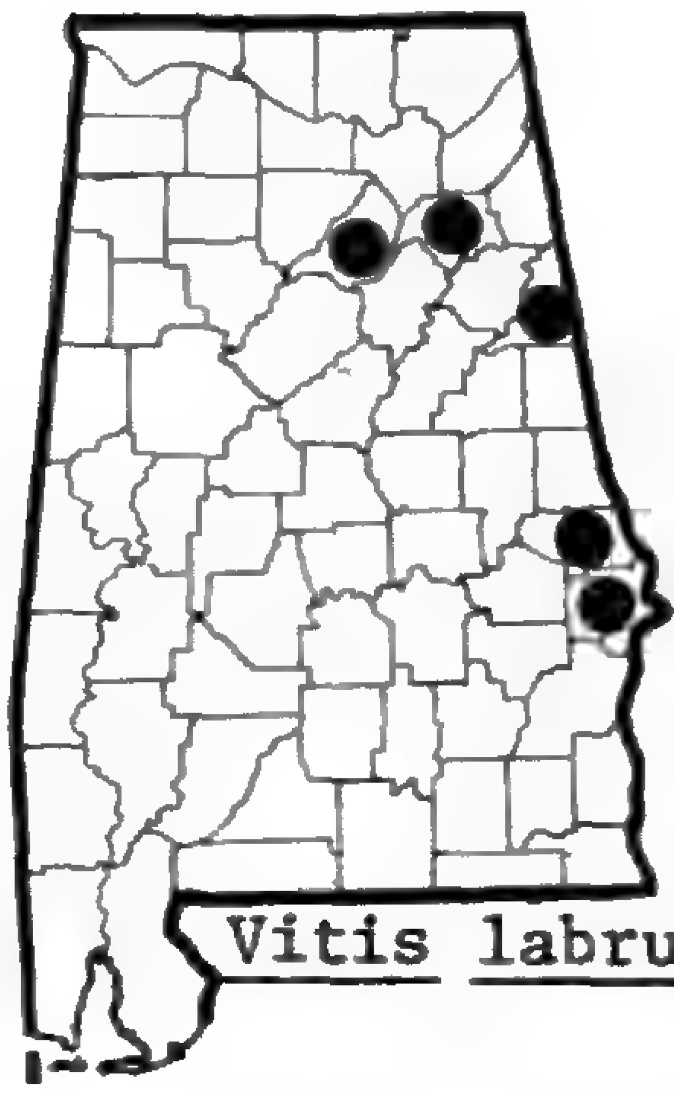
45. Tiliaceae

1. *Tilia* L., Basswood, Linn, Linden

1. *Tilia americana* L., complex. Late spring–early summer; summer. Mesic or rich woods, bluffs; throughout. *T. heterophylla* Vent.—M, H, S, RAB; *T. caro-*

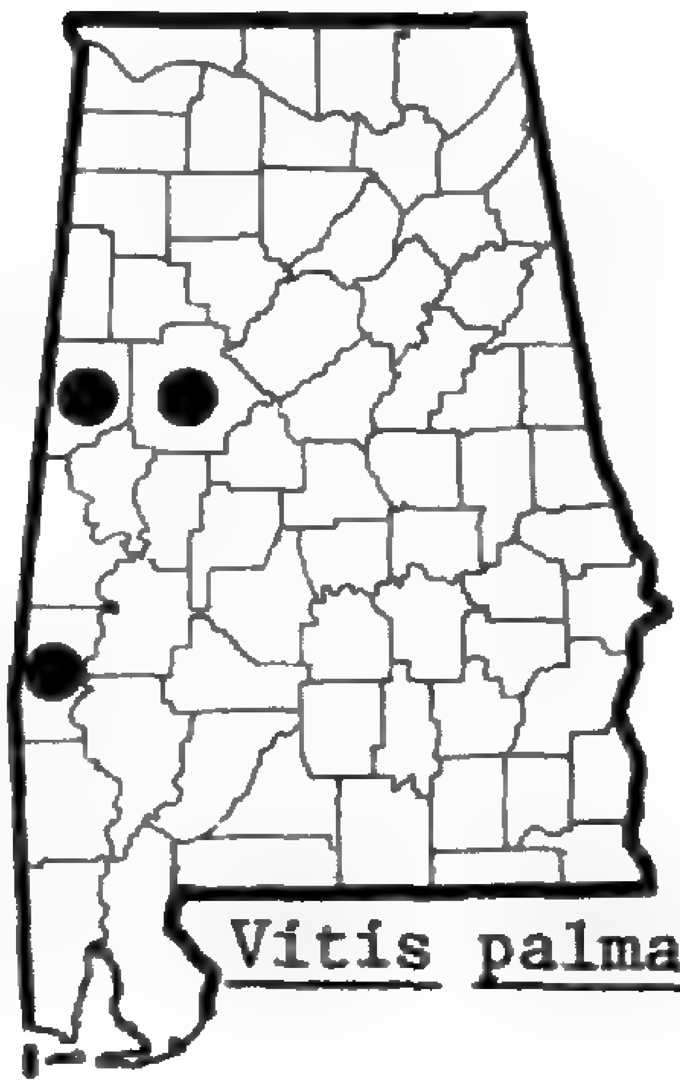


Vitis cinerea

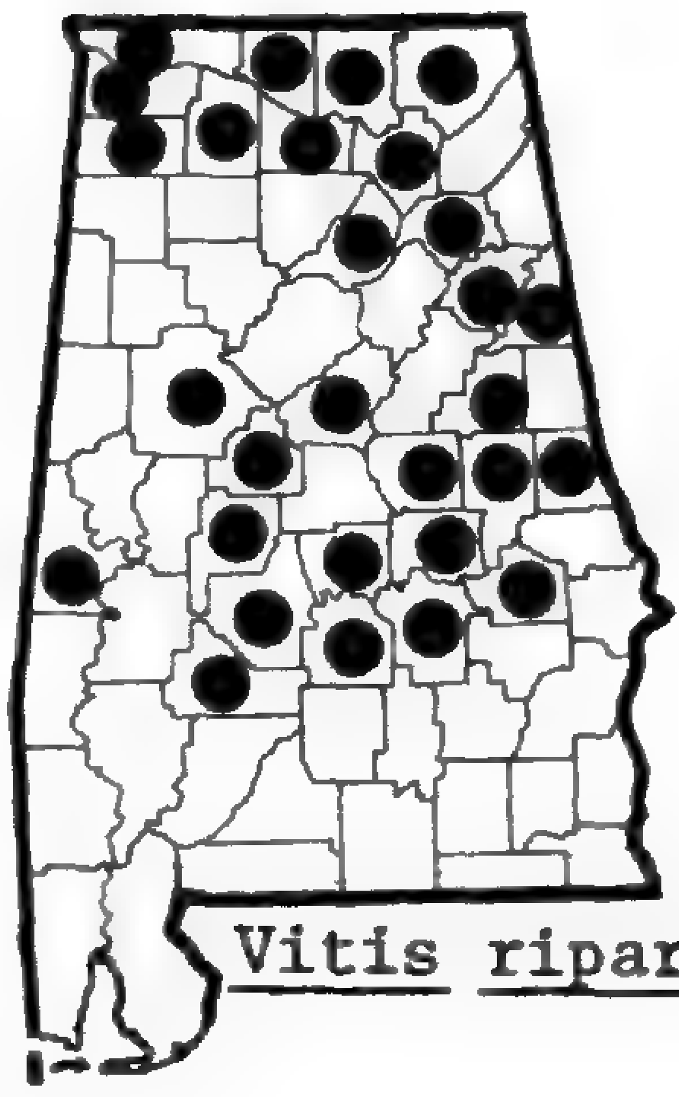


Vitis labrusca

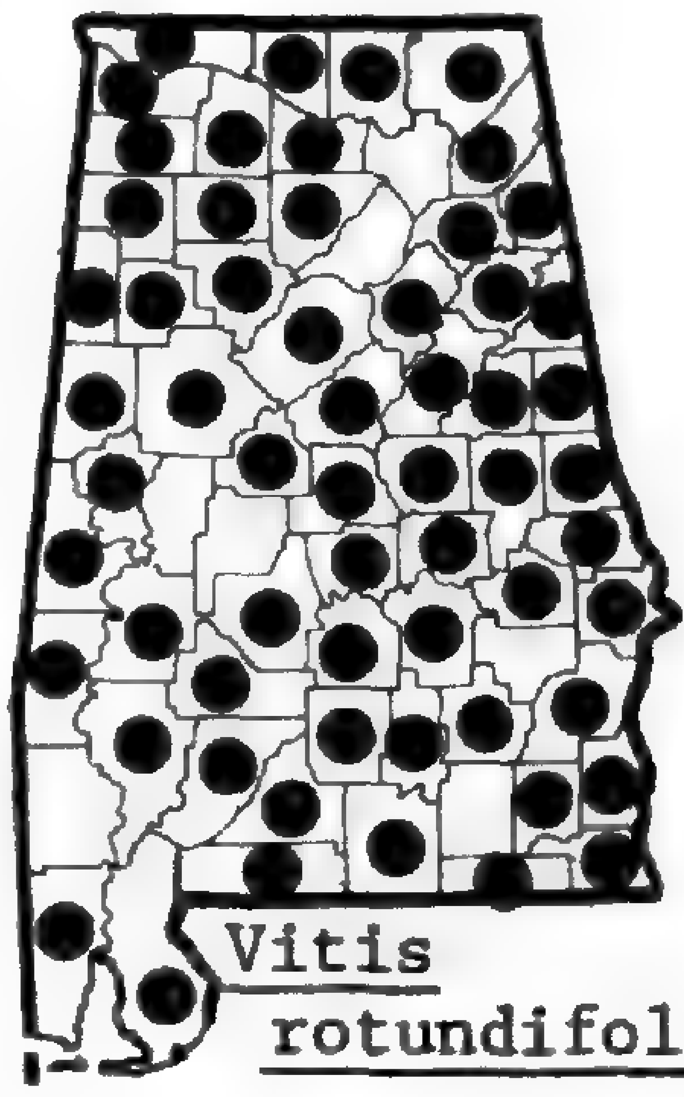
Vitis mustangensis



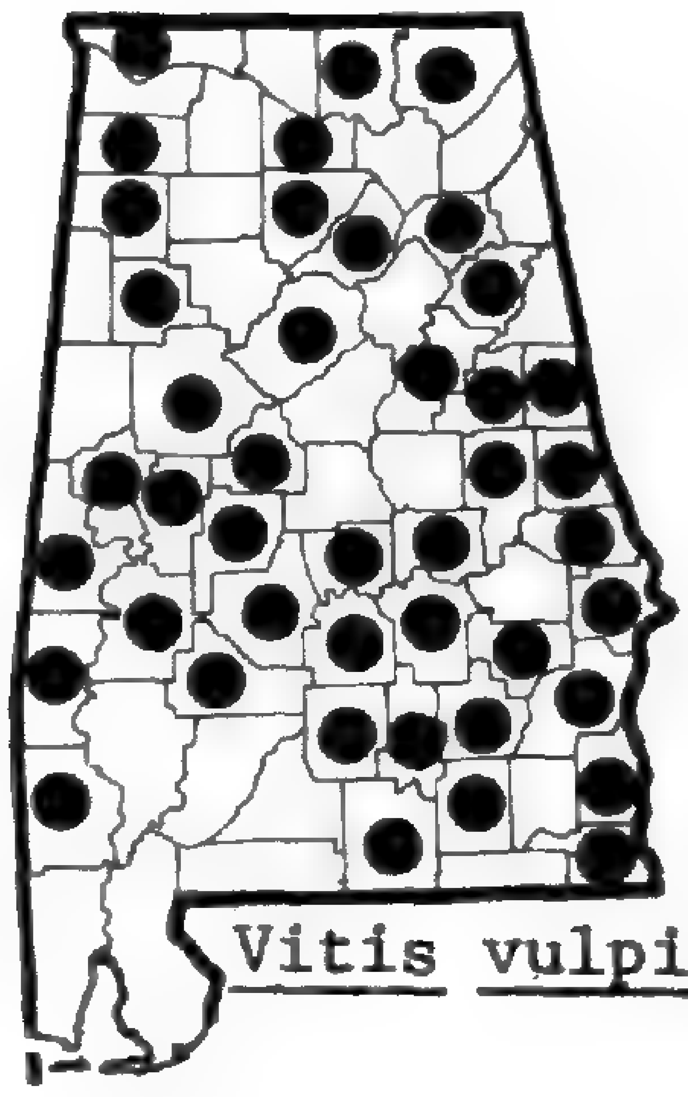
Vitis palmata



Vitis riparia

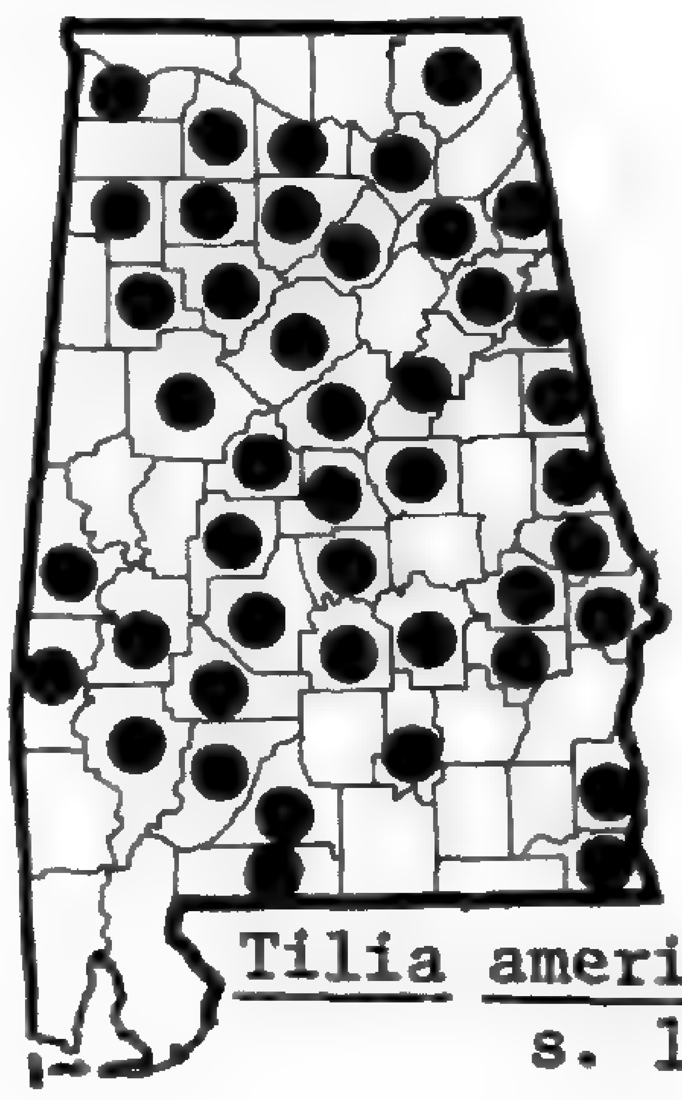


Vitis rotundifolia



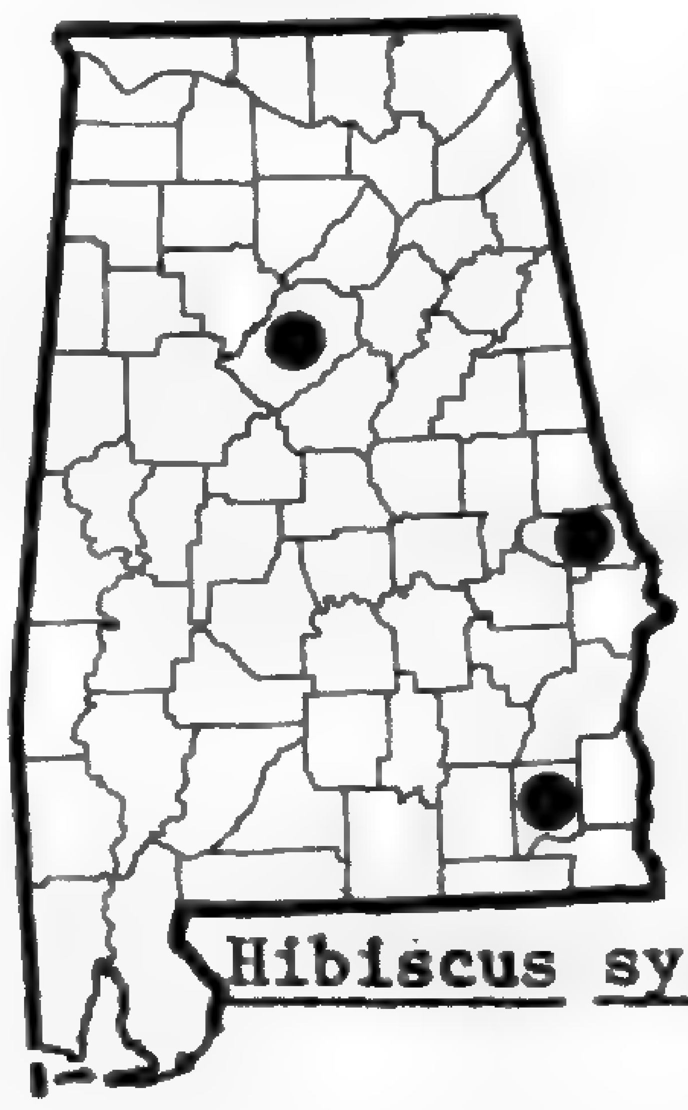
Vitis vulpina

45. TILIACEAE



Tilia americana s. l.

46. MALVACEAE



Hibiscus syriacus

liniana Mill.—S, RAB; *T. floridana* Sm.—H, S, RAB; *T. neglecta* Spach—H, S; *T. michauxii* Nutt.—S; *T. leucocarpa* Ashe, *T. australis* Sm.—H, S; *T. leucocarpa glaucescens* (Sarg.) Bush, *T. floridana alabamensis* Ashe, *T. lata* Ashe, *T. heterophylla michauxii* (Nutt.) Sarg., *T. heterophylla amphibola* Sarg.—H.—A very polymorphic group. For a recent treatment, see Jones (1968).

46. Malvaceae

1. *Hibiscus* L.

1. *H. syriacus* L., Althea, Rose of Sharon. Late spring–summer; summer–fall. Escaped to waste places, rare; CP, VR.

47. Sterculiaceae

1. *Firmiana* Marsili

1. *F. platanifolia* (L. f.) Marsili, Japanese Varnish Tree. Late spring–summer; summer. Escaped to woodlots, rare; CP. *F. platanifolia* (L. f.) R. Br.—H.

48. Theaceae

1. Leaves evergreen; sepals very unequal .... 1. *Gordonia*
1. Leaves deciduous; sepals subequal .... 2. *Stewartia*

1. *Gordonia* Ellis

1. *G. lasianthus* (L.) Ellis. Summer; summer–fall. Low ground, very rare; OCP.

2. *Stewartia* L.

1. Styles united; seeds wingless .... 1. *S. malacodendron*
1. Styles distinct; seeds winged .... 2. *S. ovata*

1. *S. malacodendron* L. Late spring–early summer; summer–fall. Mesic or rich woods, local; CP, CuP.

2. *S. ovata* (Cavanilles) Weatherby. Summer; summer–fall. Bluffs, streambanks, infrequent; CuP. *S. pentagyna* L'Her—M, H; *Malacodendron pentagynum* (L'Her) Sm.—S.

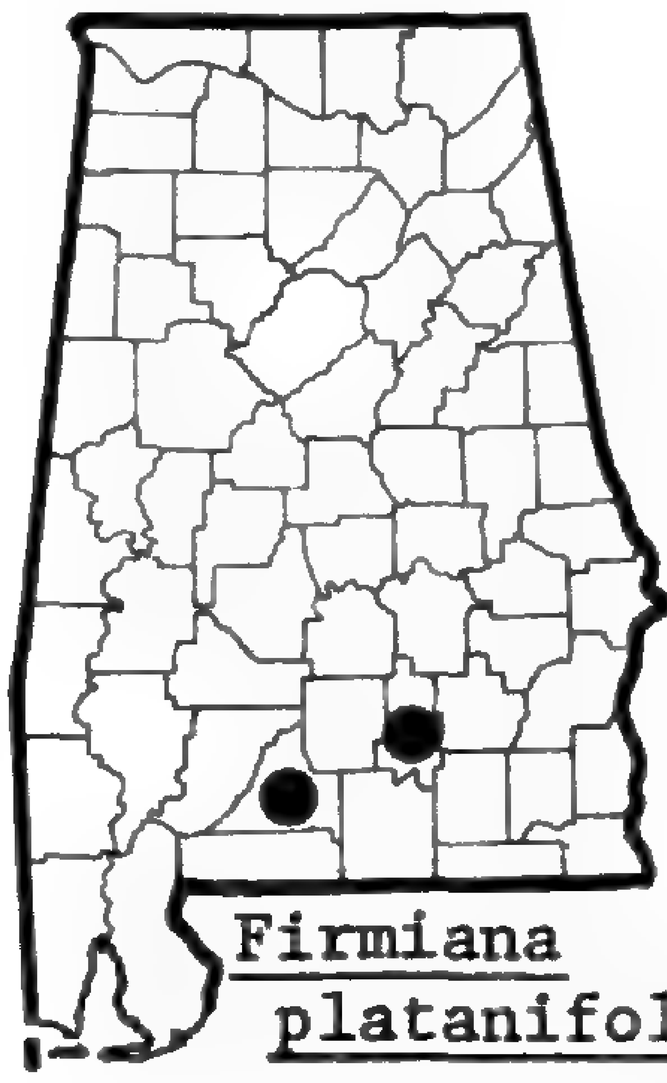
49. Hypericaceae

1. *Hypericum* L., St. John's Wort

The following treatment is adapted from that of W. P. Adams (1962).

1. Leaves clasping .... 9. *H. myrtifolium*
1. Leaves not clasping 2
    2. Mature leaves and sepals not needle-like, usually over 2 mm wide 3
        3. Perianth tetramerous 4
            4. Gynoecium 2-carpellate, 2-styled 5
                5. Pedicels elongate; bracts subtending flowers at base of pedicels .... 16. *H. suffruticosum*
                5. Pedicels compact; bracts subtending flowers approximate to the sepals 6
                    6. Plant erect .... 7. *H. hypericoides*
                    6. Plant decumbent .... 15. *H. stragalum*
            4. Gynoecium 3-carpellate, 3-styled .... 14. *H. stans*

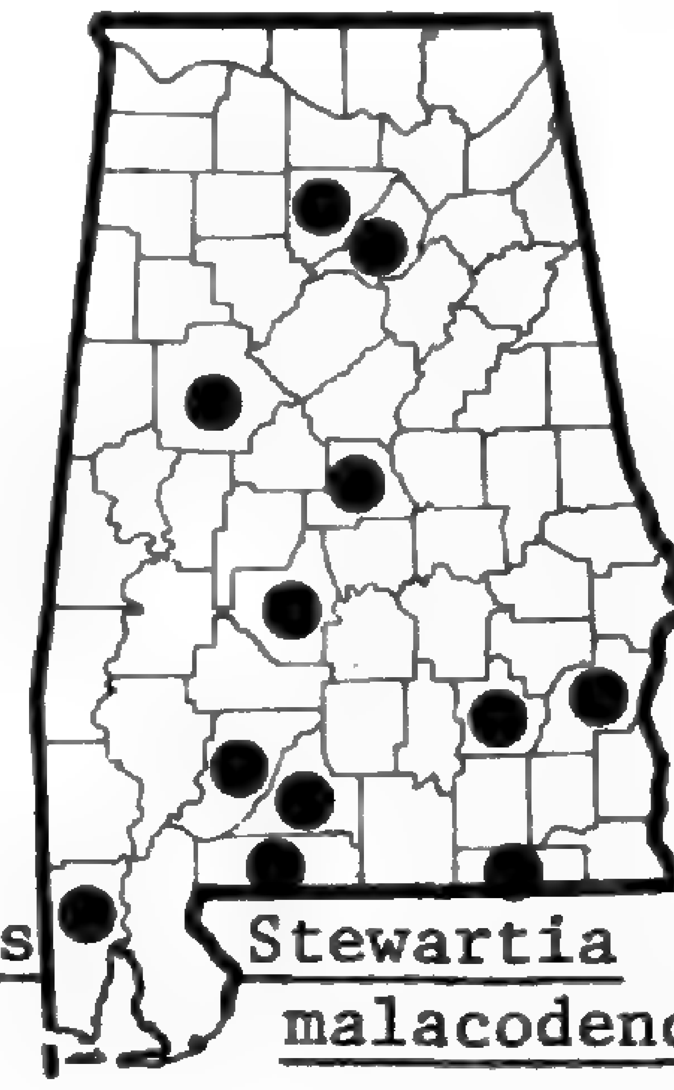
47. STERCULIACEAE



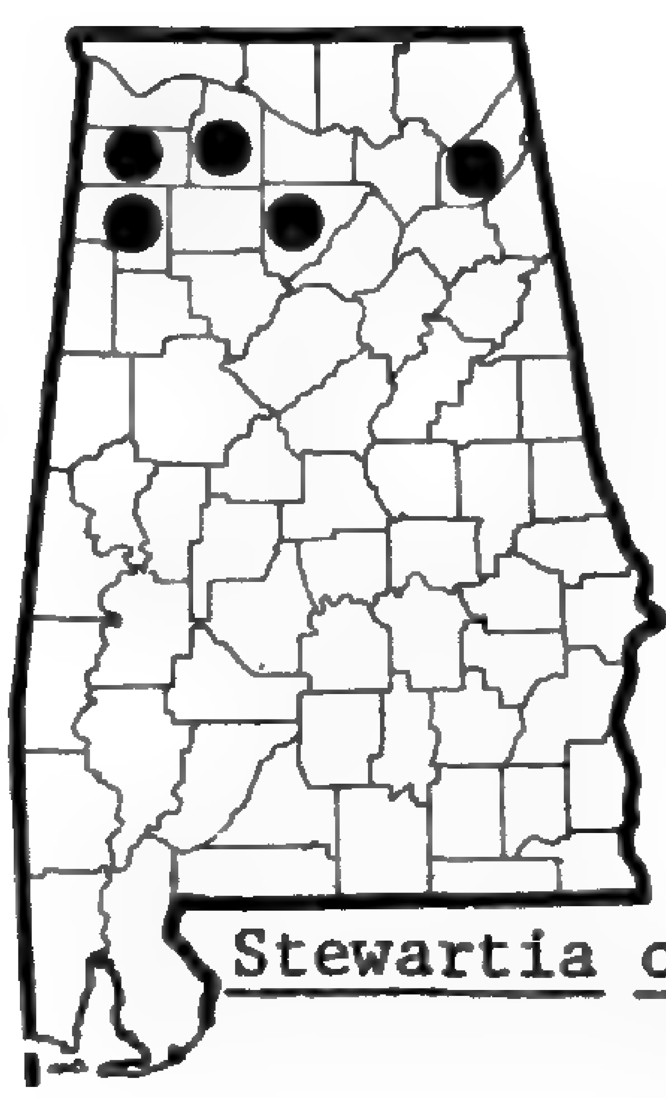
Firmiana platanifolia

48. THEACEAE

Gordonia lasianthus

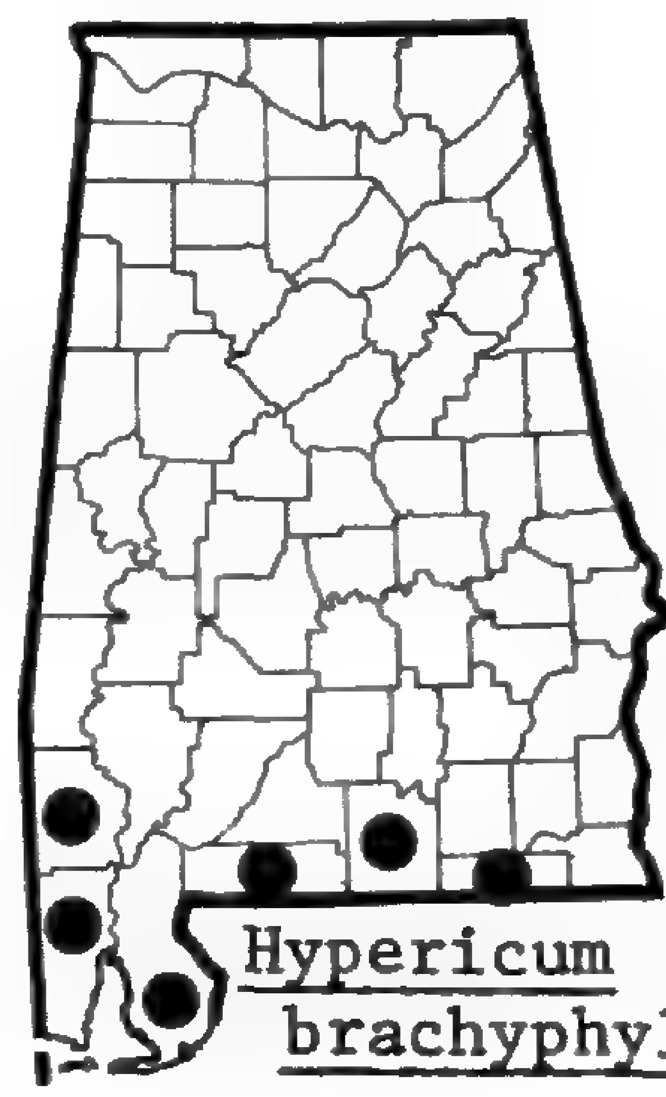


Stewartia malacodendron



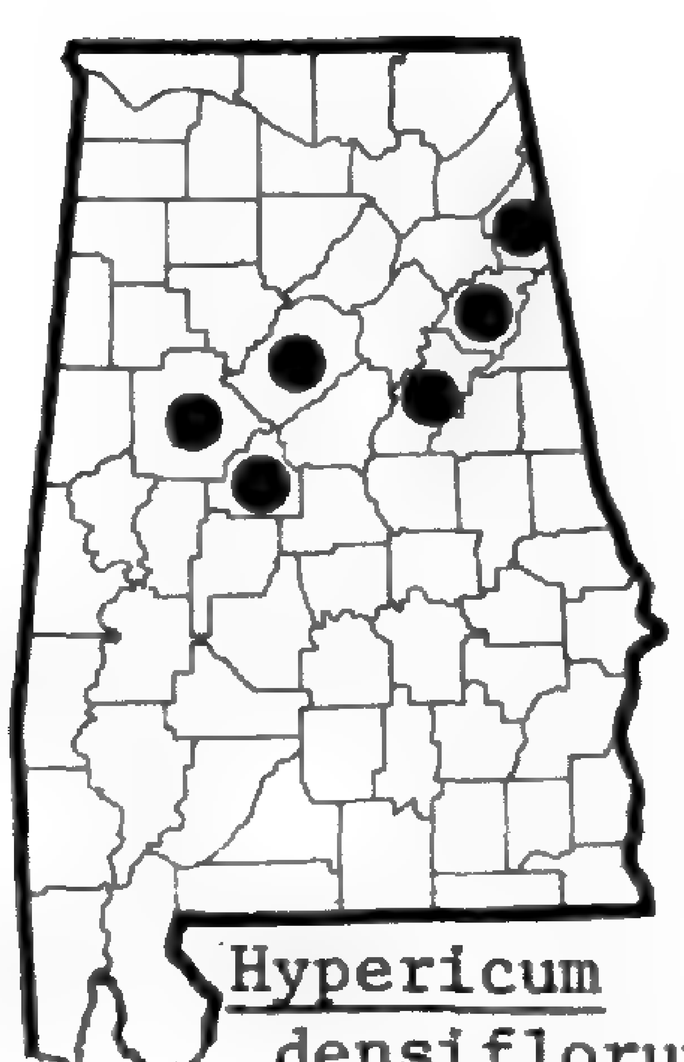
Stewartia ovata

49. HYPERICACEAE



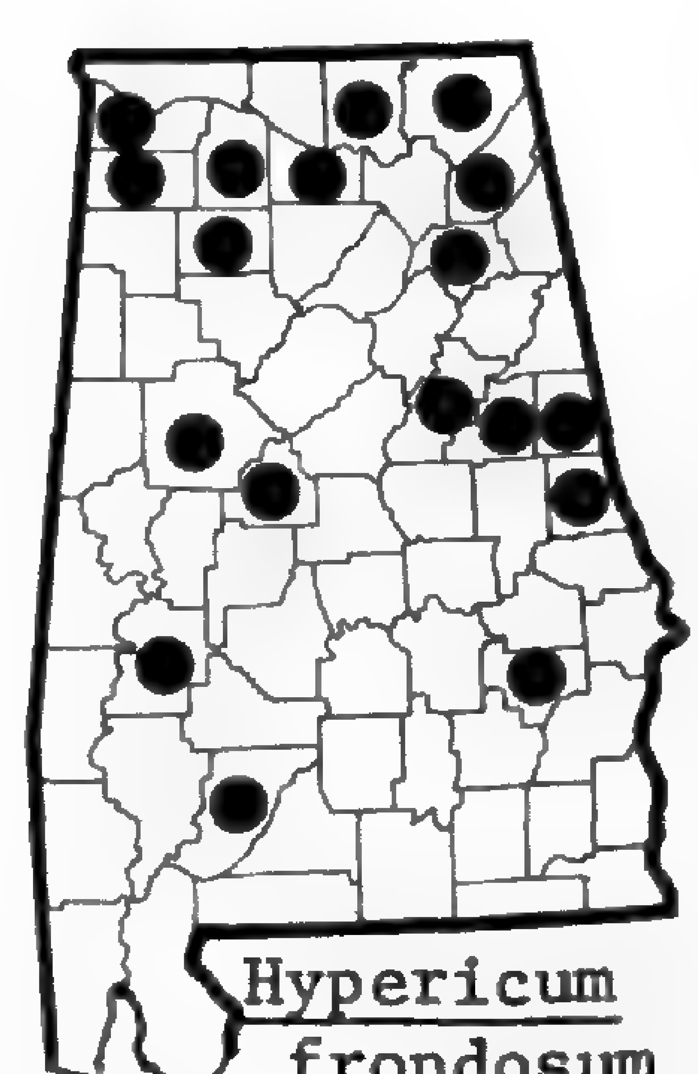
Hypericum brachyphyllum

Hypericum cistifolium



Hypericum densiflorum

Hypericum fasciculatum



Hypericum frondosum

3. Perianth pentamerous; gynoecia predominantly 3-carpellate and 3-styled 7
   7. Inflorescences, at least most, less than 3-flowered .... 5. *H. frondosum*
   7. Inflorescences predominantly more than 3-flowered 8
      8. Leaves and sepals without a basal articulation or groove 9
         9. Stamens less than 55; seeds less than 0.8 mm long .... 2. *H. cistifolium*
         9. Stamens more than 75; seeds more than 1.2 mm long .... 11. *H. nudiflorum*
      8. Leaves and sepals with a basal articulation or groove 10
         10. Largest leaves 1.5–3.0 cm long; seeds 0.7–0.8 mm long .... 6. *H. galioides*
         10. Largest leaves 3.0 cm long or longer; seeds more than 0.8 mm long 11
            11. Mature capsules less than 6 mm long and 3 mm broad; seeds reddish-brown; leaves linear or narrowly elliptic .... 3. *H. densiflorum*
            11. Mature capsules more than 7.5 mm long and 3.5 mm broad; seeds dark brown or black; leaves elliptic or wider .... 12. *H. prolificum*

2. Mature leaves and sepals needle-like, less than 2 mm wide (*H. fasciculatum* complex) 12
   12. Largest leaves regularly less than 11 mm long 13
      13. Plant decumbent .... 13. *H. reductum*
      13. Plant erect .... 1. *H. brachyphyllum*
   12. Largest leaves regularly more than 13 mm long 14
      14. Plant decumbent .... 8. *H. lloydii*
      14. Plant erect 15
         15. Bark spongy, exfoliating in thin sheets; 1- to 3-flowered inflorescences present in upper 1 or 2 leaf axils .... 4. *H. fasciculatum*
         15. Bark thin, exfoliating in flakes or narrow strips; many-flowered inflorescences present in upper 3–7 leaf axils .... 10. *H. nitidum*

Dates given below are for flowering season only, as fruits are usually persistent.

1. *H. brachyphyllum* (Spach) Steudel. Summer. Ditches, low pinelands, OCP. Closely related to species 4, 10, 13.

2. *H. cistifolium* Lamarck. Summer. Swamp ecotones; OCP. *H. opacum* T. & G.—M, H, S.

3. *H. densiflorum* Pursh. Summer. Low open stream borders, infrequent; southern CuP, VR.

4. *H. fasciculatum* Lamarck. Summer. Low ground; OCP. Forms a complex including species 1, 10, 13. *H. aspalathoides* Willd.—M, H, S.

5. *H. frondosum* Michaux. Summer. Rocky woods, often over calcareous rock, infrequent; throughout. *H. aureum* Bartr.—M, H, S.—One of Alabama's most beautiful shrubs when in bloom.

6. *H. galioides* Lamarck. Summer. Open swamp borders, low pinelands; CP. *H. ambiguum* Ell.—S; *H. galioides* var. *pallidum* Mohr—M, H.

7. *H. hypericoides* (L.) Crantz. Summer. Low and upland woods and clearings; throughout. *Ascyrum hypericoides* L.—M, H, S.

8. *H. lloydii* (Svenson) Adams. Piedmont, rare; reported by W. P. Adams (1962).

9. *H. myrtifolium* Lamarck. Flowers, fruit not seen. Ponds; OCP.

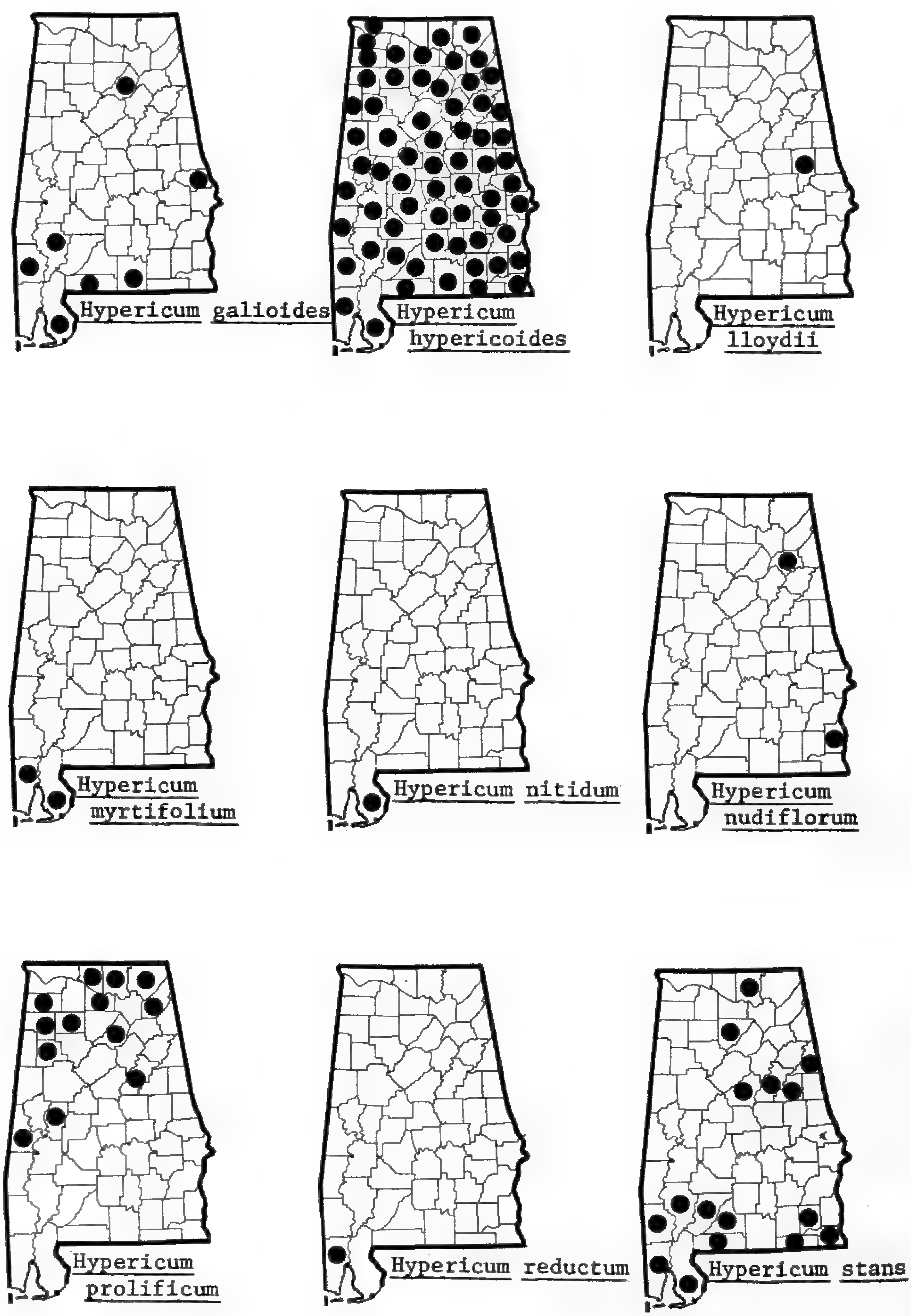
10. *H. nitidum* Lamarck. Summer. Low pinelands, creek swamps, rare; OCP.

11. *H. nudiflorum* Michaux. Summer. Open ground, very rare; CP, VR.

12. *H. prolificum* L. Summer. Rocky woods; CP, CuP, HR.

13. *H. reductum* (Svenson) Adams. Summer. Sandy woods, rare; OCP (W. P. Adams 1962). Closely related to species 1, 4, 10.

14. *H. stans* (Michaux) Adams & Robson. Summer. Low, open ground,


Hypericum galioides
Hypericum hypericoides
Hypericum lloydii
Hypericum myrtifolium
Hypericum nitidum
Hypericum nudiflorum
Hypericum prolificum
Hypericum reductum
Hypericum stans

thickets; OCP, P (rare), AM, CuP, VR, HR. *Ascyrum stans* Michx.—M, H, S; *A. cuneifolium* Chapm.—S.

15. *H. stragalum* Adams & Robson. Summer. Rocky woods and clearings; AM, VR, CuP, HR. *Ascyrum multicaule* Michx.—M. Closely related to species 7.

16. *H. suffruticosum* Adams & Robson. Summer. Reported from OCP by W. P. Adams (1962). *Ascyrum pumilum* Michx.—M, S.

50. Cactaceae

1. *Opuntia* Miller, Cactus, Prickly Pear

1. Stem segments more than 1 dm long, bearing 2–3 flattened, indurate spines at some nodes; fruit more than 3 cm broad .... 3. *O. vulgaris*
1. Stem segments less than 1 dm long, or indurate spines always less than 2 per node; fruit less than 2.5 cm broad 2
   2. Nodes, at least some, with more than 1 spine .... 2. *O. drummondii*
   2. Nodes with 1 or no spines .... 1. *O. compressa*

1. *O. compressa* (Salisbury) Macbride. Spring; summer–fall. Open, sandy or rocky ground; infrequent; throughout, but poorly collected. *O. humifusa* Raf., *O. opuntia* (L.) Coult.—M; *O. opuntia* (L.) Karst., *O. pollardi* Britt. & Rose, *O. bentonii* Griff.—S.

2. *O. drummondii* Graham. Spring; summer–fall. Dunes; OCP. *O. pes-corvi* LeConte—M; *O. tracyi* Britt.—S.

3. *O. vulgaris* Miller. Spring; summer–fall. Escaped to sandy woods and beaches; OCP.

51. Thymelaeaceae

1. *Dirca* L., Leatherwood

1. *D. palustris* L. Spring; late spring–early summer. Rich woods in circumneutral soil, rare; CP, CuP.

52. Elaeagnaceae

1. *Elaeagnus* L.

1. *E. umbellata* Thunberg. Spring; summer. Escaped, rare; CuP.

53. Lythraceae

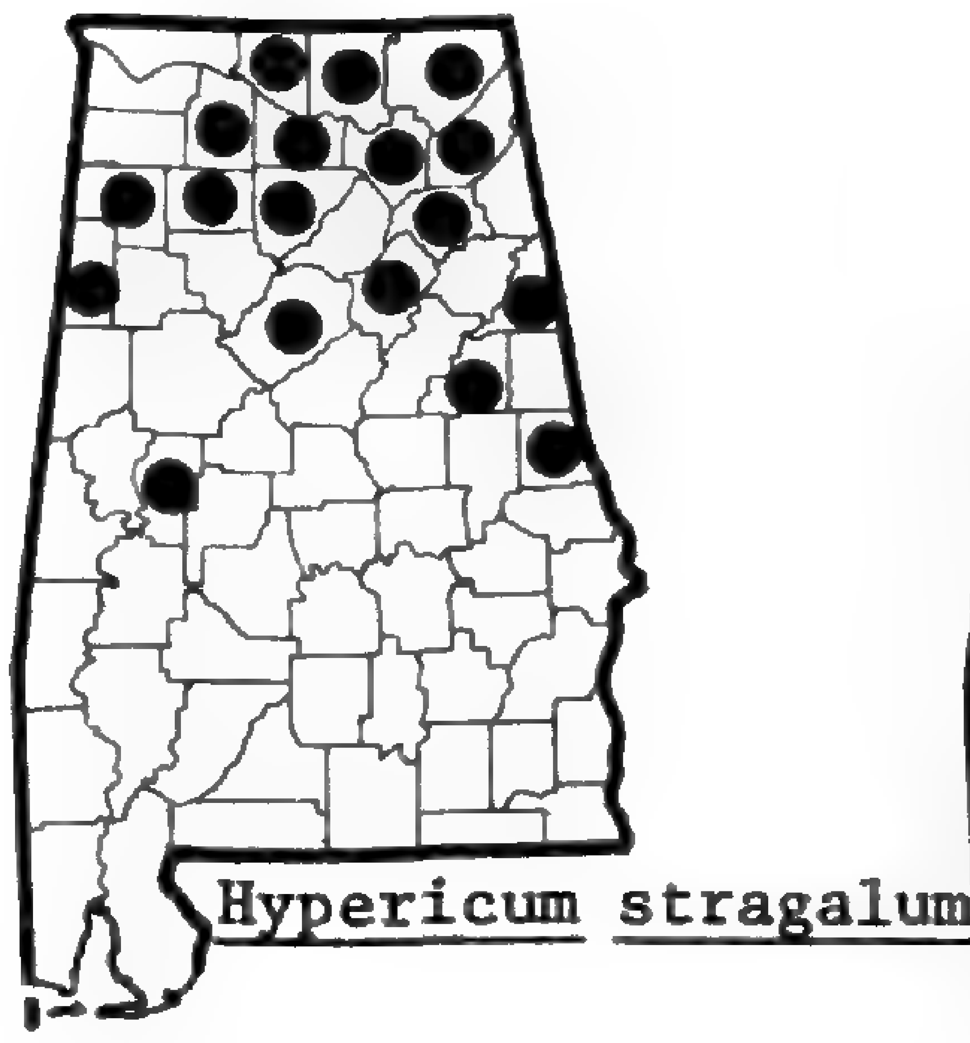
1. Inflorescences axillary, cymose .... 1. *Decodon*
1. Inflorescences terminal, paniculate .... 2. *Lagerstroemia*

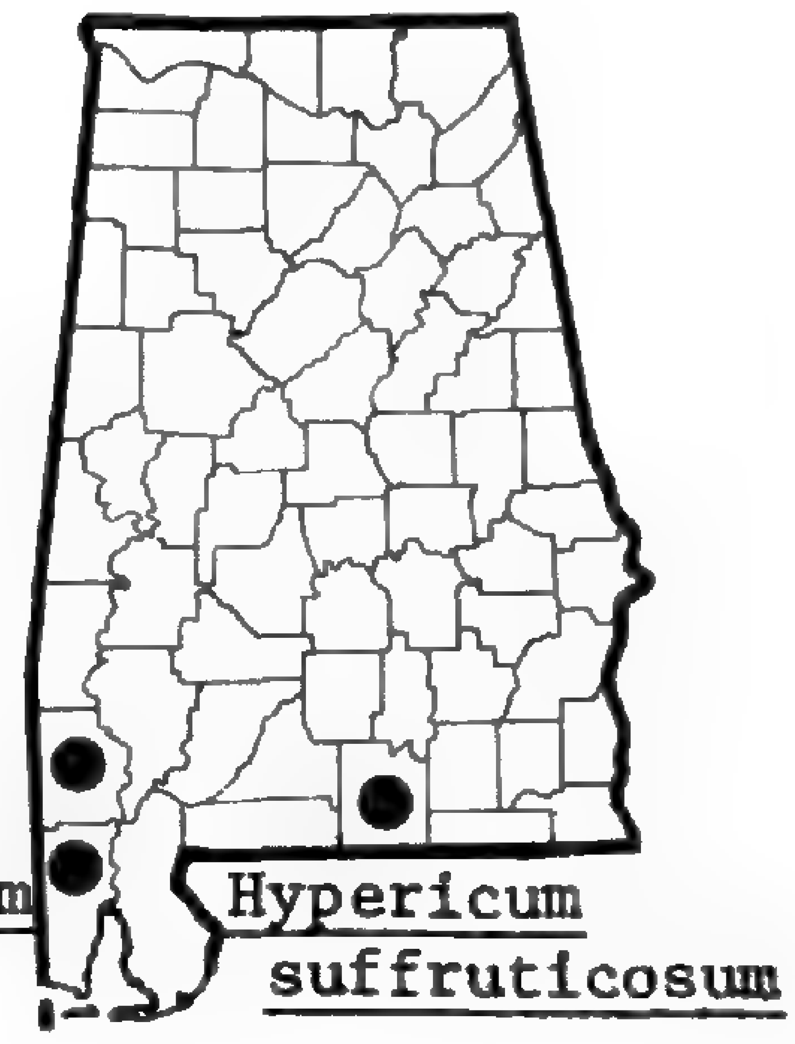
1. *Decodon* Gmelin

1. *D. verticillatus* (L.) Elliott. Summer. Pools, marshes; VR. Reported from CP, HR by Mohr (1901) and Harper (1928).

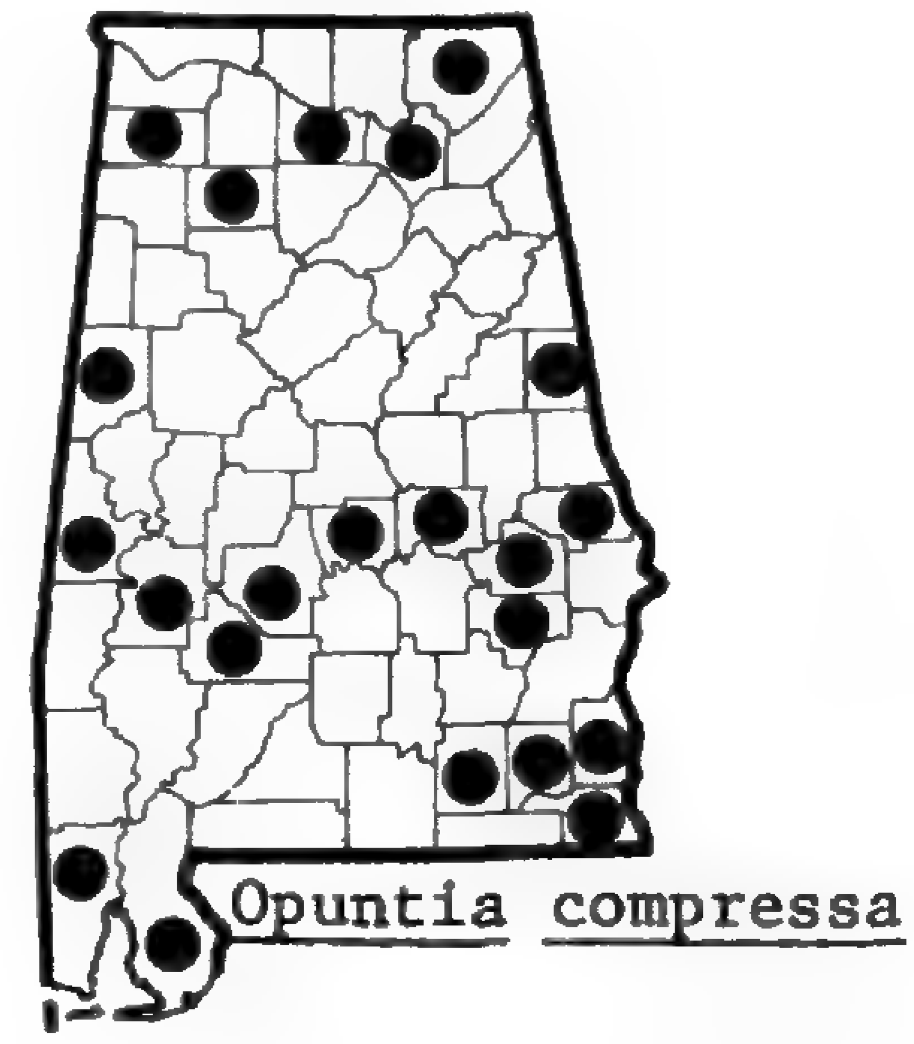
2. *Lagerstroemia* L.

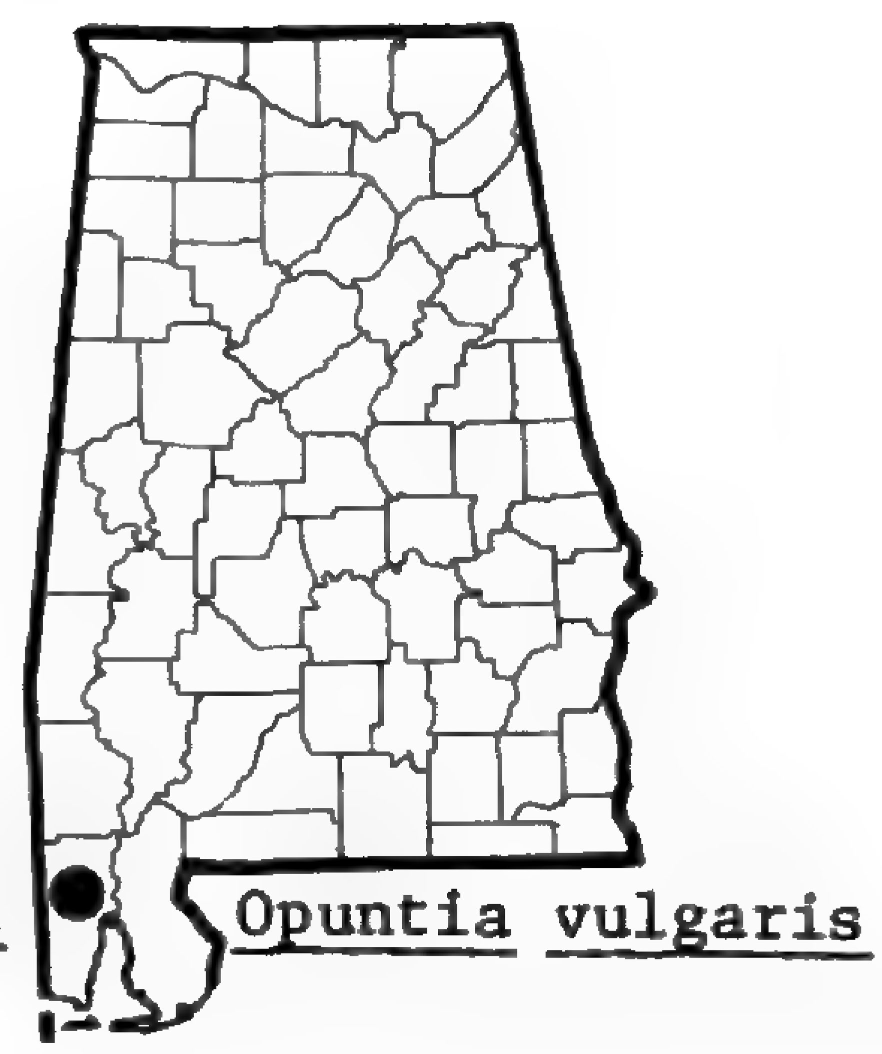
1. *L. indica* L., Crape-Myrtle. Summer; fall–winter. Persistent or rarely escaping in fencerows, waste places; principally CP.



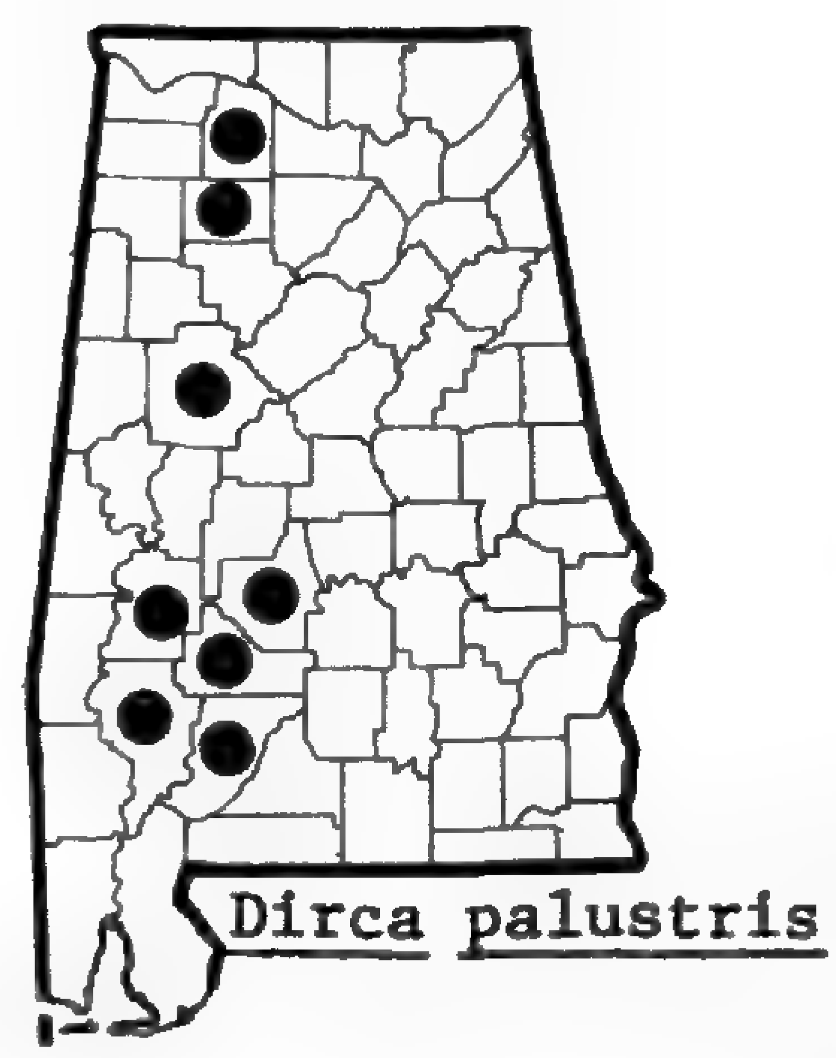


50. CACTACEAE

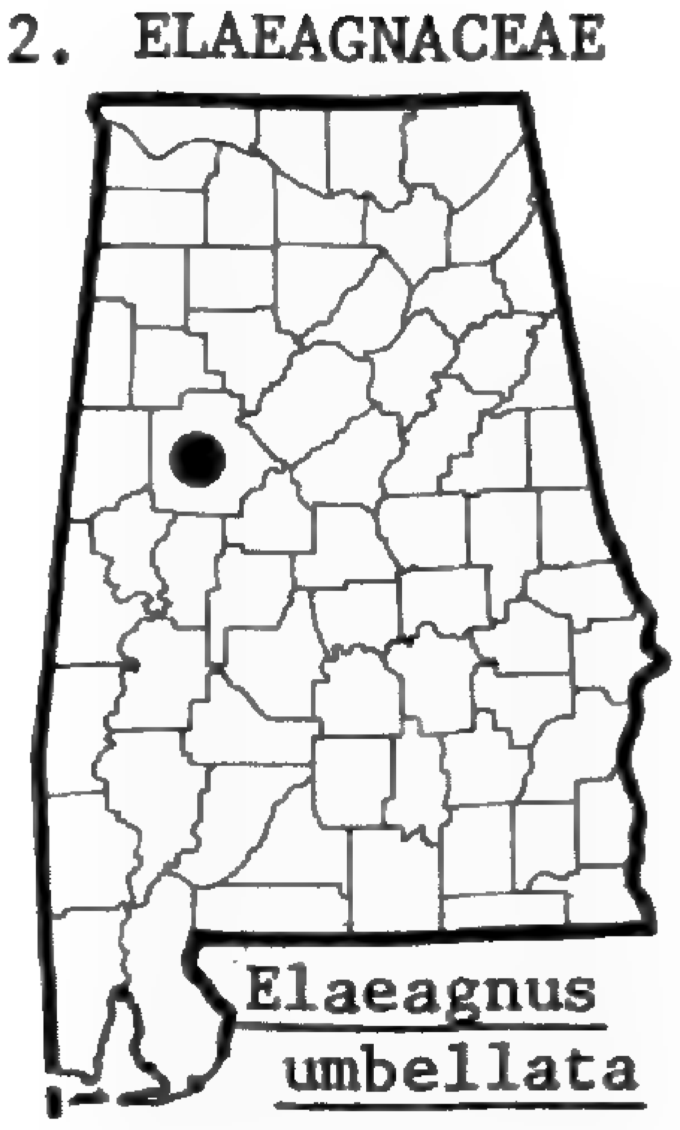




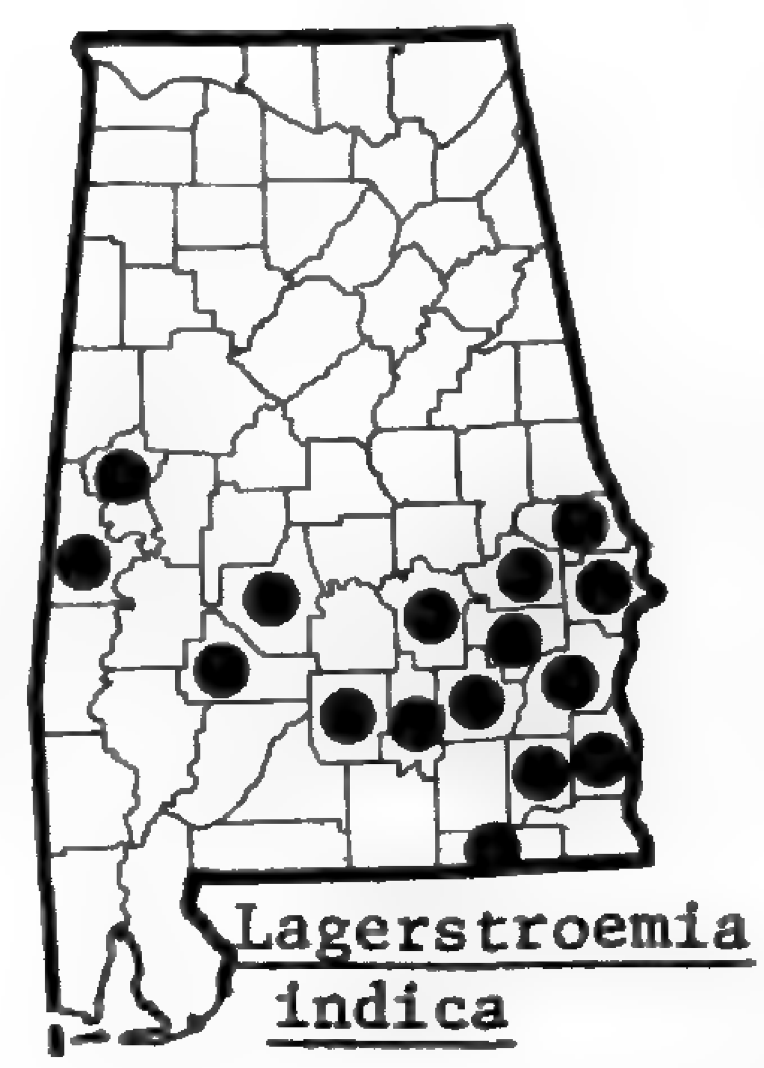
51. THYMELAEACEAE



52. ELAEAGNACEAE



53. LYTHRACEAE



54. Araliaceae

1. Leaves decompound; plant a shrub or tree .... 1. *Aralia*
1. Leaves simple; plant a vine .... 2. *Hedera*

1. *Aralia* L.

1. *A. spinosa* L., Devil's Walking-Stick, Prickly Ash. Summer–fall. Mesic woods and clearings; throughout.

2. *Hedera* L., Ivy

1. *H. helix* L. Summer; fall. Trash heap, very rare; CP.

55. Nyssaceae

1. *Nyssa* L., Gum

1. Pistillate flowers solitary; staminate flowers sessile; drupe more than 1.5 cm long .... 1. *N. aquatica*
1. Pistillate flowers in 2- or more-flowered clusters; staminate flowers pedicelled; drupe less than 1.5 cm long .... 2. *N. sylvatica*

1. *N. aquatica* L., Tupelo G. Spring; late summer–fall. Swamp forests, stream margins; CP, CuP, VR, HR.

2. *N. sylvatica* Marshall, Black G. Spring; late summer–early fall. Low and upland woods, ponds, bogs; throughout. *N. biflora* Walt.—M, H, S; *N. sylvatica* var. *biflora* (Walt.) Sarg.—RAB.—This species is very wide-ranging and variable. *Nyssa biflora* Walt. appears to deserve ecotypic status.

Nyssa ogeche Marshall, separated from *N. aquatica* L. by obtuse leaves, red fruit, and winged endocarp, has been reported (Eyde, 1963) from the OCP, but no specimens have been seen by the writer.

56. Cornaceae

1. *Cornus* L., Dogwood

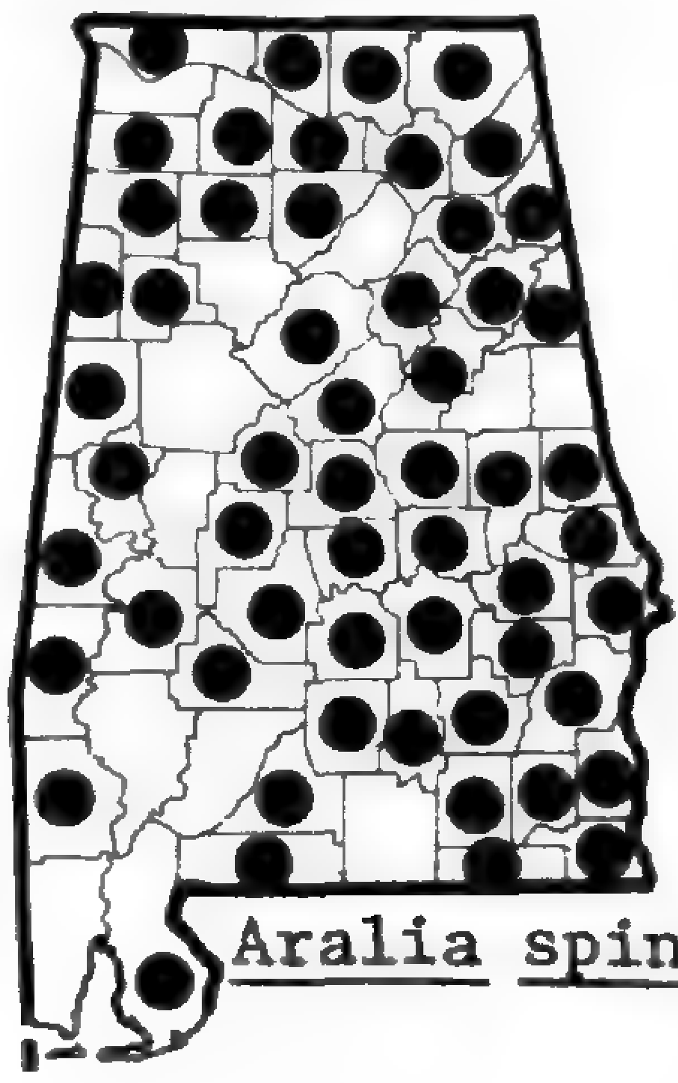
1. Leaves alternate .... 1. *C. alternifolia*
1. Leaves opposite 2
   2. Cyme head-like; bracts more than 1 cm long; drupes red .... 4. *C. florida*
   2. Cyme open; bracts minute or absent; drupes white to blue 3
      3. Pith of 1-year-old twigs reddish, brown or tan .... 2. *C. amomum*
      3. Pith of 1-year-old twigs white or cream-colored 4
         4. Leaves scabrous or scaberulous above .... 3. *C. asperifolia*
         4. Leaves smooth above .... 5. *C. stricta*

1. *C. alternifolia* L. f., Alternate-Leaved D. Spring; summer–fall. Rich or low woods, rare; CP, P, CuP. *Svida alternifolia* (L. f.) Sm.—S.

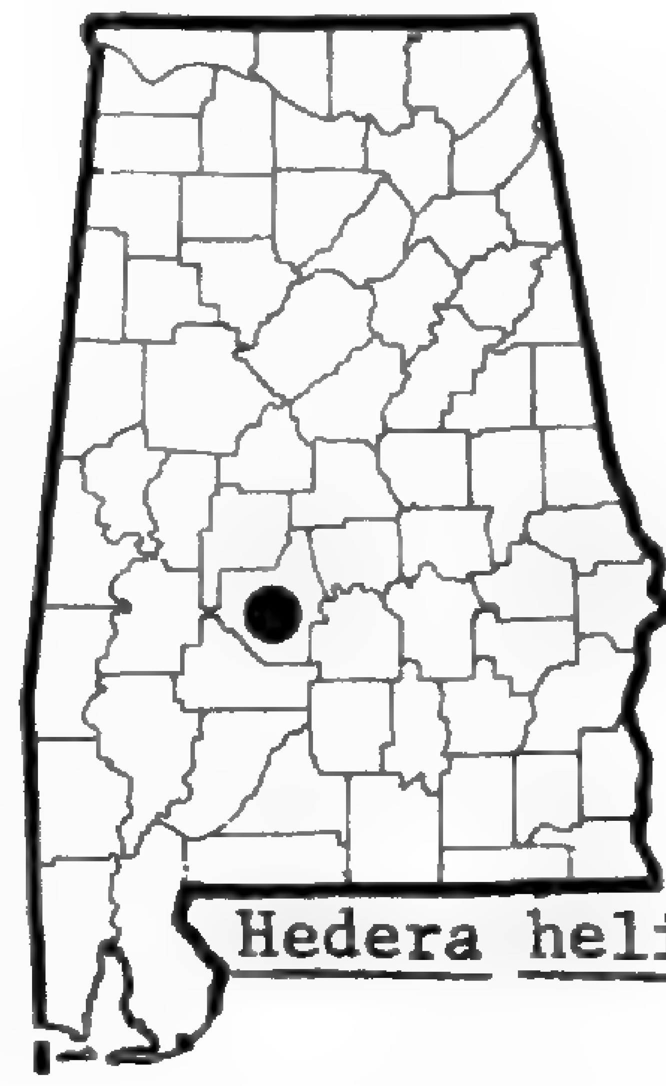
2. *C. amomum* Miller, Red-Osier D. Spring; summer. Streambanks, low woods, marshes; throughout, but more infrequent southward. *Svida amomum* (Mill.) Sm.—S; *C. stricta* Lam.—H, in part.

3. *C. asperifolia* Michaux. Spring; summer–fall. Fencerows, thickets, and woods in circumneutral situations; principally Black Belt of CP. *Svida microcarpa* (Nash) Sm., *S. asperifolia* (Michx.) Sm.—S.—Western populations of simi-

54. ARALIACEAE

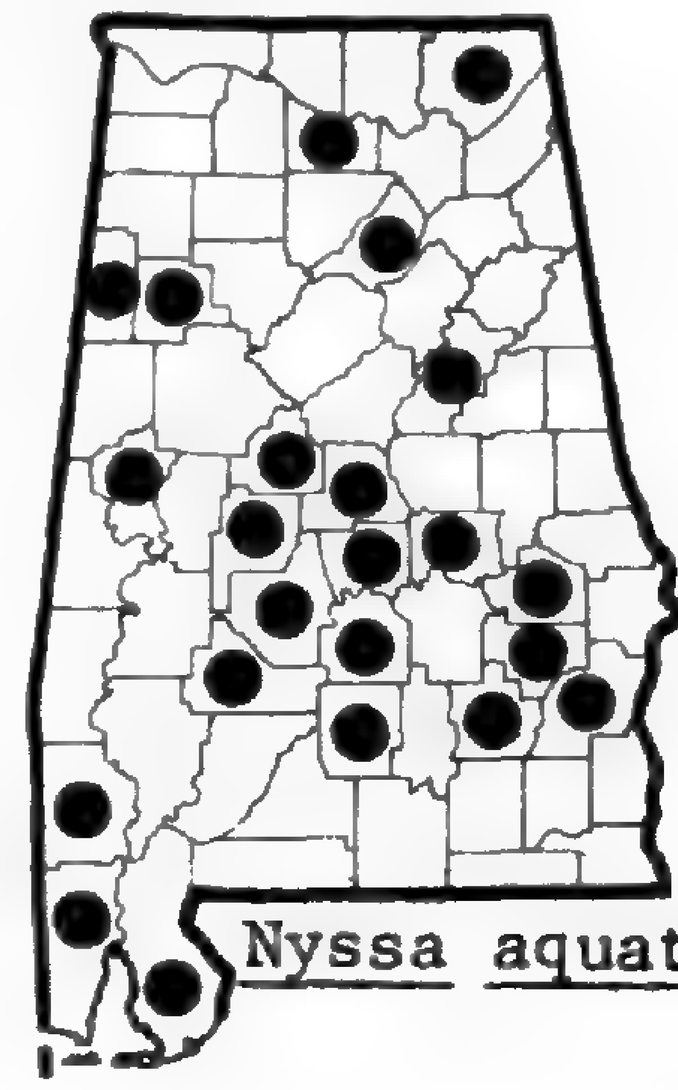


Aralia spinosa



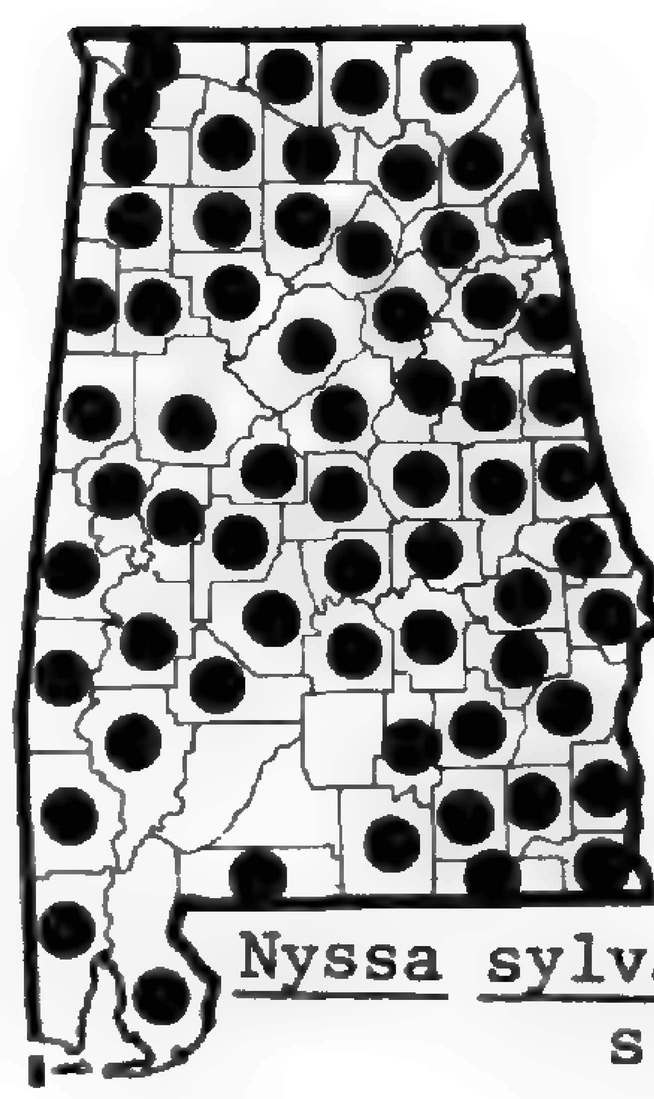
Hedera helix

55. NYSSACEAE



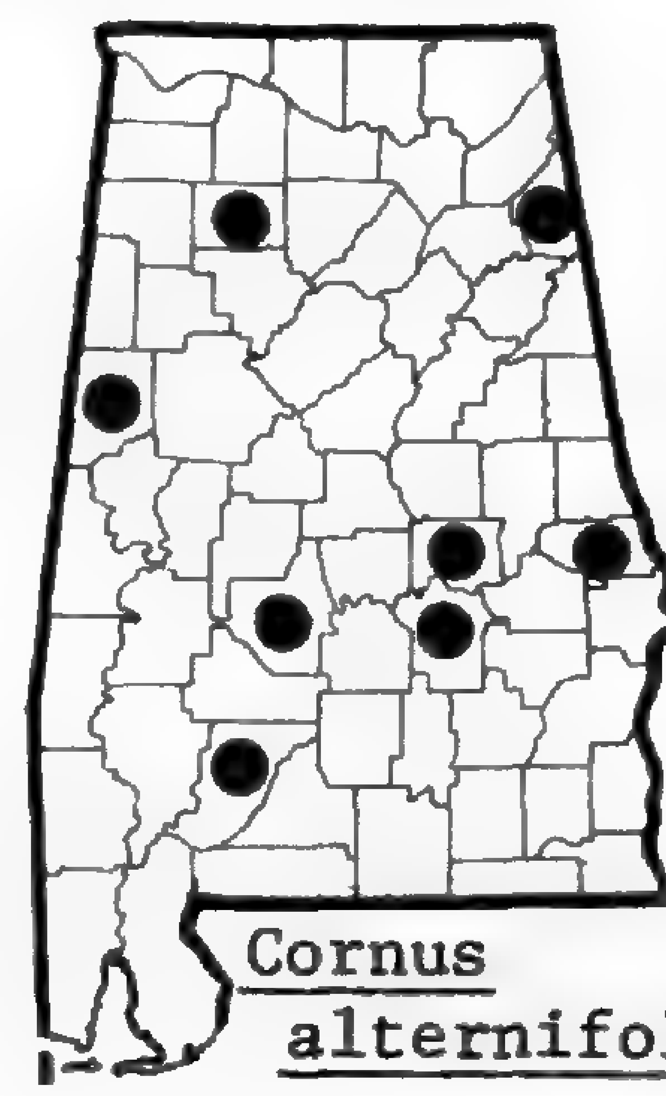
Nyssa aquatica

Nyssa ogeche

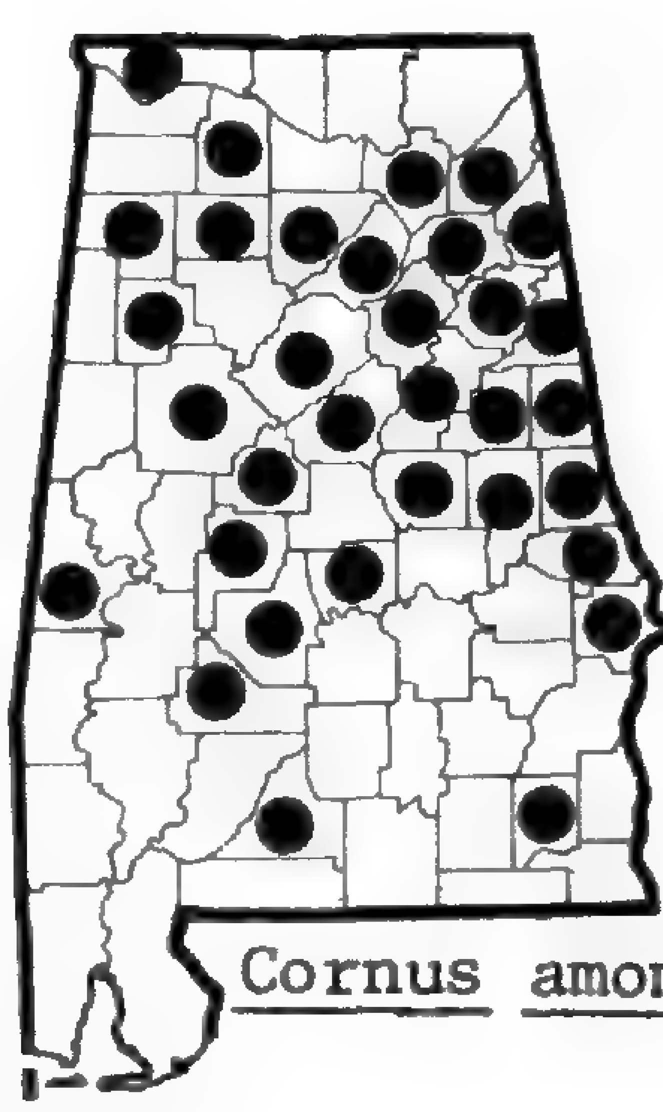


Nyssa sylvatica s. l.

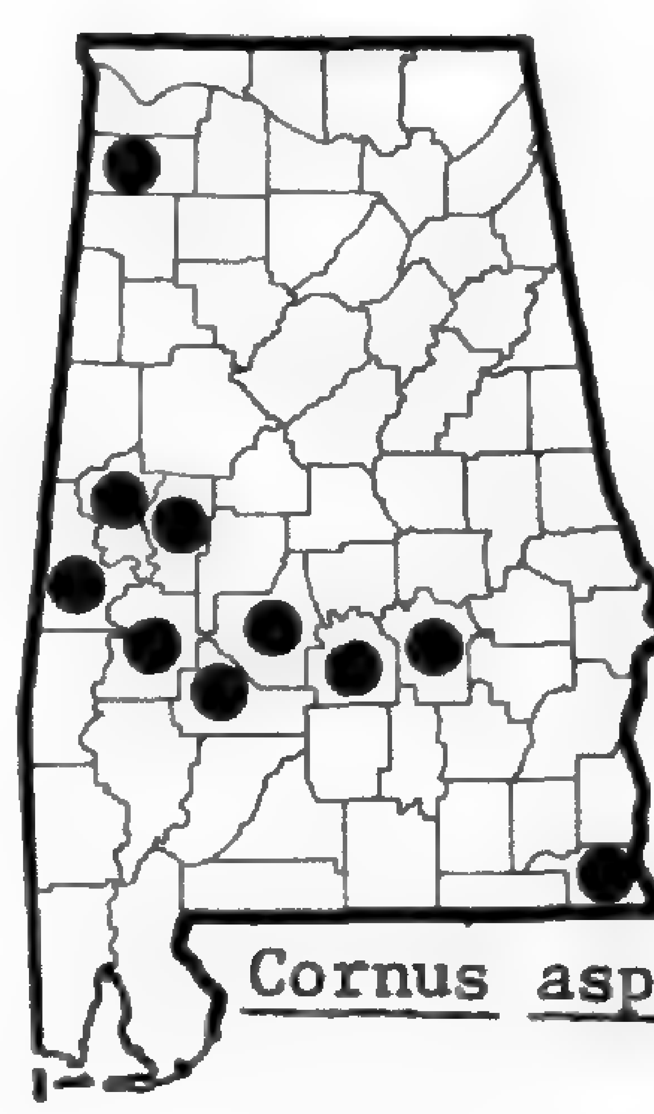
56. CORNACEAE



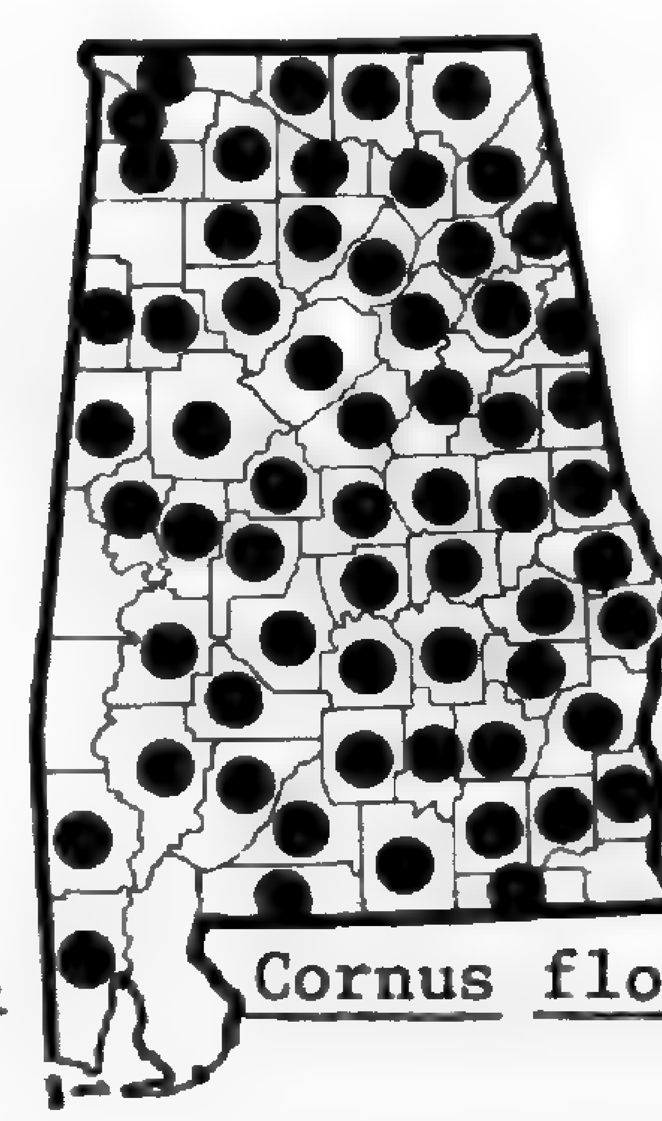
Cornus alternifolia



Cornus amomum



Cornus asperifolia



Cornus florida

lar plants, which are generally referred to *C. drummondii* C. A. Meyer, appear little different from Alabama plants.

4. *C. florida* L., Flowering D. Spring; late summer–fall. Woods, throughout. *Cynoxylon floridum* (L.) Raf.—S.

5. *C. stricta* Lamarck. Spring; summer. Ditches, low woods and swamps; throughout, but most common in CP. *Svida stricta* (Lam.) Sm.—S.

Cornus racemosa Lamarck has been credited to Alabama (Dean, 1961), but no specimens have been seen by the writer. This report should be questioned.

57. Clethraceae

1. *Clethra* L., White Alder, Sweet Pepperbush

1. *C. alnifolia* L. Summer; late summer–fall.

1. Leaves glabrous or glabrate beneath .... *C. alnifolia* var. *alnifolia*
1. Leaves densely tomentose beneath .... *C. alnifolia* var. *tomentosa*

C. alnifolia L. var. *alnifolia.* Low woods, rare; CP, CuP.

C. alnifolia L. var. *tomentosa* (Lamarck) Michaux. Swamp ecotones, bogs, seepages, low pinelands; principally southern CP. *C. tomentosa* Lam.—S.

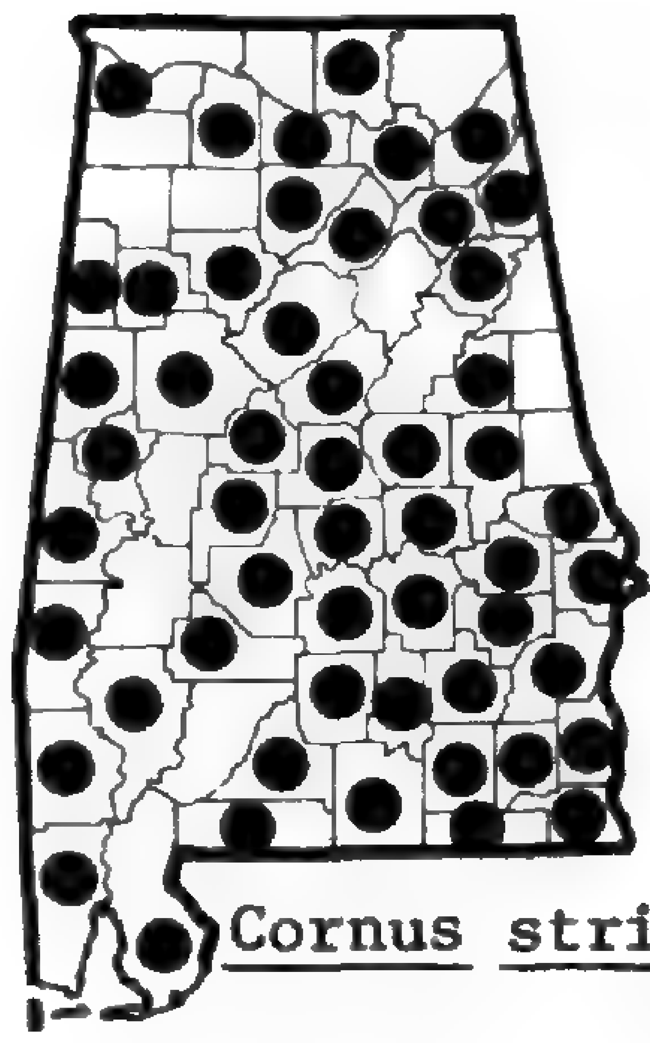
58. Empetraceae

1. *Ceratiola* Michaux, Rosemary

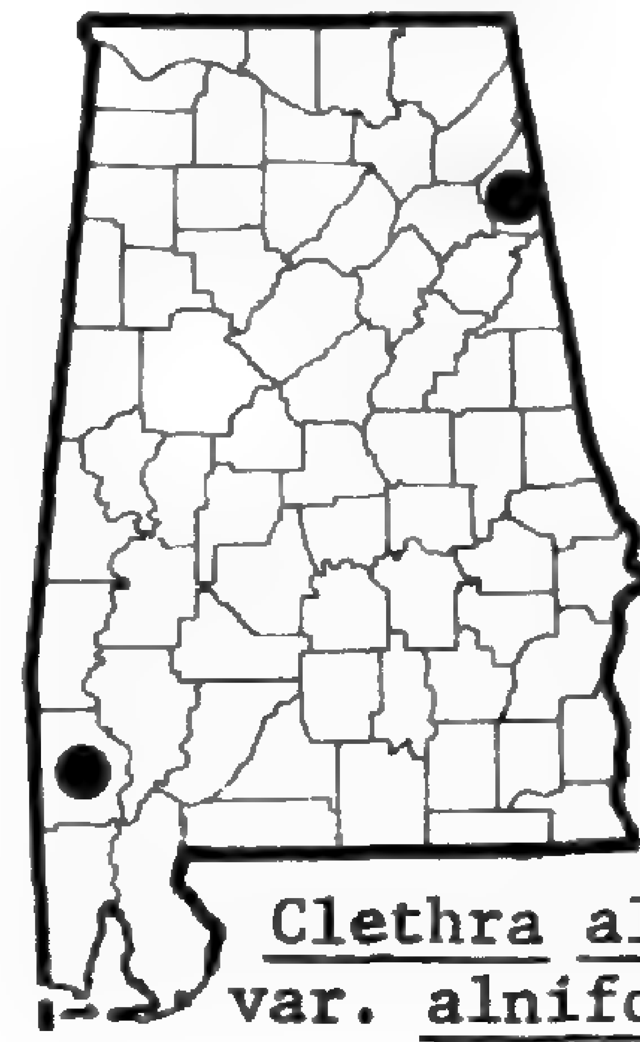
1. *C. ericoides* Michaux. Fall. Dunes, sandy woods, rare; OCP.

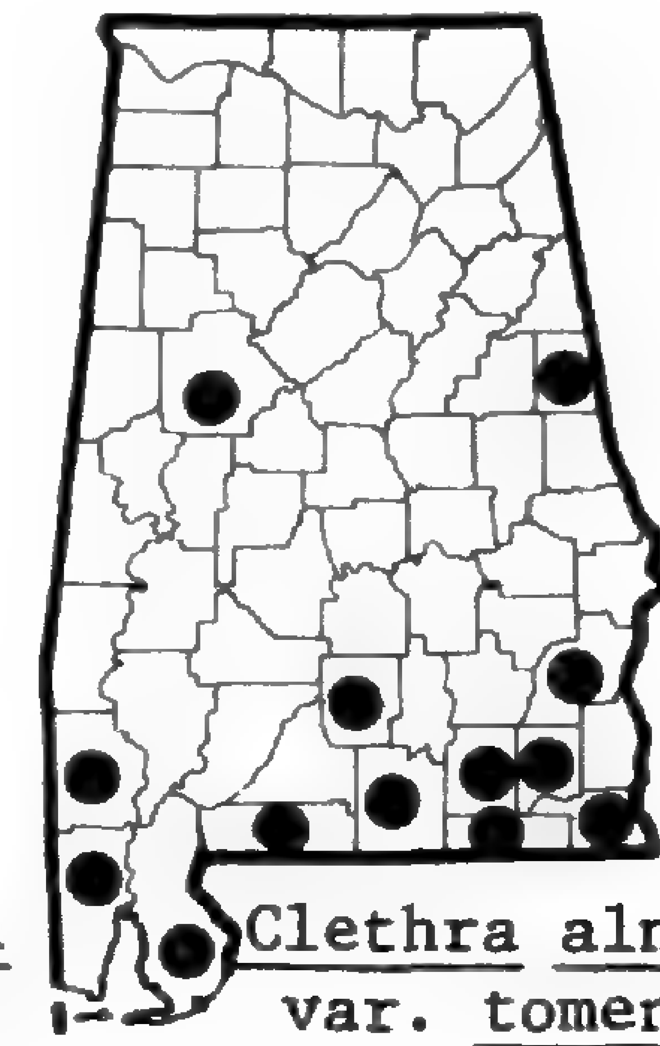
59. Ericaceae

1. Leaves variegated, evergreen .... 1. *Chimaphila*
1. Leaves green, not variegated; or leaves deciduous 2
  2. Ovary inferior 3
    3. Anthers spurred; ovules and seeds many .... 10. *Vaccinium*
    3. Anthers unappendaged; ovules and nutlets 10 .... 3. *Gaylussacia*
  2. Ovary superior 4
    4. Plant creeping 5
      5. Leaves distally toothed .... 8. *Pieris*
      5. Leaves entire .... 2. *Epigaea*
    4. Plant erect, ascending or arching 6
      6. Plant in flower 7
        7. Corolla urceolate or cylindrical 8
          8. Inflorescences axillary 9
            9. Leaves entire, often involute .... 6. *Lyonia*
            9. Leaves serrate, at least distally 10
              10. Pedicels more than 3 mm long; corolla urceolate; leaves obtuse to acute .... 8. *Pieris*
              10. Pedicels less than 2 mm long; corolla cylindrical; leaves usually acuminate .... 5. *Leucothoe*
          8. Inflorescences terminal on branches or main stems 11
            11. Ovary pubescent 12
              12. Corolla pubescent exteriorly, more than 5 mm long .... 7. *Oxydendrum*
              12. Corolla glabrous exteriorly, less than 5 mm long .... 6. *Lyonia*
            11. Ovary glabrous 13
              13. Leaves evergreen .... 8. *Pieris*
              13. Leaves deciduous .... 5. *Leucothoe*


Cornus stricta

57. CLETHRACEAE

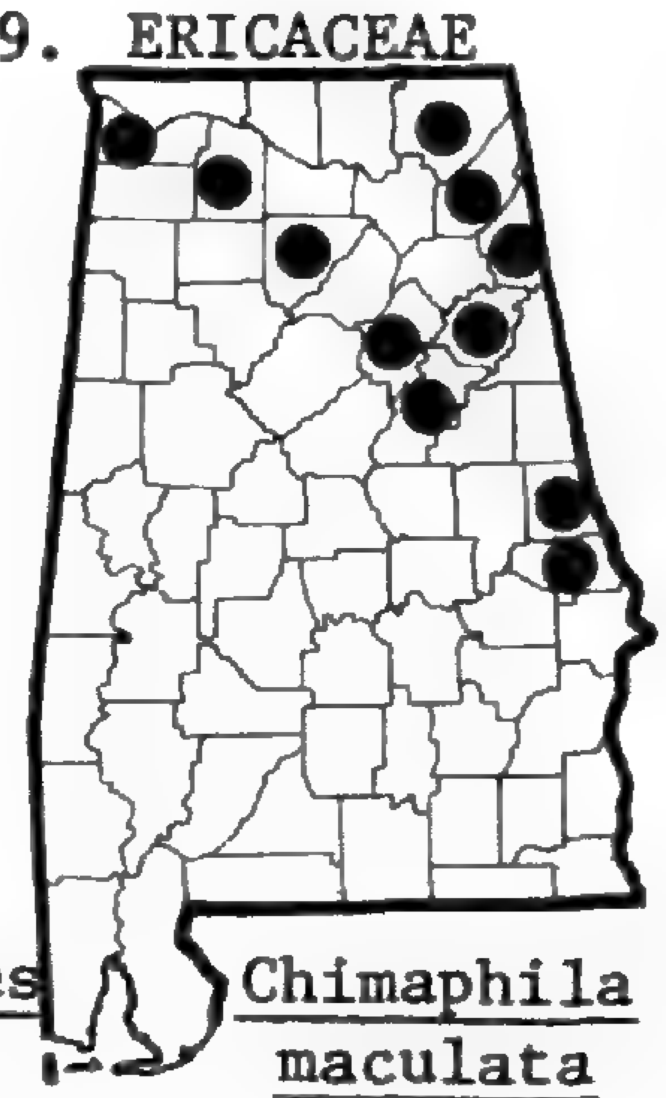

Clethra alnifolia var. alnifolia

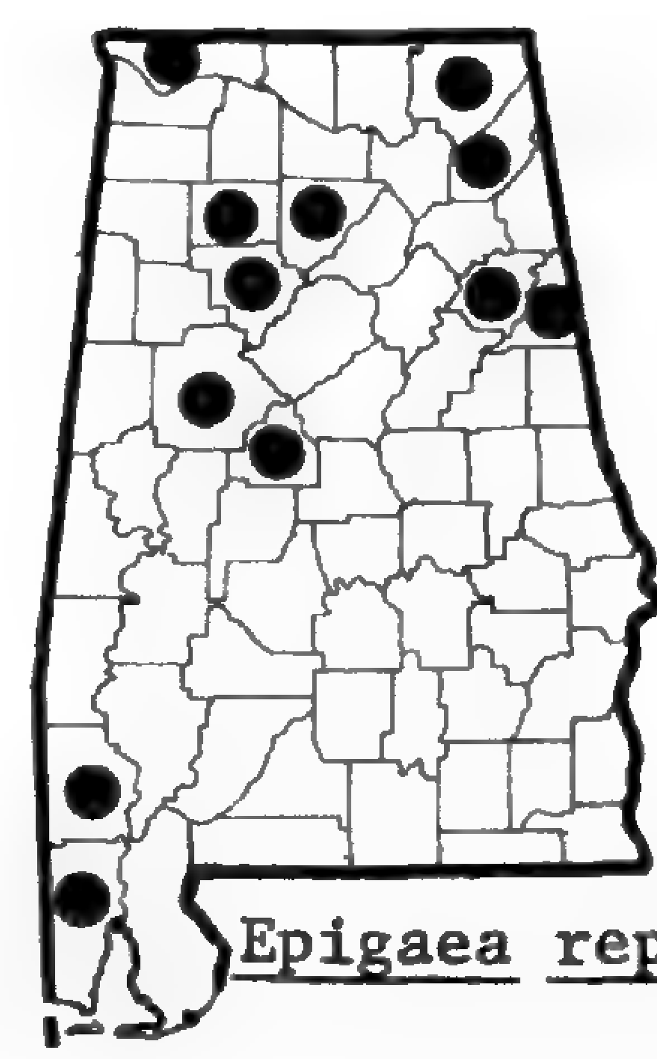

Clethra alnifolia var. tomentosa

58. EMPETRACEAE

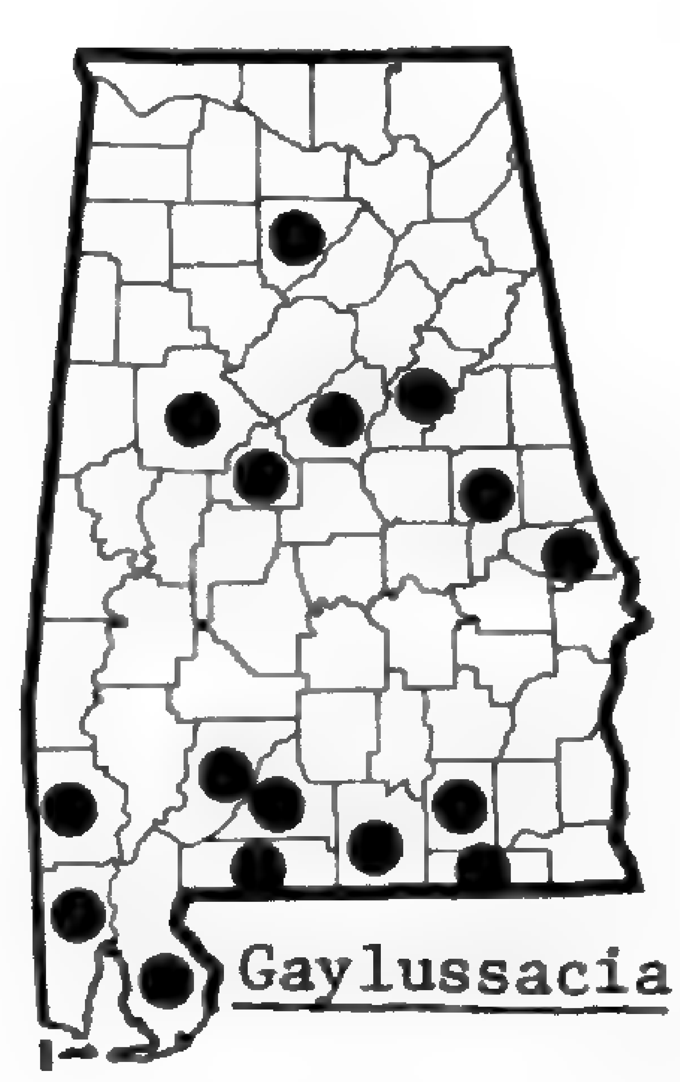

Ceratiola ericoides

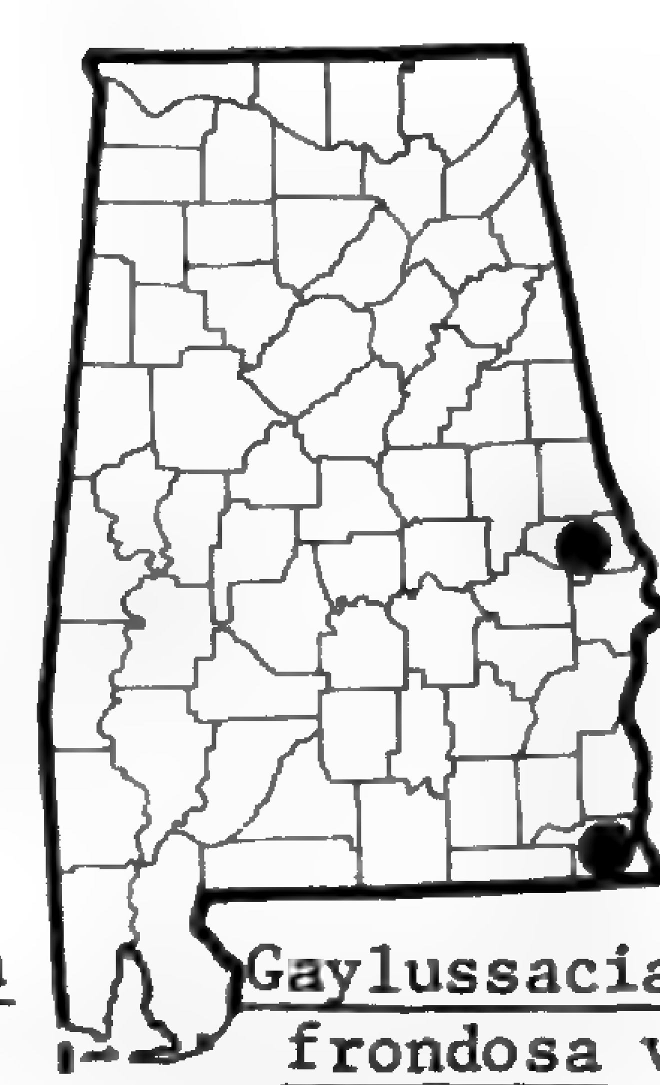
59. ERICACEAE


Chimaphila maculata


Epigaea repens


Gaylussacia baccata


Gaylussacia dumosa


Gaylussacia frondosa var. frondosa

7. Corolla campanulate, funnelform or tubular, the lobes often widely spreading distally 14
14. Corolla campanulate; anthers in corolla pouches .... 4. *Kalmia*
14. Corolla funnelform or tubular proximally, its lobes widely spreading distally, corolla lacking anther pouches .... 9. *Rhododendron*
6. Plant in fruit 15
15. Leaves entire 16
16. Capsule cylindrical, longer than broad, more than 8 mm long .... 9. *Rhododendron*
16. Capsule subglobose, broader than long, less than 6 mm long 17
17. Capsule glabrous, with longitudinal light-colored stripes along the suture lines .... 6. *Lyonia*
17. Capsule pubescent or stipitate-glandular, not longitudinally striped .... 4. *Kalmia*
15. Leaves serrate, at least distally 18
18. Capsule pubescent 19
19. Capsule subcylindric, about 2 times longer than broad, not longitudinally striped .... 7. *Oxydendrum*
19. Capsule subglobose, broader than long, with longitudinal light-colored stripes along the suture lines .... 6. *Lyonia*
18. Capsule glabrous 20
20. Inflorescences terminal on branches; leaves deciduous .... 5. *Leucothoe*
20. Inflorescences axillary; leaves evergreen 20
21. Leaves obtuse to acute .... 8. *Pieris*
21. Leaves, at least most, acuminate .... 5. *Leucothoe*

1. *Chimaphila* Pursh, PIPSISSEWA

1. *C. maculata* (L.) Pursh, SPOTTED WINTERGREEN. Spring; summer–fall. Rich and upland woods; CuP, VR.

2. *Epigaea* L., TRAILING ARBUTUS

1. *E. repens* L. Spring. Open, rocky woods, infrequent to rare; AM, CuP, VR.

3. *Gaylussacia* HBK, HUCKLEBERRY

1. Bracts of raceme longer than pedicels, persisting until fruits mature .... 2. *G. dumosa*
1. Bracts of raceme shorter than pedicels, soon deciduous 2
2. Leaves glandular on both surfaces 3
3. Branchlets, inflorescences and fruits stipitate-glandular .... 4. *G. mosieri*
3. Branchlets, inflorescences and fruits not stipitate-glandular .... 1. *G. baccata*
2. Leaves glandular only beneath .... 3. *G. frondosa*

1. *G. baccata* (Wang.) K. Koch. Credited to Alabama by Ahles in RAB; no specimens seen by the writer. *Decachaena baccata* (Wang.) Sm.—S.

2. *G. dumosa* (Andrz.) Torrey & Gray, GOPHER-BERRY. Spring; summer–fall. Sandy woods or open ground, infrequent; OCP, CP, VR. *Lasiococcus dumosus* (Andr.) Sm.—S.

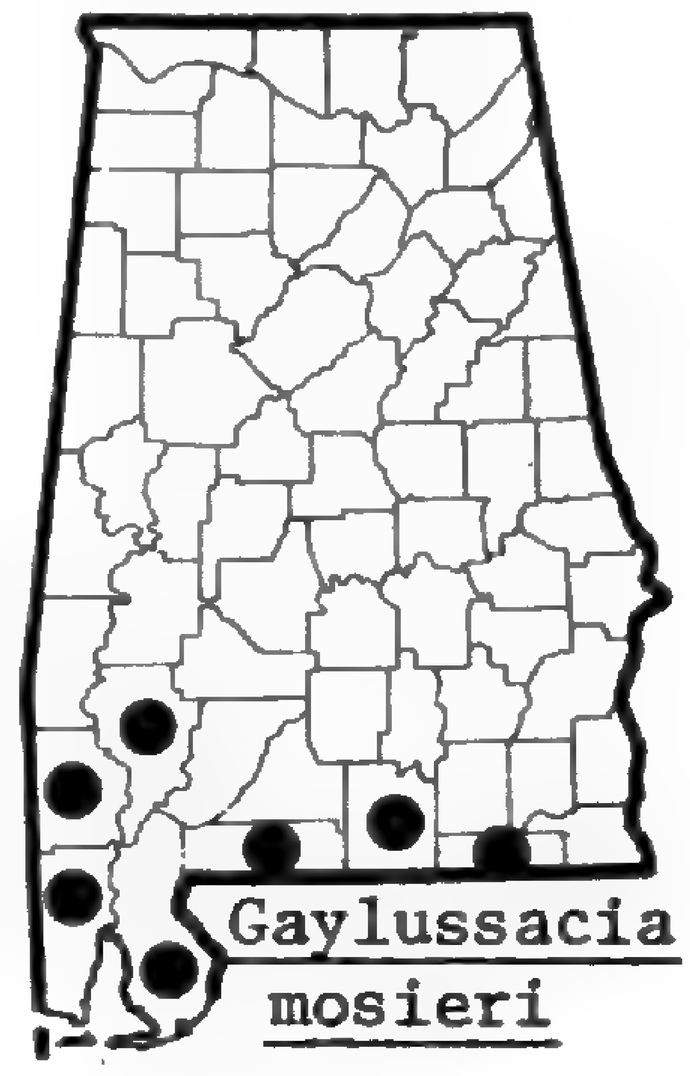
3. *G. frondosa* (L.) Torrey & Gray. Spring; summer.

1. Corolla about 4 mm long; sepals ⅓ or less as long as corolla tube 2
2. Leaves glabrate to puberulent beneath .... *G. frondosa* var. *frondosa*
2. Leaves densely pubescent beneath .... *G. frondosa* var. *tomentosa*
1. Corolla about 3 mm long; sepals more than ⅓ the length of corolla tube .... *G. frondosa* var. *nana*

G. frondosa (L.) Torrey & Gray var. *frondosa*. Low, open woods, rare; OCP, P. *Decachaena frondosa* (L.) T & G.—S.

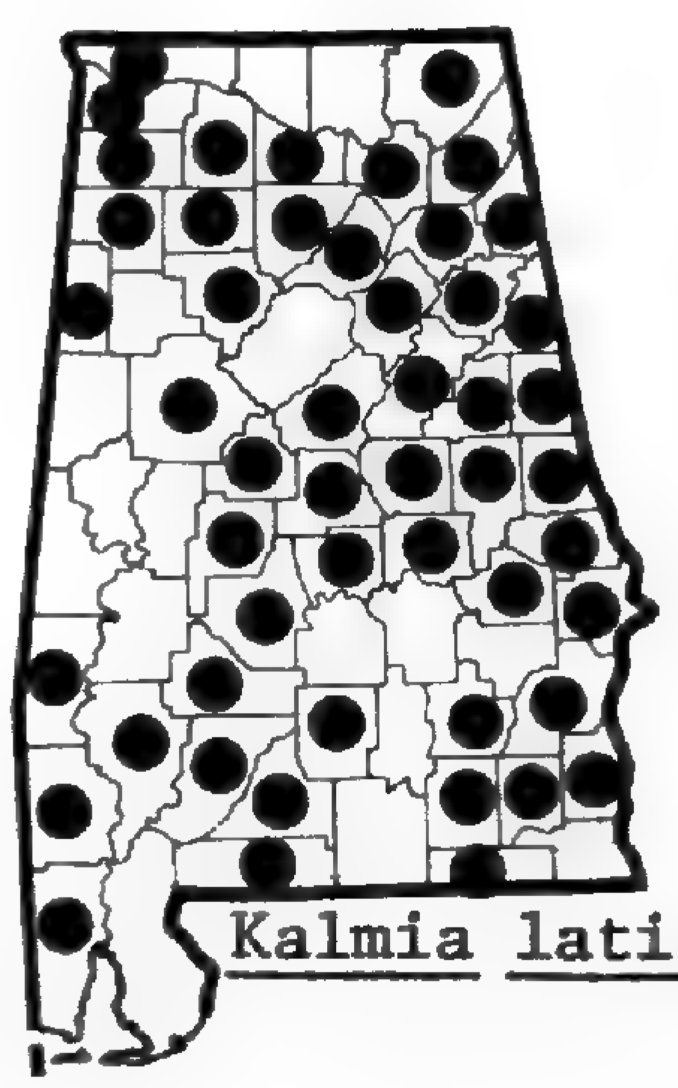
Gaylussacia frondosa var. nana

Gaylussacia frondosa var. tomentosa

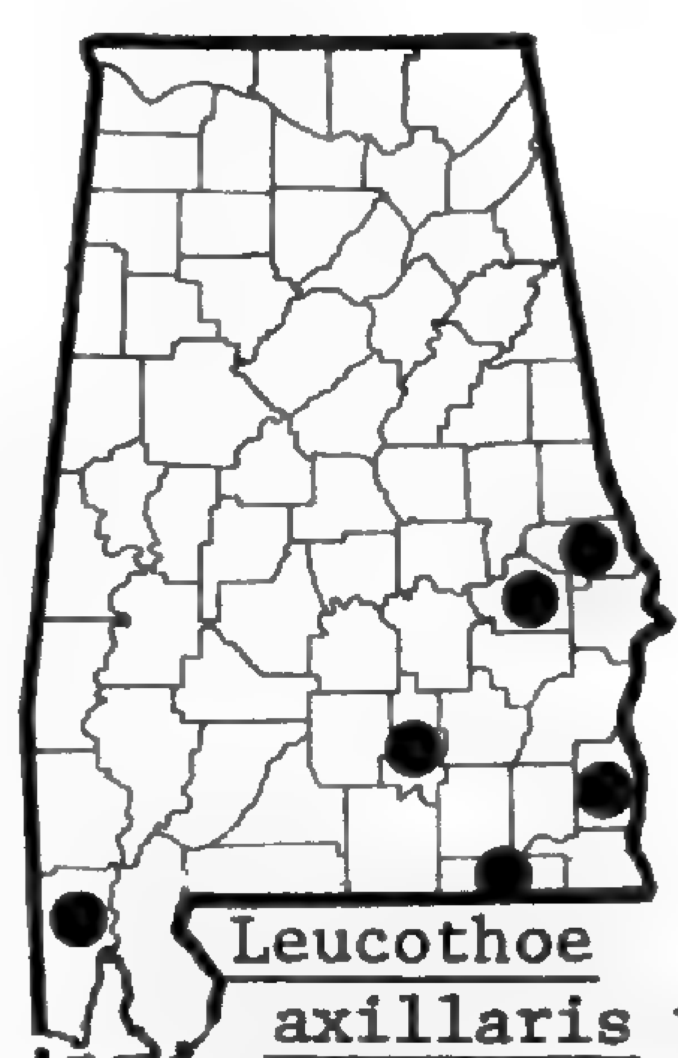


Gaylussacia mosieri

Kalmia hirsuta

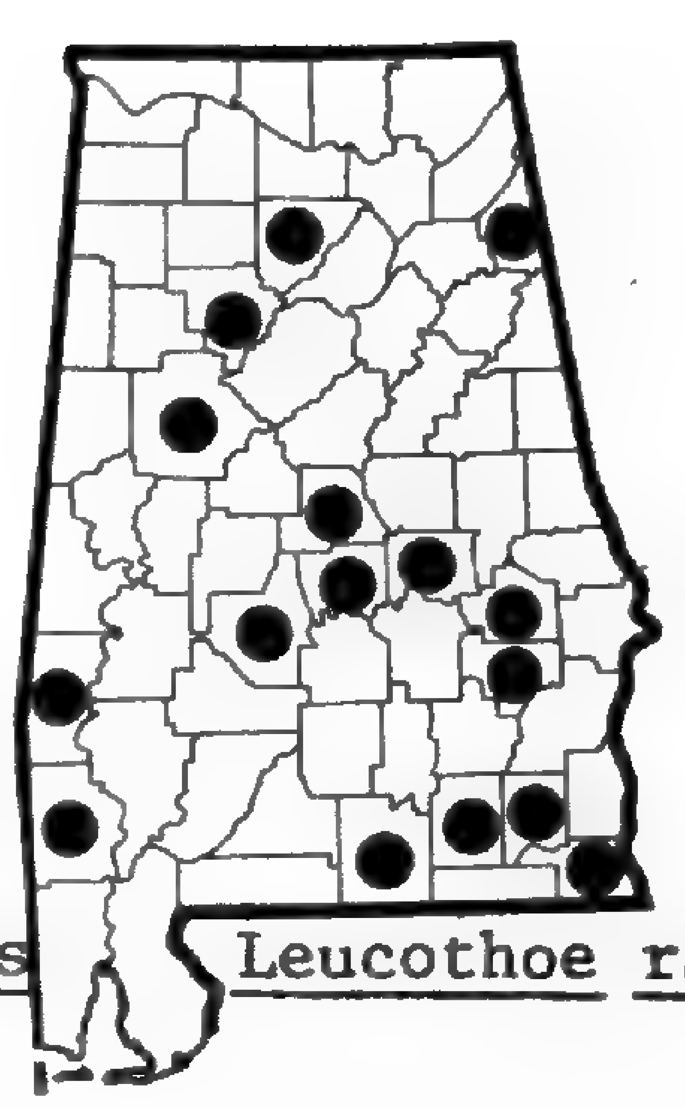


Kalmia latifolia

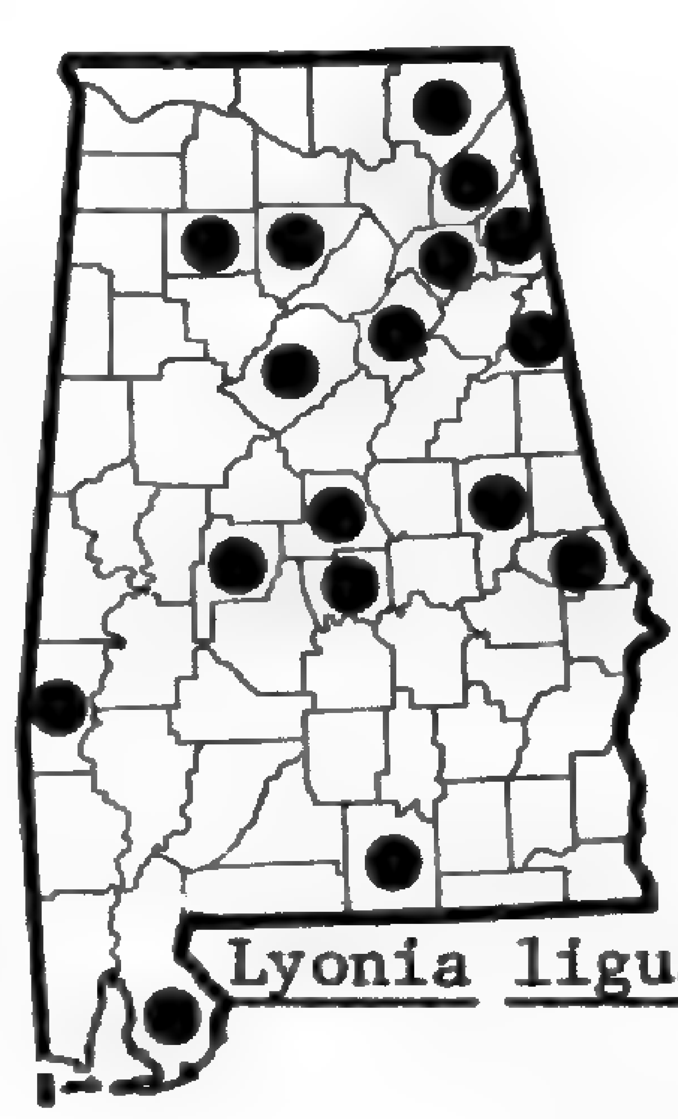


Leucothoe axillaris var. axillaris

Leucothoe axillaris var. editorum



Leucothoe racemosa



Lyonia ligustrina

G. frondosa (L.) Torrey & Gray var. *nana* Gray. Sandy ground; OCP. *Decachaena nana* (Gray) Sm.—S.

G. frondosa (L.) Torrey & Gray var. *tomentosa* Gray. Reported by Ahles in RAB; no specimens seen by the writer. *Decachaena tomentosa* (Pursh) Sm.—S.

4. *G. mosieri* Small. Spring; summer. Creek swamps, rare; OCP. *Lasiococcus mosieri* Sm.—S.

4. *Kalmia* L.

1. Twigs hirsute .... 1. *K. hirsuta*
1. Twigs glabrous .... 2. *K. latifolia*

1. *K. hirsuta* Walter, Wicky. Late spring–early summer; late summer–fall. Low pinelands, rare, OCP. *Kalmiella hirsuta* (Walt.) Sm.—S.

2. *K. latifolia* L., Mountain Laurel. Spring; summer–fall. Rocky or rich woods; throughout, but more common northward.

5. *Leucothoe* D. Don

1. Leaves evergreen; inflorescences axillary .... 1. *L. axillaris*
1. Leaves deciduous; inflorescences terminal .... 2. *L. racemosa*

1. *L. axillaris* (Lamarck) D. Don. Spring; late summer–fall.

1. Petioles 8 mm or less long; leaves acute to abruptly acuminate .... *L. axillaris* var. *axillaris*
1. Petioles 8 mm long or longer; leaves acuminate .... *L. axillaris* var. *editorum*

L. axillaris (Lam.) D. Don var. *axillaris*. Swamp forests, seepages, rare; CP. *L. catesbaei* (Walt.) Gray—S.

L. axillaris (Lam.) D. Don var. *editorum* (Fernald & Schubert) Ahles. Mesic woods, rare; AM.

2. *L. racemosa* (L.) Gray. Spring; late summer–fall. Bogs, seepages, ditches, pond margins; CP, CuP. *Eubotrys racemosa* (L.) Nutt.—S.

6. *Lyonia* Nuttall

1. Leaves deciduous; corolla globose; capsule 4.5 mm or less long .... 1. *L. ligustrina*
1. Leaves evergreen; corolla subcylindrical; capsule more than 4.5 mm long .... 2. *L. lucida*

1. *L. ligustrina* (L.) DC. Spring; late summer–fall. Bogs, seepages, pond margins, infrequent; CP, P, AM, VR, CuP. *Xolisma ligustrina* (L.) Britt., *X. ligustrina foliosiflora* (Michx.) Mohr—M; *Cholisma ligustrina* (L.) Britt.—H; *Arsenococcus ligustrinus* (L.) Sm.—S.

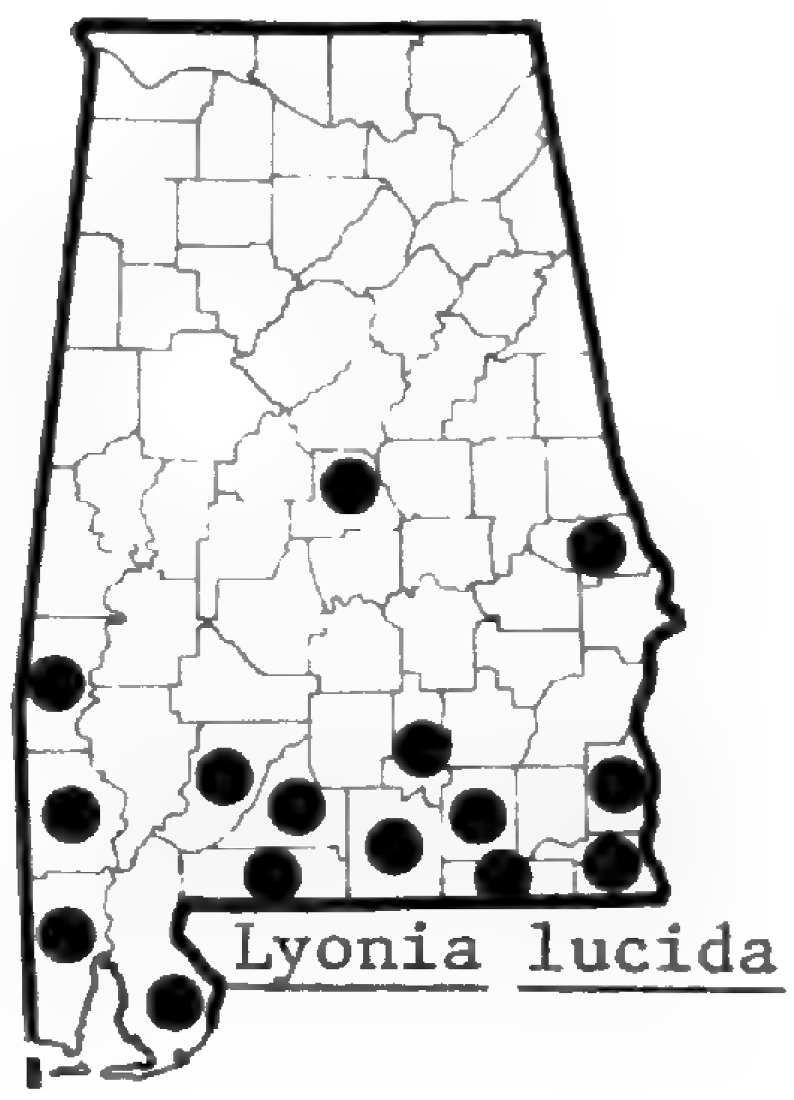
2. *L. lucida* (Lamarck) K. Koch. Spring; late summer–fall. Low woods, low pinelands, creek swamps; chiefly southern CP, but rare in southern P and AM. *Pieris nitida* (Bartr.) B. & H.—M, H; *Desmothamnus lucidus* (Lam.) Sm.—S.

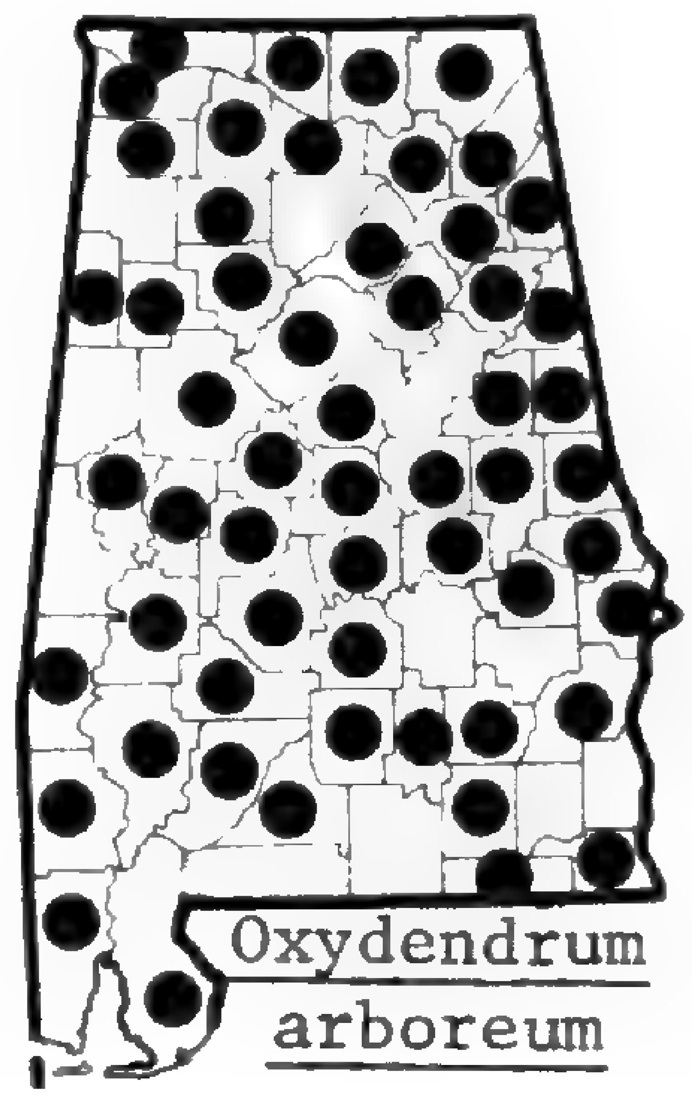
7. *Oxydendrum* DC., Sourwood

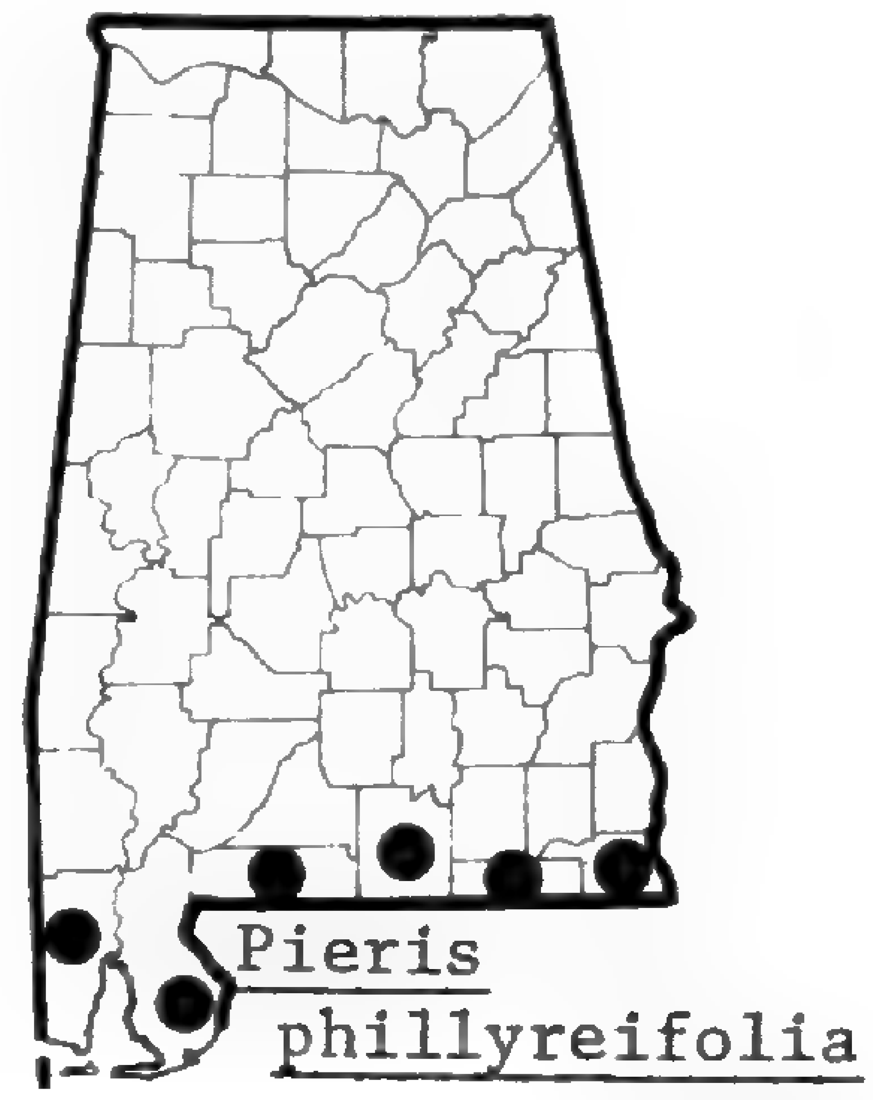
1. *O. arboreum* (L.) DC. Late spring–summer; late summer–fall. Upland woods; throughout.

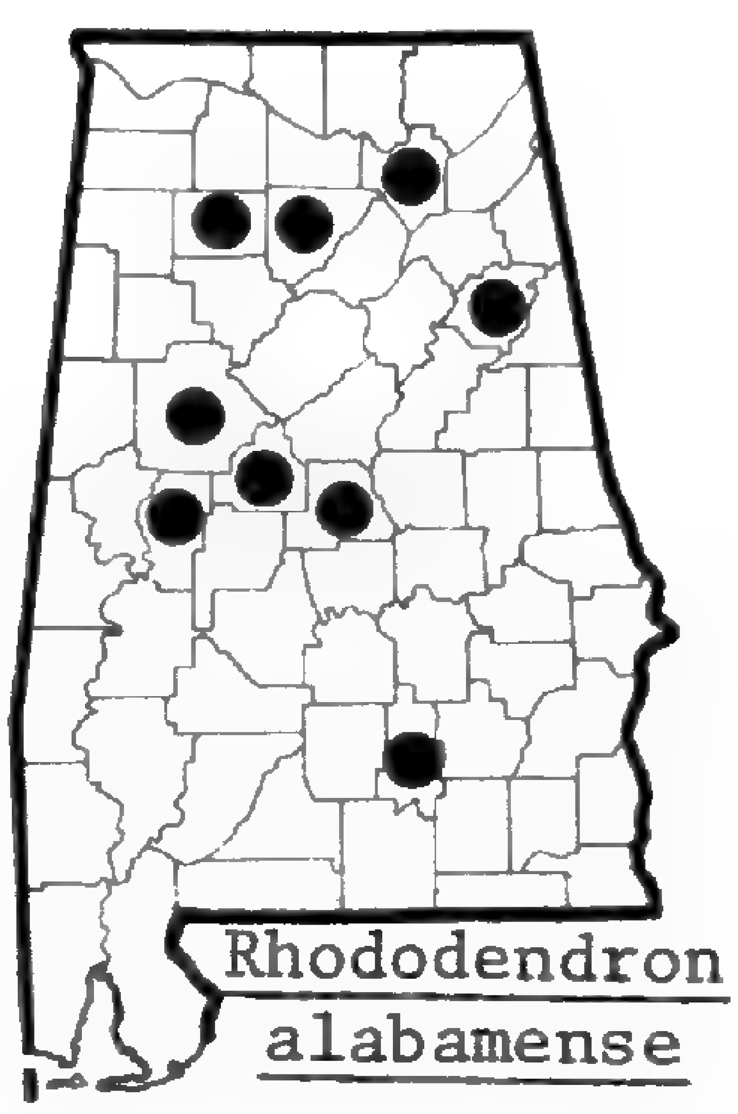
8. *Pieris* D. Don

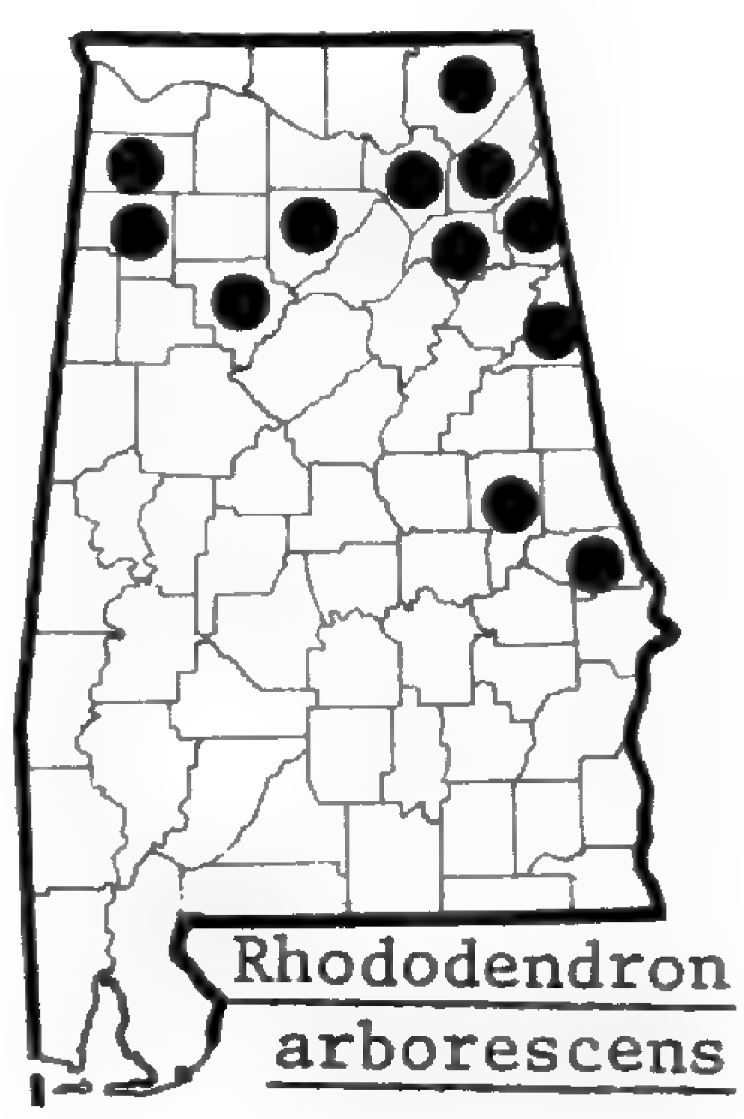
1. *P. phillyreifolia* (Hooker) DC. Late winter–spring; summer–fall. Ponds, swamp margins, infrequent; OCP.

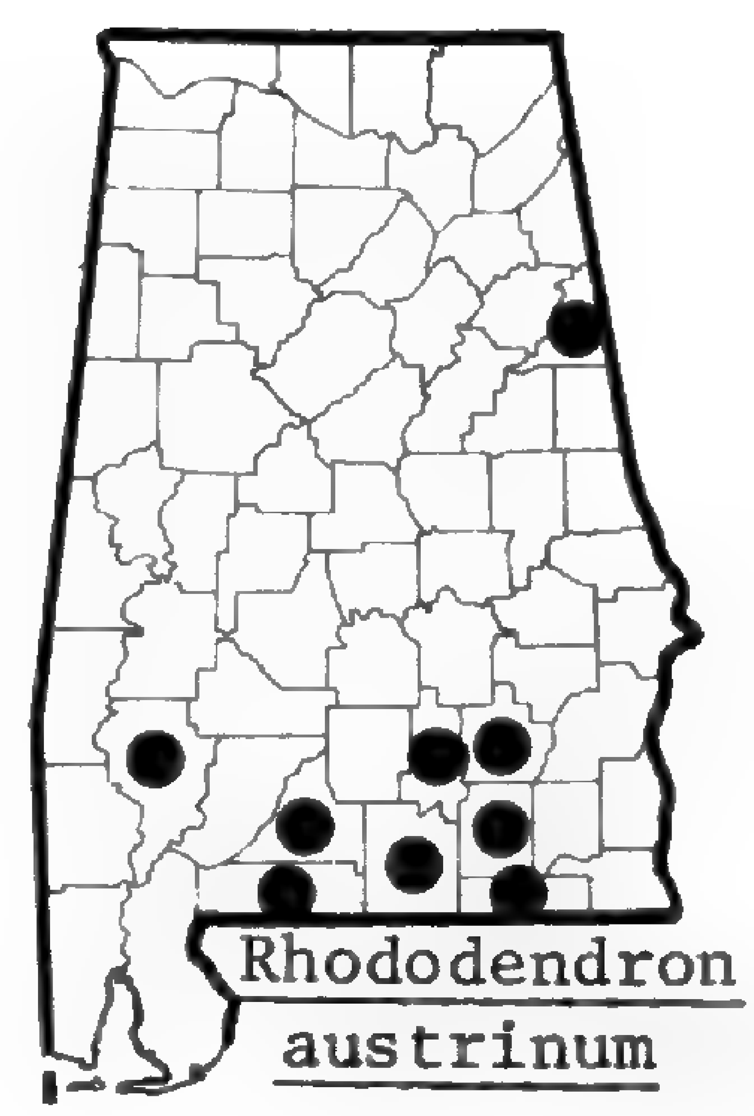

Lyonia lucida

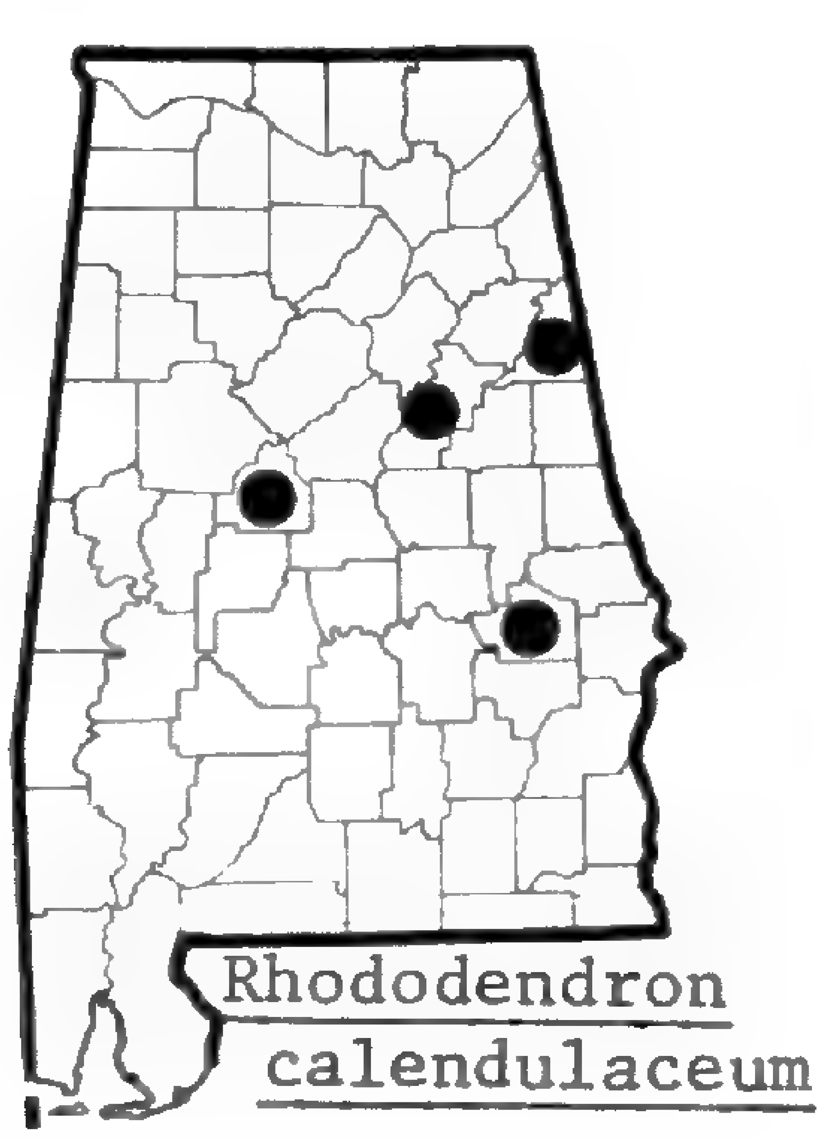

Oxydendrum arboreum

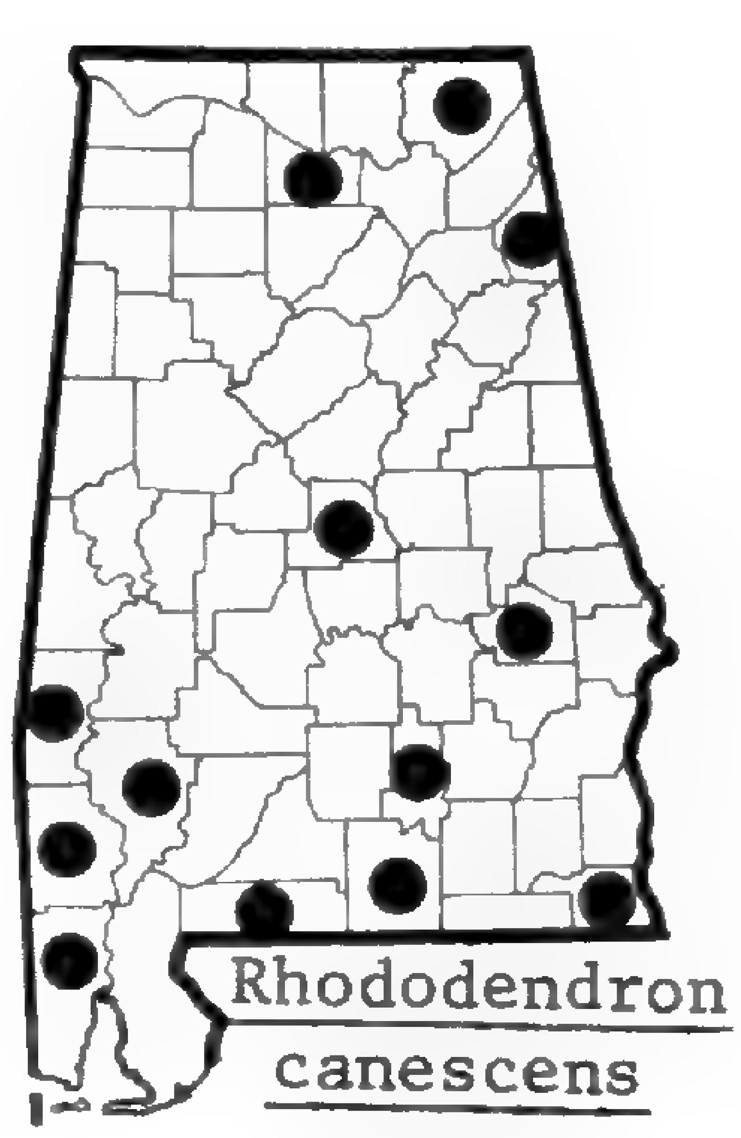

Pieris phillyreifolia

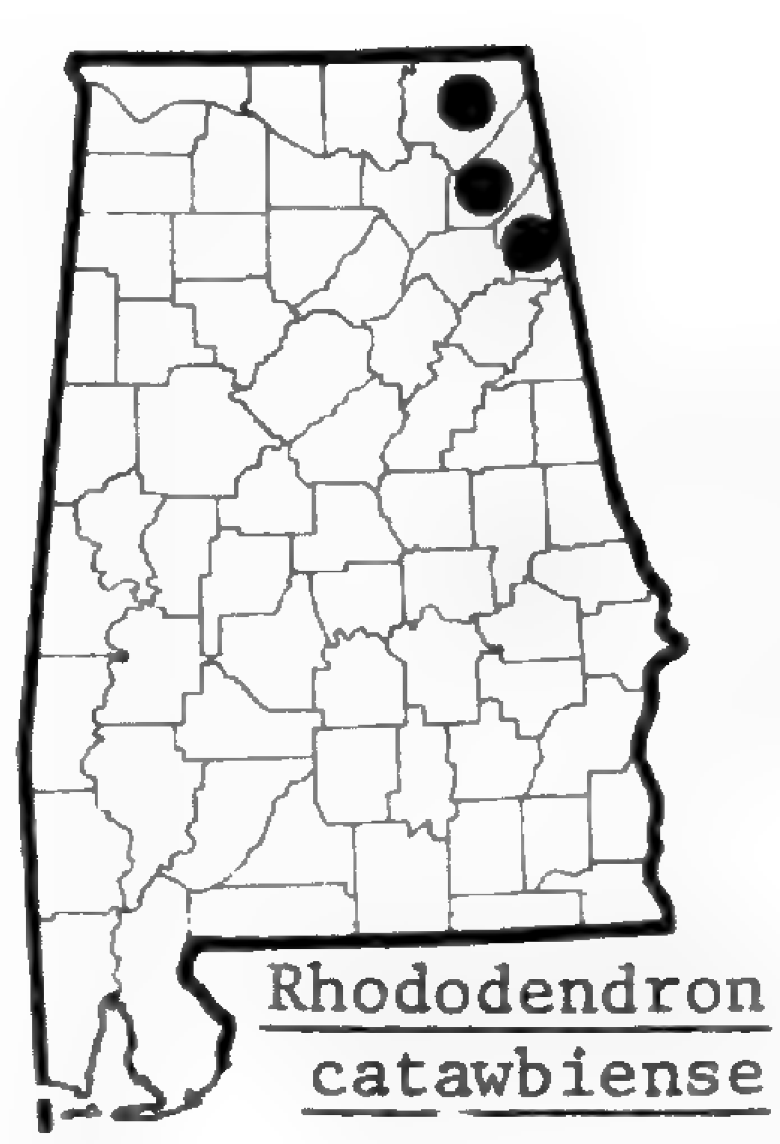

Rhododendron alabamense


Rhododendron arborescens


Rhododendron austrinum


Rhododendron calendulaceum


Rhododendron canescens


Rhododendron catawbiense

9. *Rhododendron* L.

1. Leaves evergreen, entire; stamens 10 2
  2. Leaves punctate beneath .... 8. *R. minus*
  2. Leaves not punctate beneath .... 6. *R. catawbiense*
1. Leaves deciduous, serrulate or ciliate; stamens 5–7 3
  3. Twigs glandular or glabrous 4
    4. Twigs glandular 5
      5. Mature bud scales pubescent abaxially .... 3. *R. austrinum*
      5. Mature bud scales glabrous abaxially .... 11. *R. viscosum*
    4. Twigs glabrous .... 2. *R. arborescens*
  3. Twigs eglandular, pubescent 6
    6. Corolla tube eglandular, capsule not canescent 7
      7. Leaves canescent above, at least along the midvein .... 7. *R. flammeum*
      7. Leaves not canescent above .... 10. *R. prunifolium*
    6. Corolla tube glandular; capsule canescent, at least basally 8
      8. Leaves not pubescent beneath 9
        9. Pedicels and calyces eglandular .... 9. *R. periclymenoides*
        9. Pedicels and calyces glandular .... 11. *R. viscosum*
      8. Leaves pubescent beneath 10
        10. Pedicels and calyces eglandular 11
          11. Corollas red, orange, or yellow .... 7. *R. flammeum*
          11. Corollas pink or white 12
            12. Leaves strigose or hirsute beneath, at least along the midveins .... 9. *R. periclymenoides*
            12. Leaves canescent beneath, midveins not strigose or hirsute .... 5. *R. canescens*
        10. Pedicels or calyces glandular 13
          13. Mature bud scales pubescent abaxially 14
            14. Corollas orange, red or yellow; pedicels and capsules not hoary 15
              15. Canescence on upper sides of leaves confined to midveins .... 4. *R. calendulaceum*
              15. Canescence on upper sides of leaves distributed over the surfaces and veins .... 1. *R. alabamense*
            14. Corollas pink or white; pedicels and capsules hoary 5. *R. canescens*
          13. Mature bud scales not pubescent abaxially 16
            16. Leaves canescent above, at least along the midvein 17
              17. Canescence on upper surfaces of leaves confined to midveins .... 4. *R. calendulaceum*
              17. Canescence on upper sides of leaves distributed over the surfaces and midveins .... 1. *R. alabamense*
            16. Leaves glabrous above, even along the midveins .... 11. *R. viscosum*

1. *R. alabamense* Rehder, Azalea. Spring; summer–fall. Upland woods; rare; CP, CuP, VR. *Azalea alabamensis* (Rehd.) Sm.—S.

2. *R. arborescens* (Pursh) Torrey, Azalea. Spring–early summer; summer–fall. Streambanks, seepages; P, CuP. *Azalea arborescens* Pursh—M, H, S.

3. *R. austrinum* Rehder, Azalea. Summer; fall. Rich woods, infrequent; CP, AM. *Azalea austrina* Sm.—S.—Very showy.

4. *R. calendulaceum* (Michaux) Torrey, Flame Azalea. Spring; summer. Rocky woods, rare; P, AM. *Azalea calendulacea* Michx.—S.

5. *R. canescens* (Michx) Sweet, Azalea. Spring; summer. Moist woods, infrequent; CP, CuP. *Azalea canescens* Michx.—S.

6. *R. catawbiense* Michaux, Pink Rhododendron, Rosebay. Spring; summer–fall. Rocky woods; CuP.

7. *R. flammeum* (Michaux) Sargent, FLAME AZALEA. Spring; summer–fall. Rocky woods, local; AM. *Azalea speciosa* Willd.—S.—Very showy.

8. *R. minus* Michaux. Spring; summer–fall. Mesic, rocky woods, infrequent; AM, CP. *R. punctatum* Andr.—H; *R. carolinianum* Rehd.—S.

9. *R. periclymenoides* (Michaux) Shinners, AZALEA. Spring; summer–fall. Upland woods and seepages; throughout. *Azalea nudiflora* L.—M, H, S; *A. lutea* L.—H; *R. nudiflorum* (L.) Torr.—RAB.

10. *R. prunifolium* Millais, AZALEA. Spring. Reported from rich woods of southeastern CP. *Azalea prunifolia* Sm.—H, S.

11. *R. viscosum* (L.) Torrey var. *serrulatum* (Small) Ahles, AZALEA. Summer; summer–fall. Low ground, rare; CP. *Azalea viscosa* L.—M, H, S; *A. viscosa glauca* (Lam.) Michx.—M.

10. *Vaccinium* L., BLUEBERRY

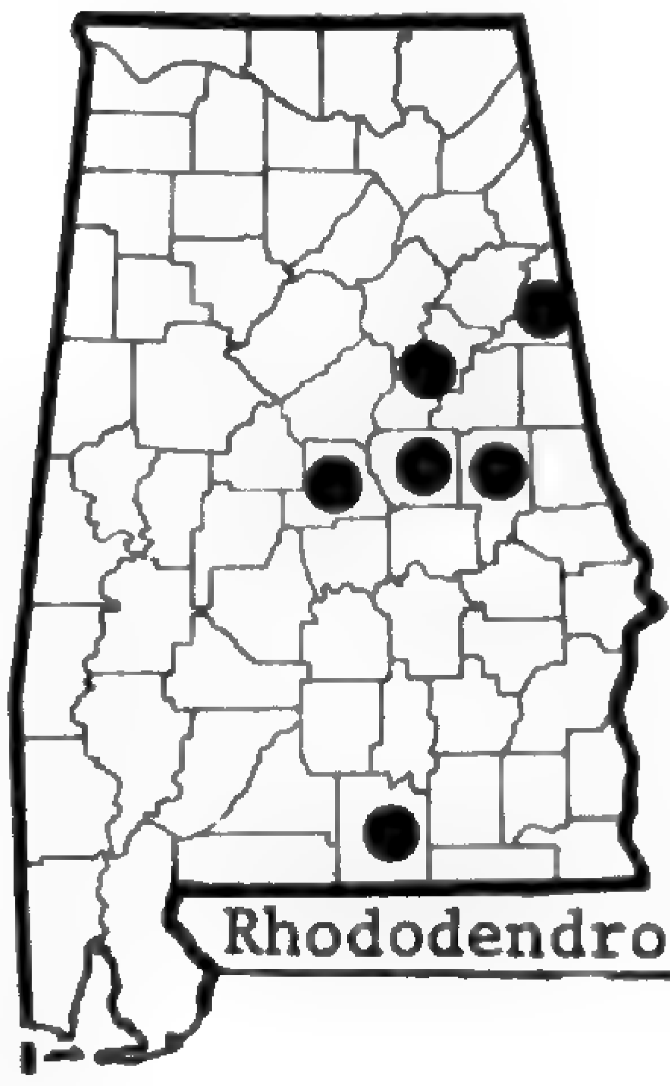
1. Plant in flower 2
  2. Stamens exerted beyond the corolla 3
    3. Corolla lobes 4 .... 8. *V. erythrocarpum*
    3. Corolla lobes 5 .... 12. *V. stamineum*
  2. Stamens included within the corolla 4
    4. Corolla campanulate .... 2. *V. arboreum*
    4. Corolla urceolate .... KEY 1
1. Plant in fruit 5
  5. Bracts leaf-like 6
    6. Leaf margins regularly serrulate .... 8. *V. erythrocarpum*
    6. Leaf margins not serrulate, sometimes remotely glandular 7
      7. Pedicels glabrous .... 2. *V. arboreum*
      7. Pedicels pubescent 8
        8. Distal half of pedicel woolly-pubescent; fruit green to purplish, sometimes pubescent .... 12. *V. stamineum*
        8. Distal half of pedicel glabrate, remotely pubescent; fruit black, glabrous .... 2. *V. arboreum*
  5. Bracts scale-like .... KEY 1

KEY 1

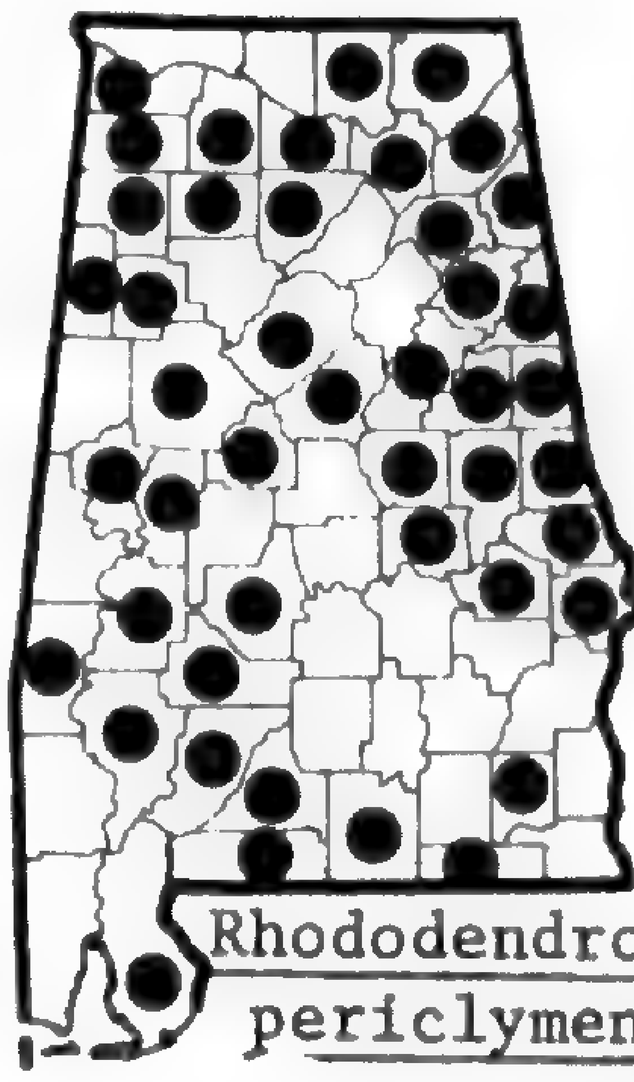
(Adapted from Camp, 1942)

1. Leaves evergreen 2
  2. Plant 1 m or less tall 3
    3. Leaves glandular .... 10. *V. myrsinites*
    3. Leaves eglandular .... 6. *V. darrowii*
  2. Plant 1.5 m tall or taller 4
    4. Leaves glandular .... 3. *V. ashei*
    4. Leaves eglandular .... 9. *V. fuscatum*
1. Leaves deciduous 5
  5. Leaves minutely stipitate-glandular beneath 6
    6. Glands abundant and conspicuous; leaves spatulate to oblanceolate .... 1. *V. amoenum*
    6. Glands sparse, inconspicuous; leaves broadly oblanceolate to elliptic .... 3. *V. ashei*
  5. Leaves eglandular beneath 7
    7. Leaves serrate 8
      8. Leaves averaging 3 cm or less long .... 7. *V. elliottii*
      8. Leaves averaging more than 3 cm long 9
        9. Plant 1 m or less tall .... 11. *V. pallidum*
        9. Plant 1.5 m tall or taller 10
          10. Twigs glabrous .... 5. *V. corymbosum*
          10. Twigs pubescent .... 4. *V. atrococcum*
    7. Leaves entire 11

Rhododendron flammeum

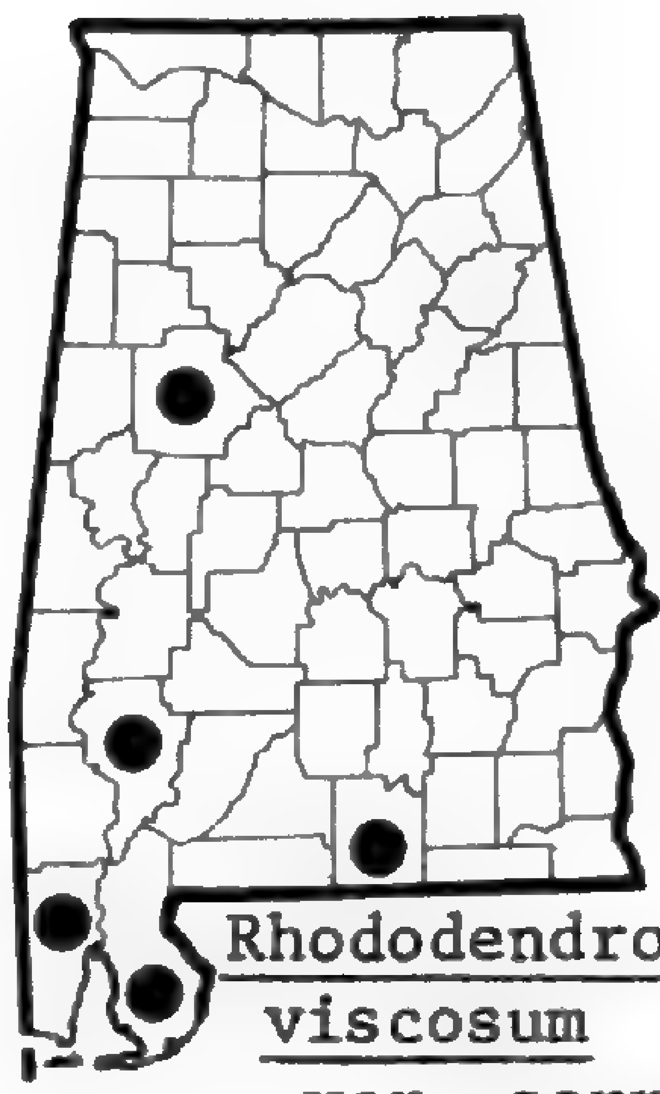


Rhododendron minus

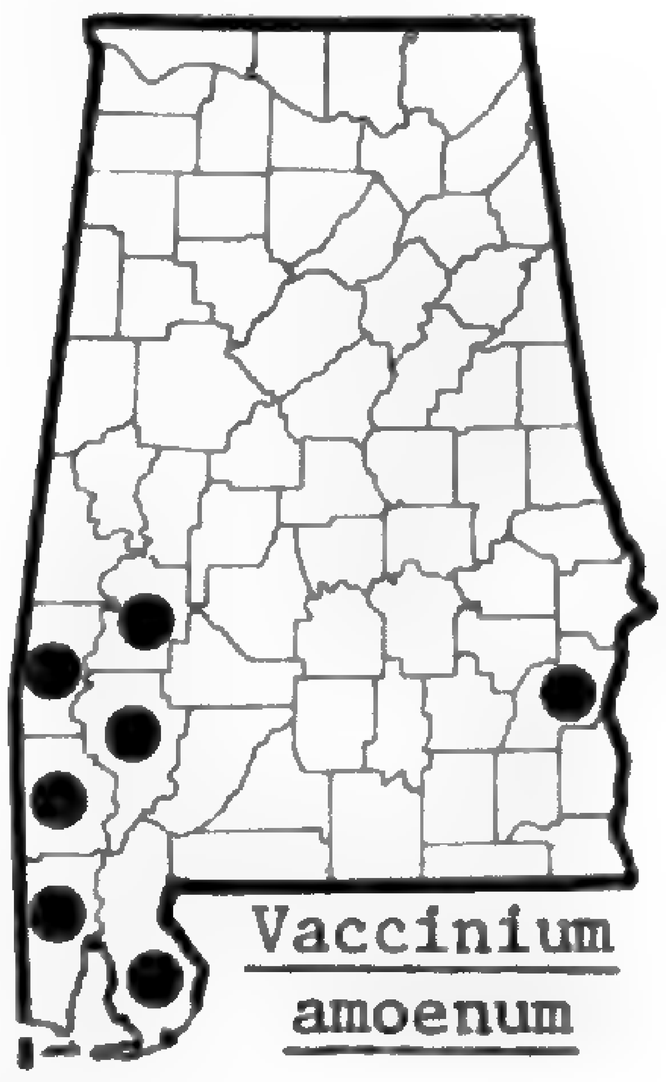


Rhododendron periclymenoides

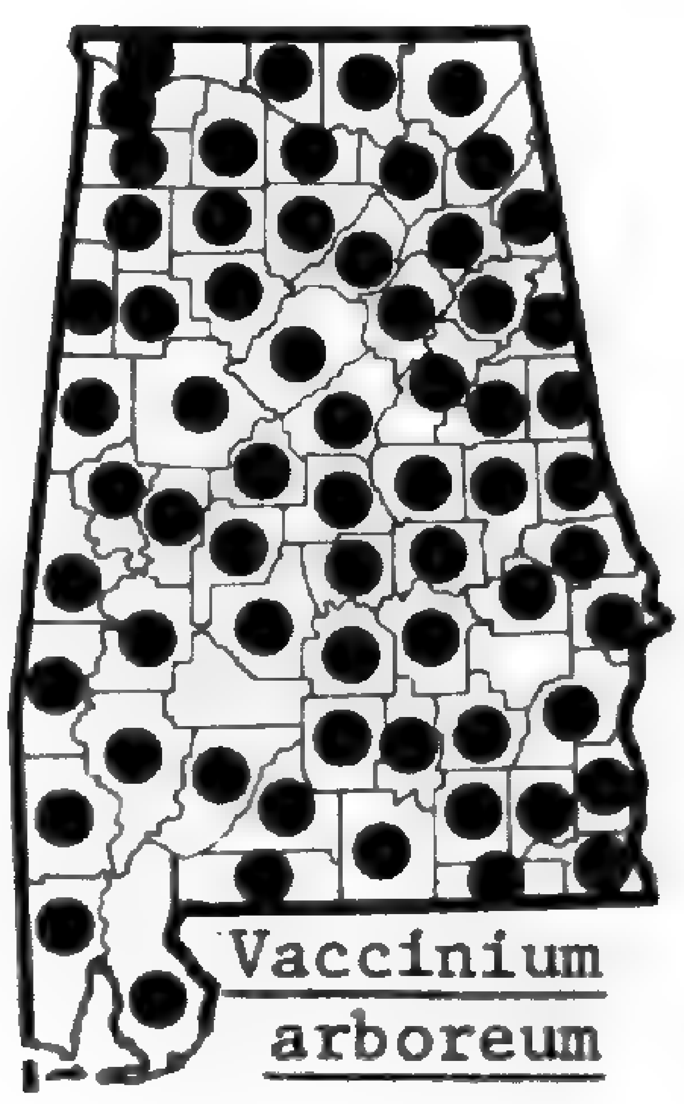
Rhododendron prunifolium



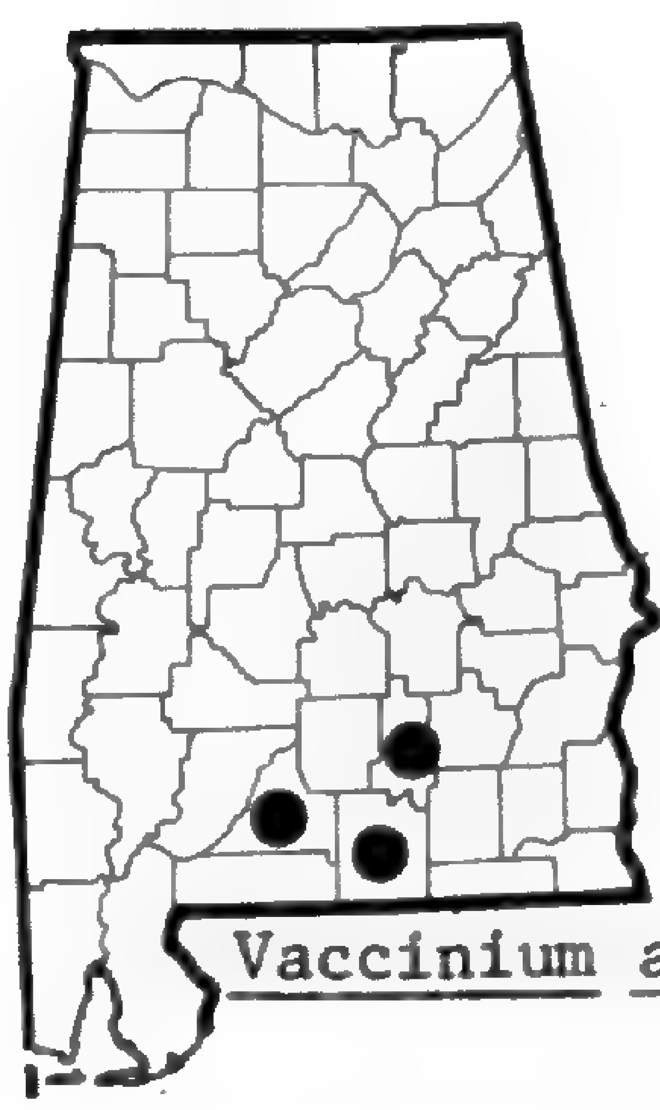
Rhododendron viscosum var. *serrulatum*



Vaccinium amoenum

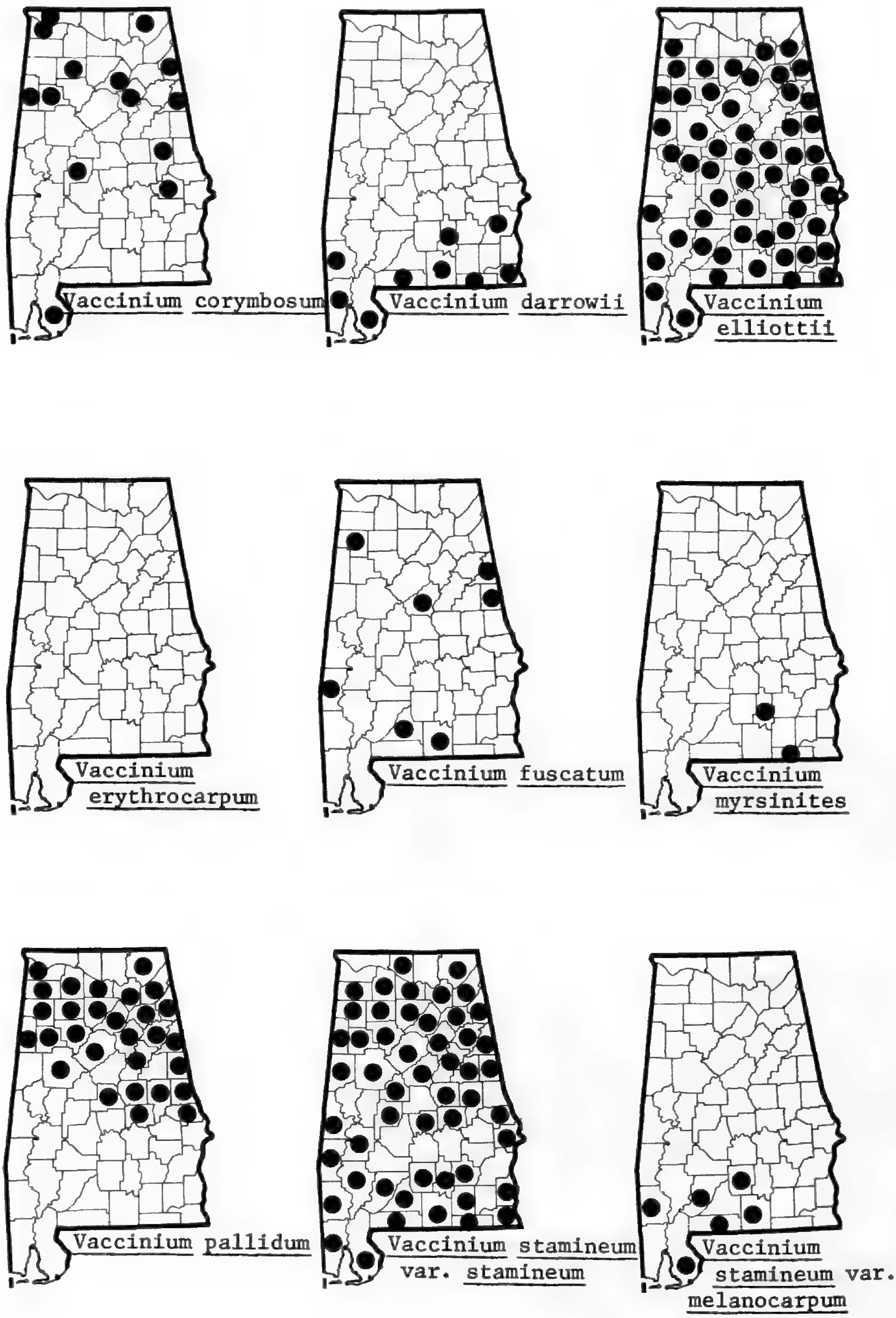


Vaccinium arboreum



Vaccinium ashei

Vaccinium atrococcum


Vaccinium corymbosum
Vaccinium darrowii
Vaccinium elliottii
Vaccinium erythrocarpum
Vaccinium fuscatum
Vaccinium myrsinites
Vaccinium pallidum
Vaccinium stamineum var. stamineum
Vaccinium stamineum var. melanocarpum

11. Plant 1 m or less tall .... 11. *V. pallidum*
11. Plant 1.5 m tall or taller 12
  12. Twigs glabrous .... 5. *V. corymbosum*
  12. Twigs pubescent .... 4. *V. atrococcum*

Most of the taxa listed here are in great need of biosystematic study and reassessment.

1. *V. amoenum* Aiton. Spring; summer. Sandy ground; CP. *V. virgatum* Ait., *V. corymbosum amoenum* (Ait.) Gray—M; *Cyanococcus amoenus* (Ait.) Sm., *C. virgatus* (Ait.) Sm., *C. tenellus* (Ait.) Sm.—S; *V. tenellum* Ait.—M, RAB.

2. *V. arboreum* Marshall, Sparkleberry. Spring; fall. Upland woods, thickets, open areas; throughout. *Batodendron arboreum* (Marsh.) Nutt.—H, S.

3. *V. ashei* Reade. Spring; summer. Upland woods, rare, south-central OCP. Probably a segregate of species 5.

4. *V. atrococcum* (Gray) Porter. Late winter–spring. Deciduous woods, P, CuP, HR. *Cyanococcus atrococcus* (Gray) Sm., *C. margarettae* (Ashe) Sm.—S.

5. *V. corymbosum* L., Highbush B. Late winter–spring; summer. Mesic upland slopes or seepages, infrequent; throughout. *Cyanococcus simulatus* Sm.—S.

6. *V. darrowii* Camp. Spring; summer. Sandy woods; southern CP.

7. *V. elliottii* Chapman. Spring; late spring–early summer. Moist or sandy woods, streambanks; CP, P, AM, CuP, VR. *Cyanococcus elliottii* (Chapm.) Sm. —S.

8. *V. erythrocarpum* Michaux. Spring; summer. Reported from CuP by Dean (1961). *Hugeria erythrocarpa* (Michx.) Sm.—S.

9. *V. fuscatum* Aiton. Spring; summer. Upland woods; CP, AM, VR. *Cyanococcus fuscatus* (Ait.) Sm.—S.—Probably a segregate of species 5.

10. *V. myrsinites* Lamarck. Sandy woods, CP. *V. myrsinites glaucum* Gray—M; *Cyanococcus myrsinites* (Lam.) Sm.—S.

11. *V. pallidum* Aiton, Low-Bush B. Spring; summer. Upland woods; P, AM, VR, CuP. *V. vacillans* Torr.—RAB; *Cyanococcus pallidus* (Ait.) Sm., *C. vacillans* (Kalm) Rydb., *C. tallapusae* Cov.—S.

12. *V. stamineum* L. Spring; summer–fall.

1. Branches and fruit glabrous or glabrate .... *V. stamineum* var. *stamineum*
1. Branches and fruit pubescent .... *V. stamineum* var. *melanocarpum*

V. stamineum L. var. *stamineum*. Upland woods; throughout. *V. melanocarpum* Mohr, *V. melanocarpum candicans* Mohr—M; *Polycodium melanocarpum* (Mohr) Sm., *P. stamineum* (L.) Greene—H, S; *P. neglectum* Sm., *P. candicans* Sm., *P. melanocarpum* (Mohr) Sm.—S.

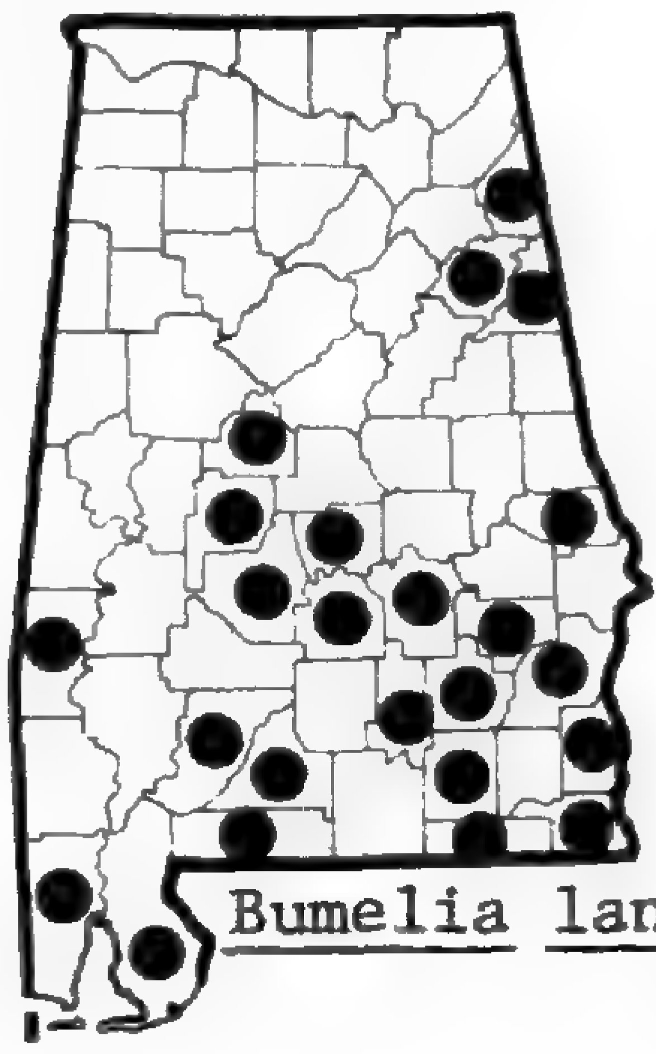
V. stamineum L. var. *melanocarpum* Mohr. Xeric woods; principally CP. *V. melanocarpum sericeum* Mohr—M; *Polycodium macilentum* Sm., *P. depressum* Sm.—S.

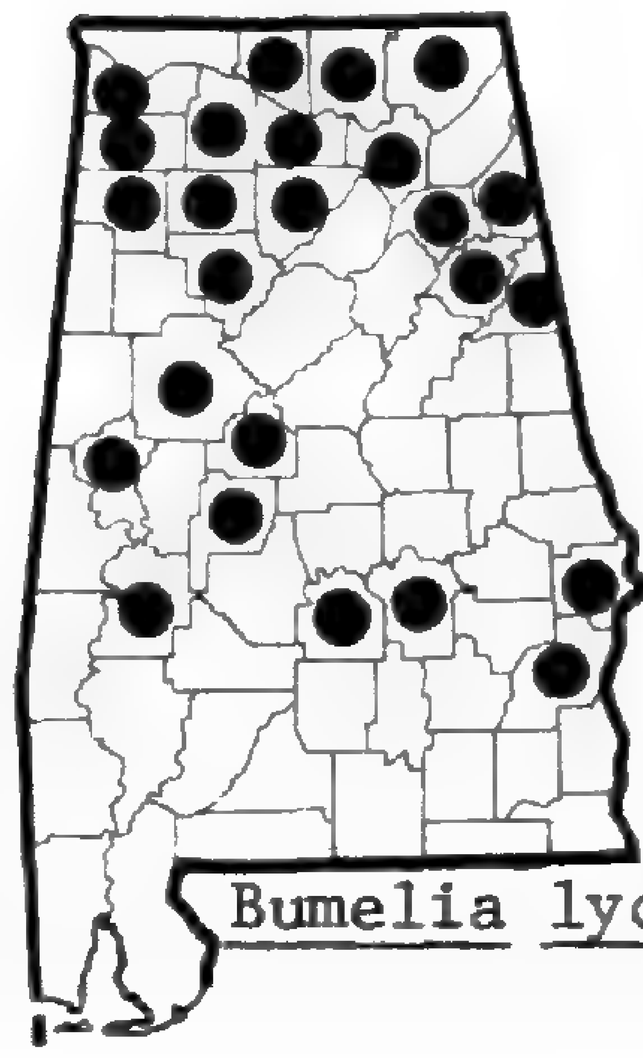
60. Sapotaceae

1. *Bumelia* Swartz

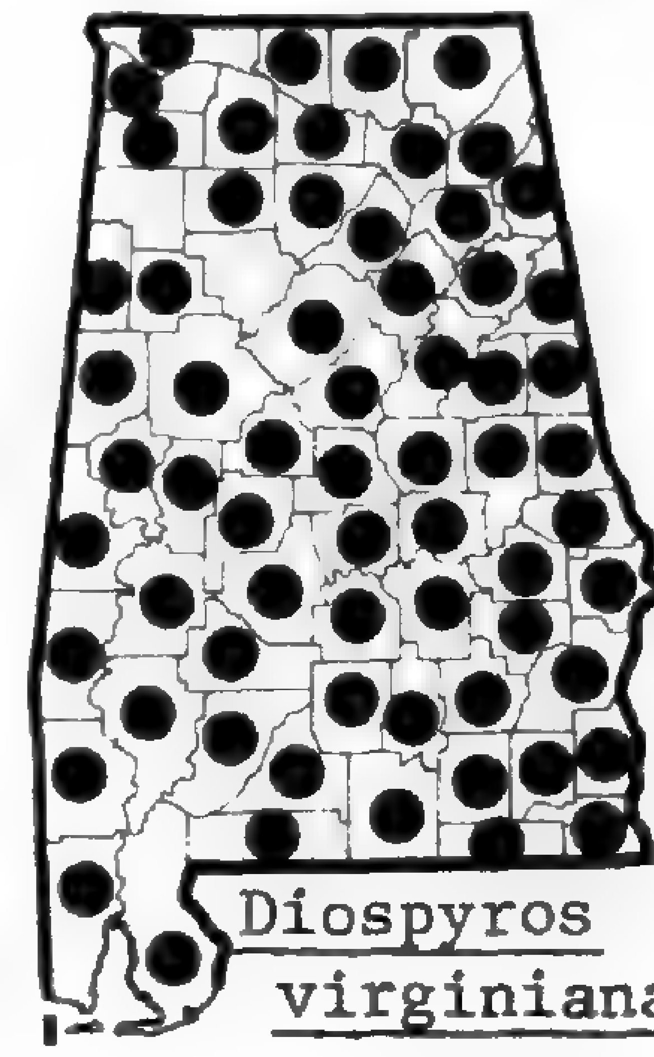
1. Leaves tomentose beneath .... 1. *B. lanuginosa*
1. Leaves glabrous beneath, at least at maturity .... 2. *B. lycioides*

60. SAPOTACEAE

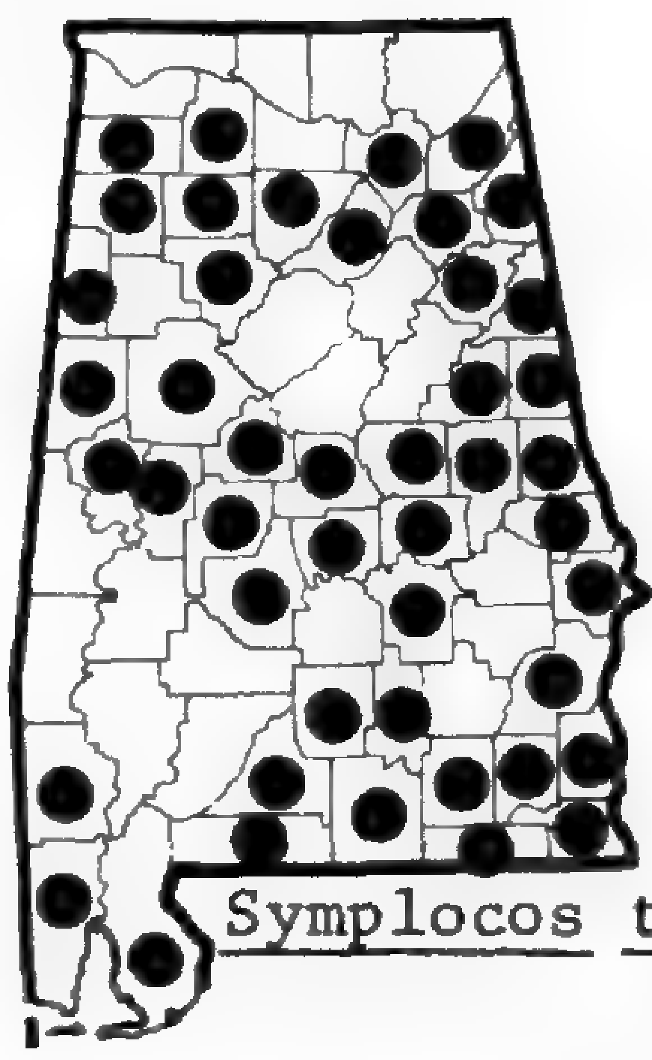

Bumelia lanuginosa


Bumelia lycioides

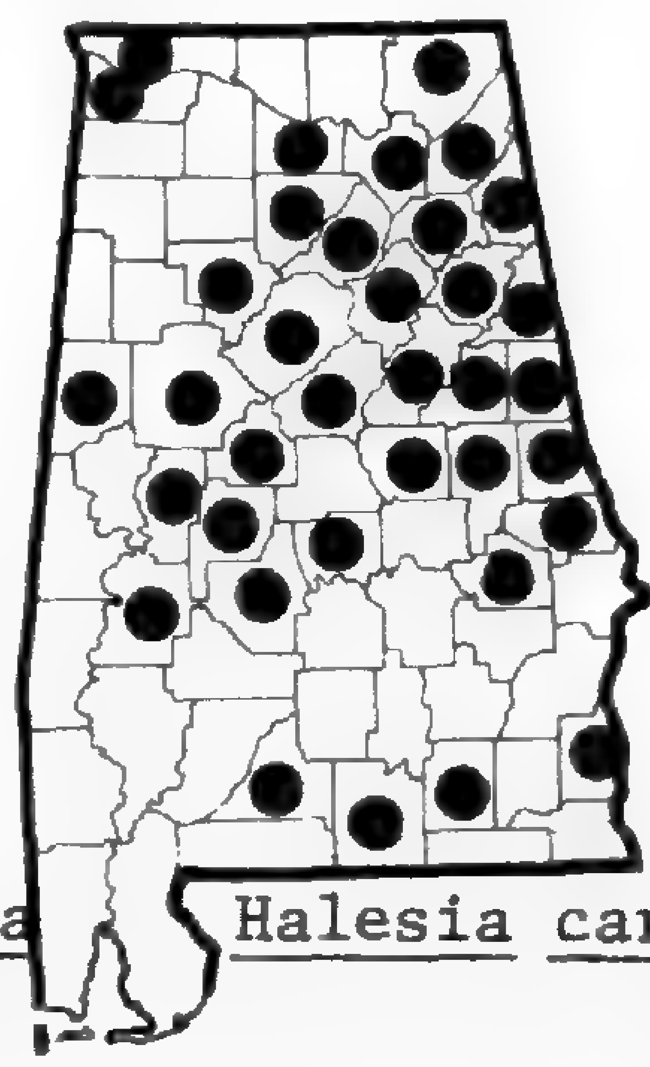
61. EBENACEAE

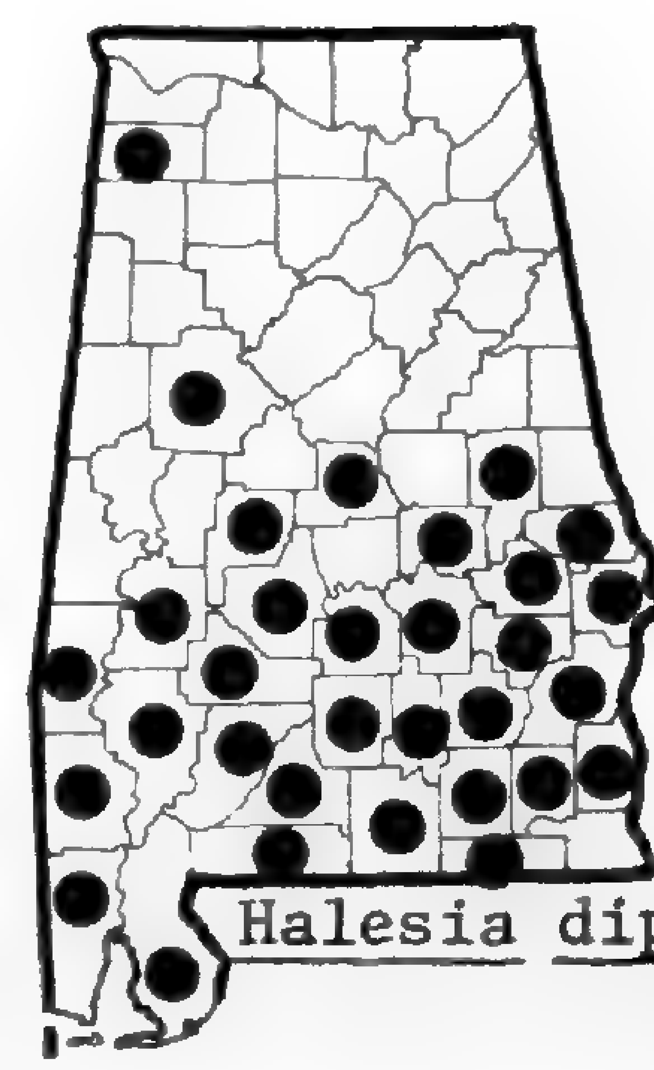

Diospyros virginiana

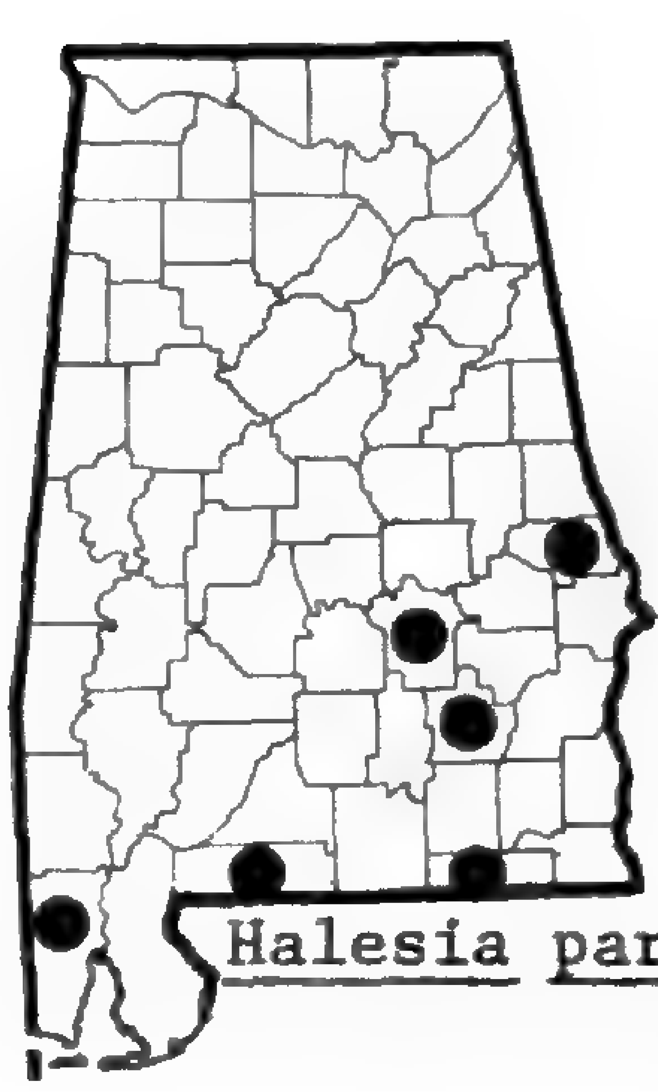
62. SYMPLOCACEAE

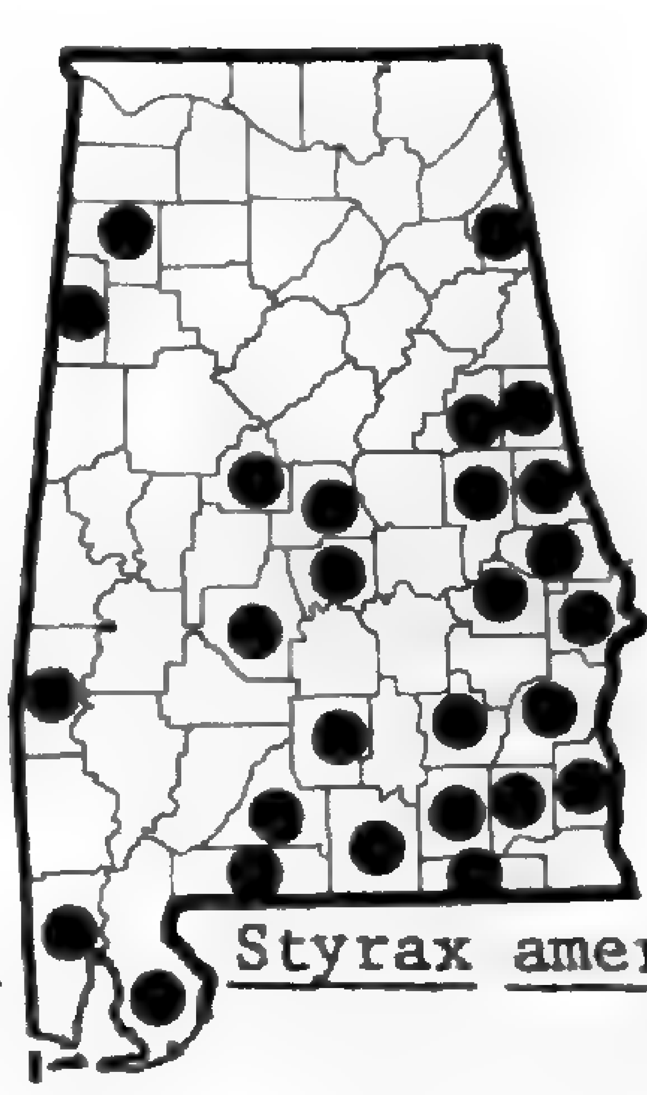

Symplocos tinctoria

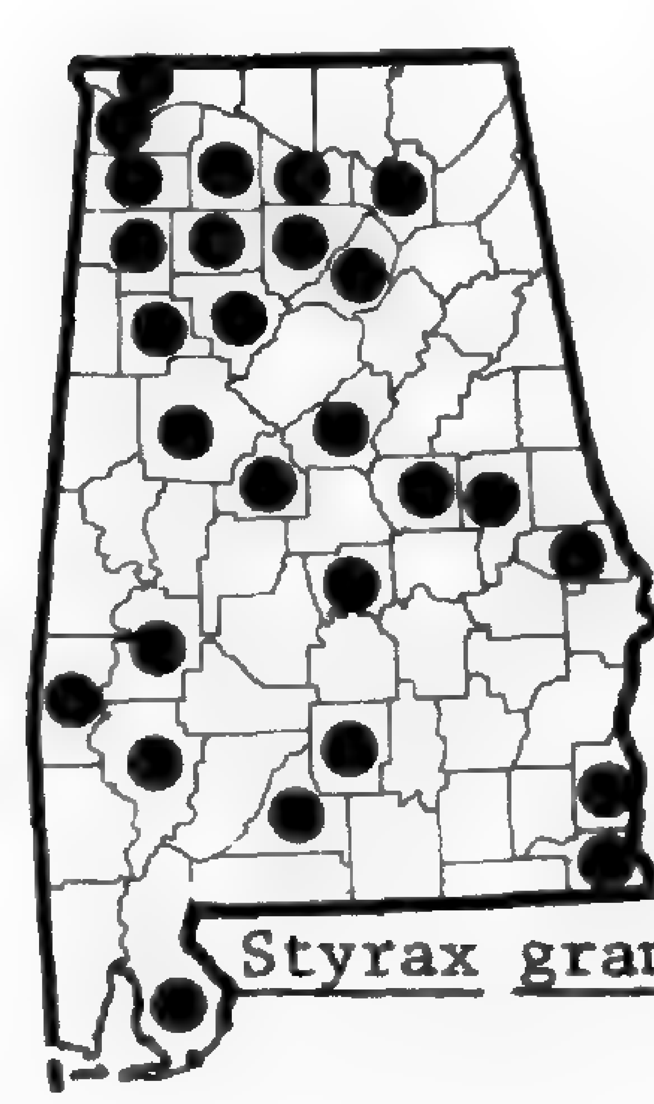
63. STYRACACEAE


Halesia carolina


Halesia diptera


Halesia parviflora


Styrax americana


Styrax grandifolia

1. *B. lanuginosa* (Michaux) Persoon. Late spring–early summer; late summer–fall. Thickets, mesic or alluvial woods; principally CP.

2. *B. lycioides* (L.) Gaertner. Late spring–summer; fall. Thickets, rich or alluvial woods, usually in circumneutral soil; CP, AM, VR, CuP, HR.

Alabama is considered by Small (1933) to be within the range of *Bumelia reclinata* Vent.

61. Ebenaceae

1. *Diospyros* L., Persimmon

1. *D. virginiana* L. Spring; late summer–fall. Woodlands, thickets, fields; throughout.

62. Symplocaceae

1. *Symplocos* Jacquin

1. *S. tinctoria* (L.) L'Her, Horse-Sugar, Sweet-Leaf, Sweet Bay. Spring; summer. Rich or alluvial woods, infrequent; throughout.

63. Styracaceae

1. Corolla lobes 4; fruit winged .... 1. *Halesia*
1. Corolla lobes 5; fruit wingless .... 2. *Styrax*

1. *Halesia* Ellis *ex* L., Silverbell

1. Corolla lobes shorter than corolla tube; wings of fruit subequal 2
    2. Corolla less than 1.5 cm long; fruit clavate .... 3. *H. parviflora*
    2. Corolla 1.5 cm long or longer; fruit ellipsoid to obovoid .... 1. *H. carolina*
1. Corolla lobes longer than corolla tube; one pair of fruit wings 2 or more times as wide as the other pair of wings .... 2. *H. diptera*

1. *H. carolina* L. Spring; summer. Alluvial or rich upland woods; throughout, but infrequent to the south and westward. *Mohrodendron carolinum* (L.) Britt.—M.

2. *H. diptera* Ellis. Spring; summer. Bluffs, mesic woods; CP and adjacent P, AM, CuP. *Mohrodendron dipterum* (L.) Britt.—M.—*Halesia diptera* Ell. var. *magniflora* Godfrey is infrequent in the CP.

3. *H. parviflora* Michaux. Spring; summer. Mesic woods; CP.

2. *Styrax* L.

1. Leaves stellate-pubescent over the lower surfaces; racemes 5- or more-flowered .... 2. *S. grandifolia*
1. Leaves glabrous beneath, or sparsely stellate-pubescent only on the principal veins; racemes 4- or less-flowered, or flowers solitary .... 1. *S. americana*

1. *S. americana* Lamarck. Spring; summer. Swamp forests, alluvial and low woods and thickets, more frequent southeastward; CP, P, AM, VR (rare). *S. pulverulenta* Michx.—M, H, S.

2. *S. grandifolia* Aiton. Spring; summer. Ravines, mesic slopes; CP, P, CuP, HR.

64. OLEACEAE

1. Leaves pinnately compound .... 3. *Fraxinus*
1. Leaves simple 2
   2. Leaves serrate or crenate .... 2. *Forestiera*
   2. Leaves entire 3
      3. Petals linear, united only at base; leaves deciduous .... 1. *Chionanthus*
      3. Petals united into a salverform or funnelform corolla; leaves evergreen or partially so 4
         4. Inflorescences axillary .... 5. *Osmanthus*
         4. Inflorescence terminal .... 4. *Ligustrum*

1. *Chionanthus* L., GRANDSIR GRAYBEARD, FRINGE TREE

1. *C. virginicus* L. Spring; summer. Rocky or dry woods, bluffs; throughout. Widely transplanted as an ornamental.

2. *Forestiera* Poiret

1. Leaves gradually acuminate; fruit 2 or more times longer than broad .... 1. *F. acuminata*
1. Leaves obtusely acuminate; fruit less than 2 times as long as broad .... 2. *F. ligustrina*

1. *F. acuminata* (Michaux) Poiret. Spring. Swamp forests, river banks, local and rare; CP, reported from HR. *Adelia acuminata* Michx.—M, H.

2. *F. ligustrina* (Michaux) Poiret. Summer; late summer–fall. Dry woods and thickets, local and infrequent; CP (rare), VR (rare), P, CuP, HR. *F. pubescens* Nutt.—S; *Adelia ligustrina* Michx.—M, H.

3. *Fraxinus* L., ASH

1. Twigs 4-angled or 4-winged .... 4. *F. quadrangulata*
1. Twigs not winged 2
   2. Samara winged to the base, its body flattened .... 2. *F. caroliniana*
   2. Samara not winged to the base, its body terete 3
      3. Samara body usually less than 12 mm long, its wing decurrent less than ⅓ of body length .... 1. *F. americana*
      3. Samara body usually more than 12 mm long, its wing decurrent more than ⅓ of body length 4
         4. Samara body more than 2 mm broad .... 5. *F. tomentosa*
         4. Samara body less than 2 mm broad .... 3. *F. pennsylvanica*

Except for species 4, staminate or sterile material is impossible to determine satisfactorily.

1. *F. americana* L., AMERICAN A., WHITE A. Spring; summer–fall.

1. Twigs, petioles and lower surfaces of leaflets glabrous or glabrate .... *F. americana* var. *americana*
1. Twigs, petioles and lower surfaces of leaflets densely pubescent .... *F. americana* var. *biltmoreana*

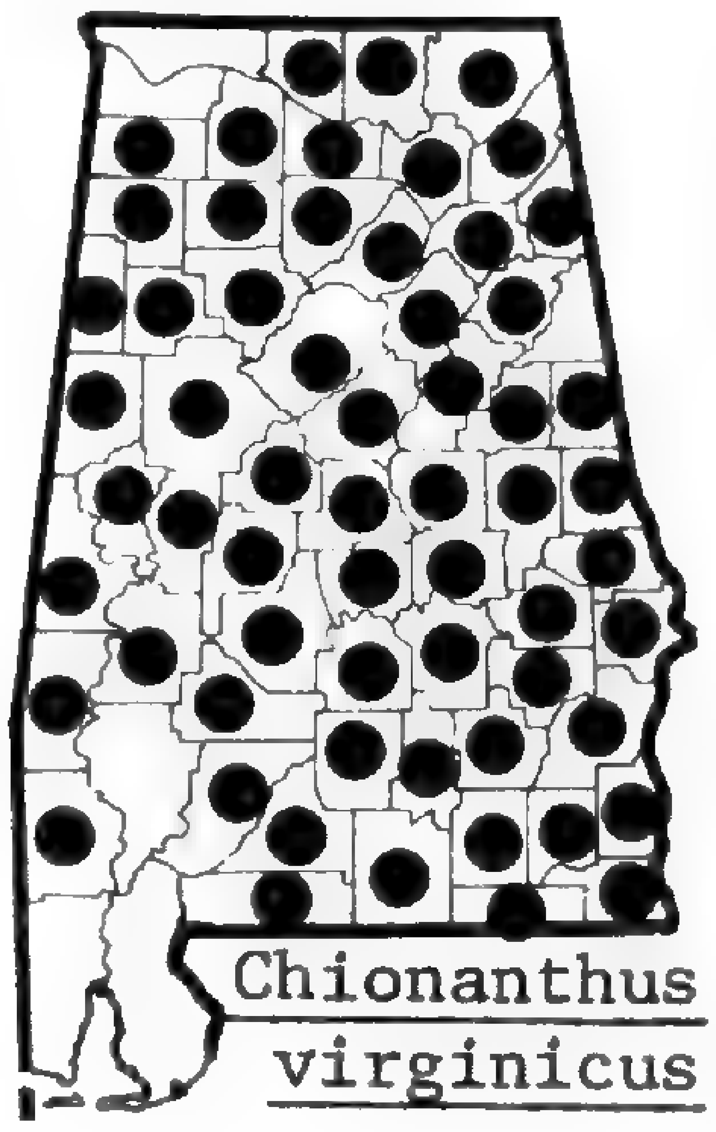
F. americana L. var. *americana*. Rich or low woods, infrequent to rare; throughout. *F. americana curtissii* (Vasey) Sudw.—M.

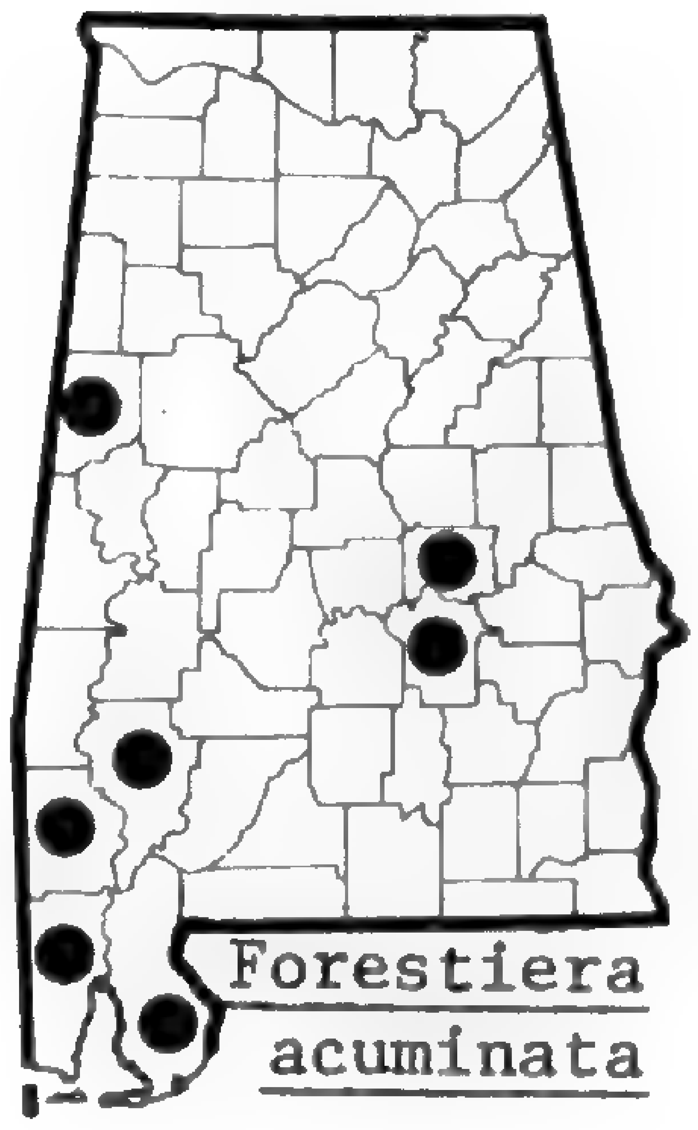
F. americana L. var. *biltmoreana* (Beadle) Wright *ex* Fernald. Dry, rich, or low woods; throughout, becoming rare southward. *F. biltmoreana* Bead.—M, S.

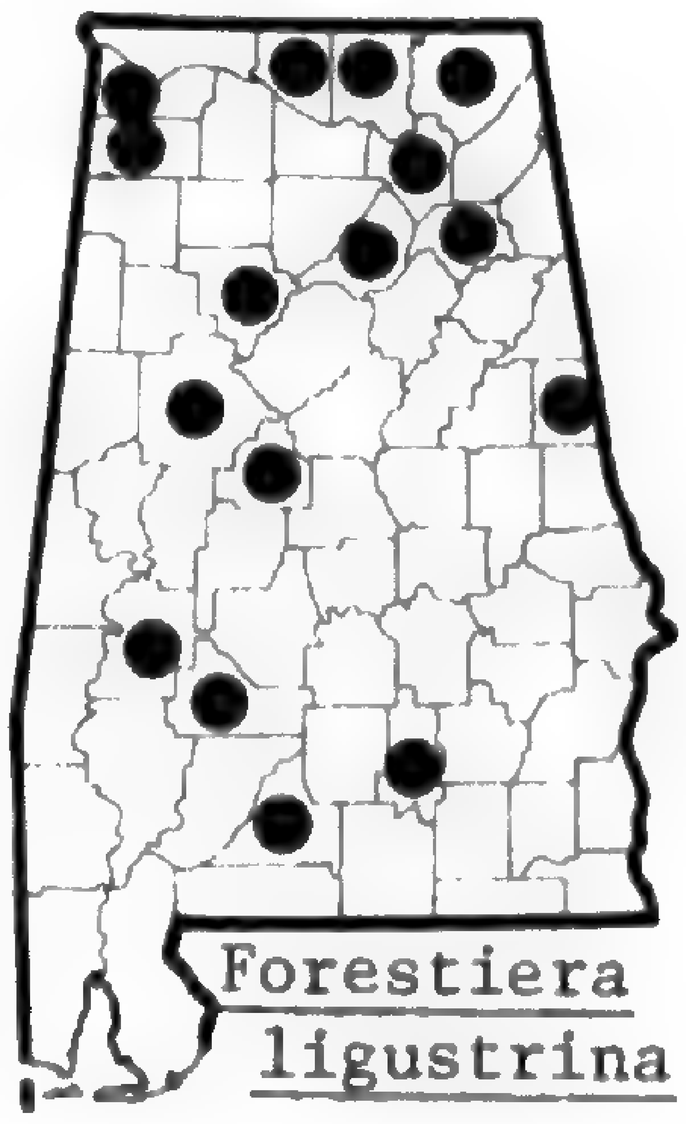
2. *F. caroliniana* Miller. Spring; summer–fall. Swamp forests; CP. *F. pauciflora* Nutt.—S.

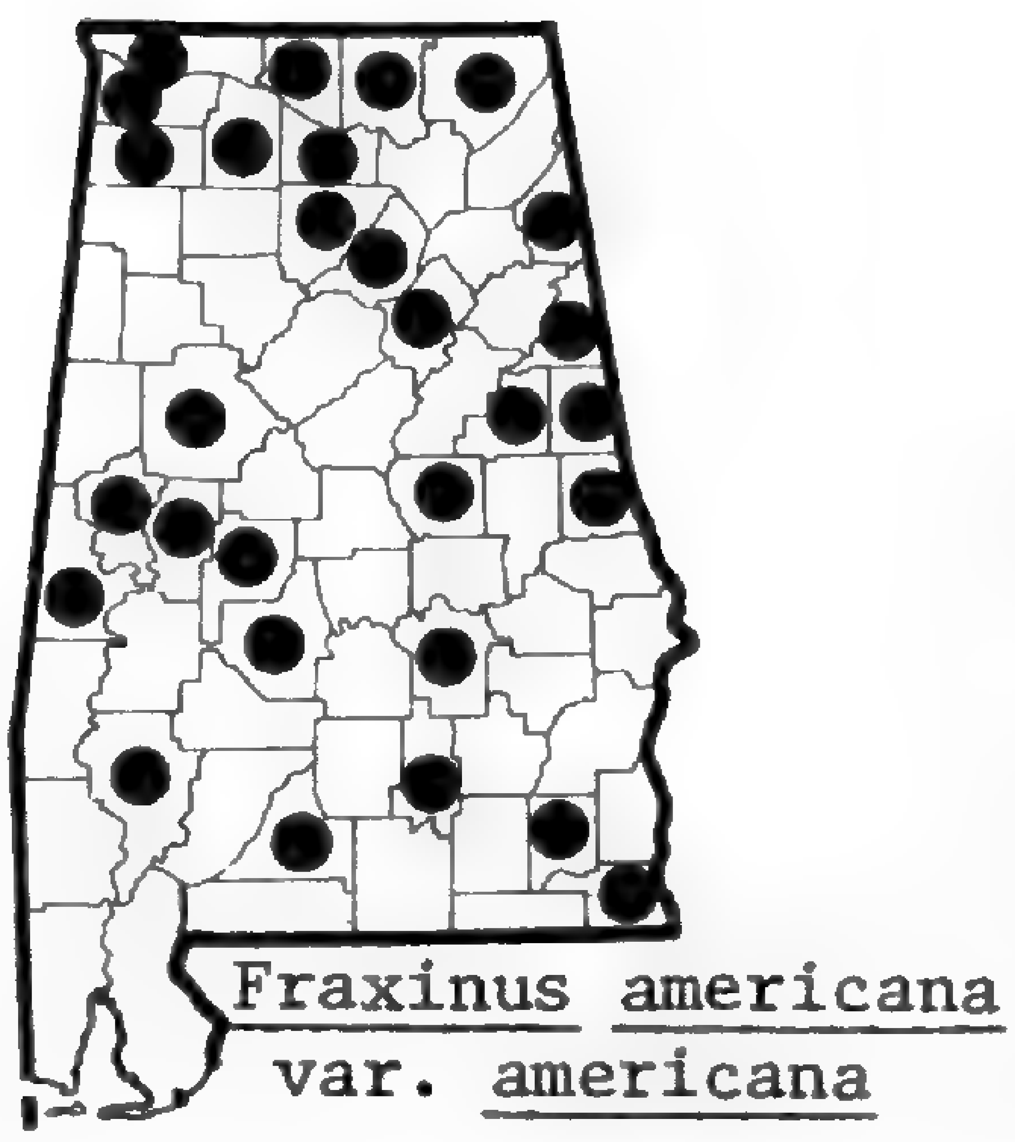
3. *F. pennsylvanica* Marshall, GREEN A. Spring; summer–fall. Low thickets

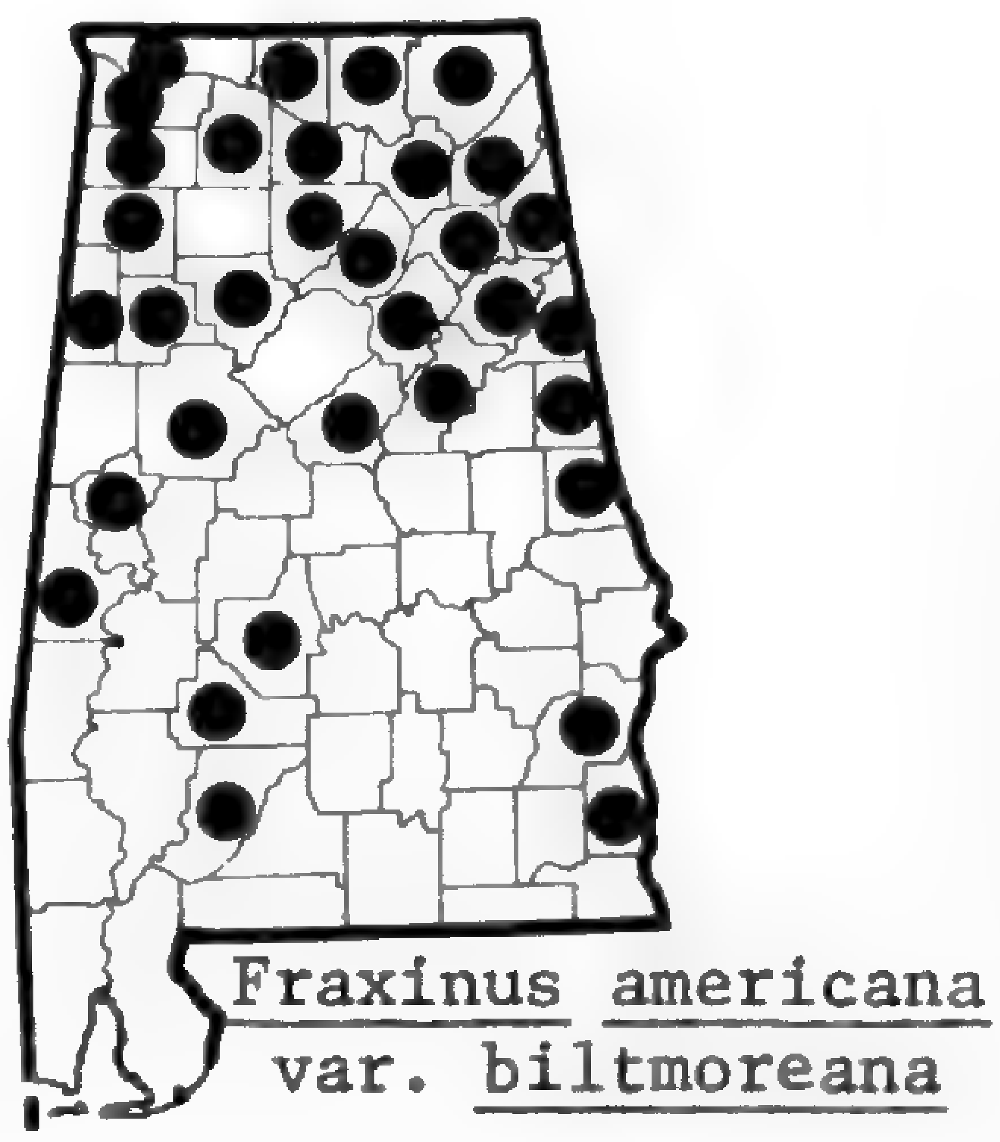
64. OLEACEAE

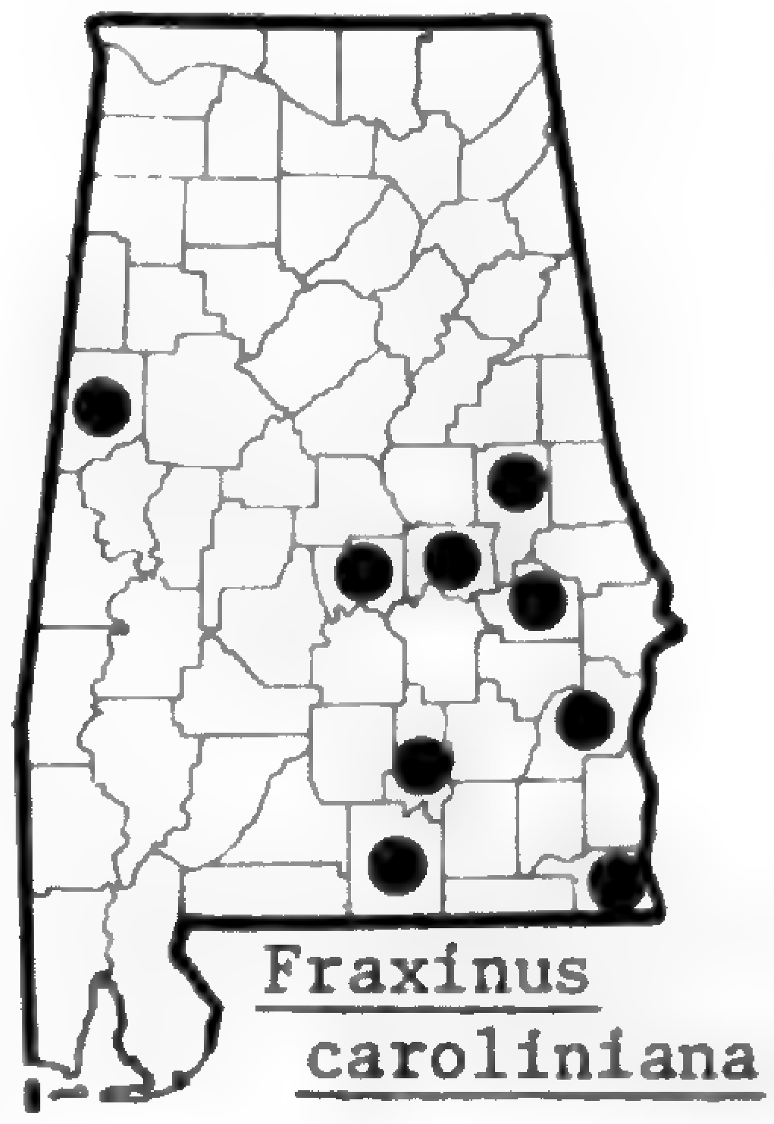

Chionanthus
virginicus

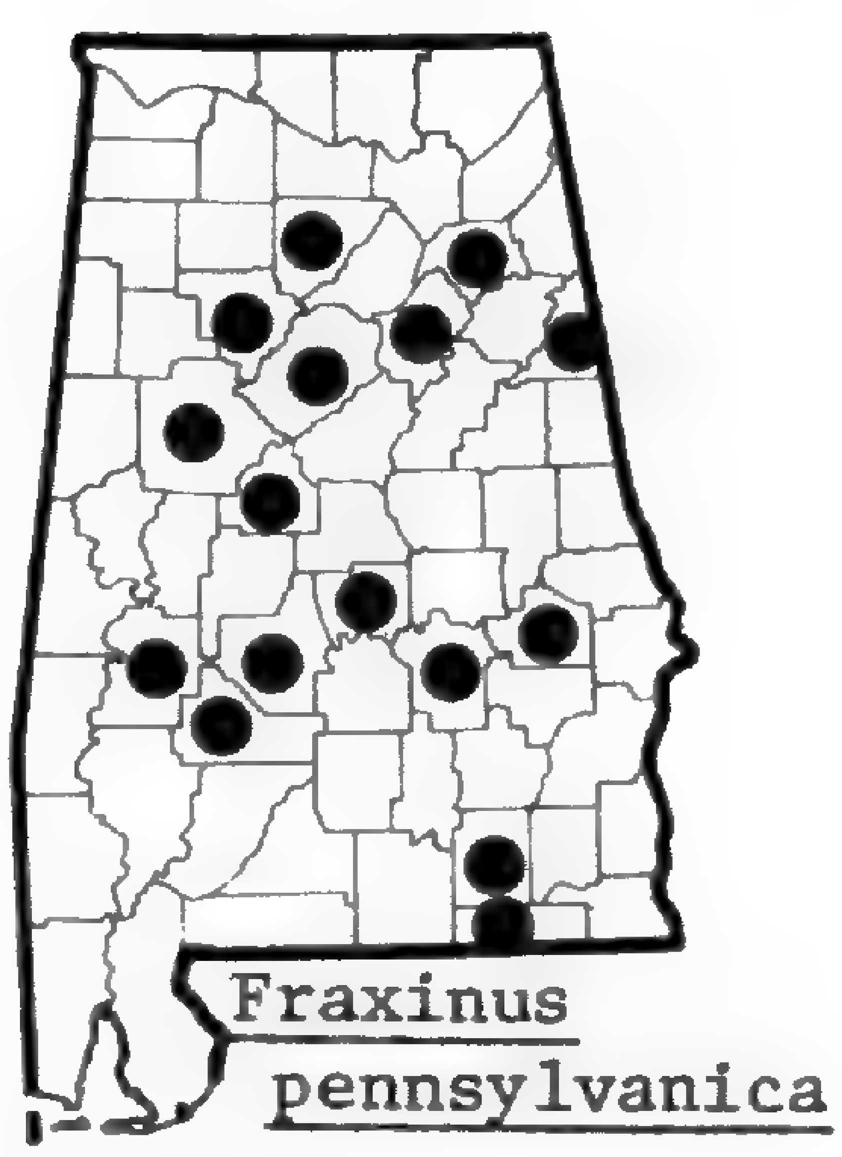

Forestiera
acuminata


Forestiera
ligustrina


Fraxinus americana
var. americana


Fraxinus americana
var. biltmoreana


Fraxinus
caroliniana


Fraxinus
pennsylvanica


Fraxinus
quadrangulata


Fraxinus
tomentosa

and woods; CP, P, VR, CuP. *F. lanceolata* Borkh.—M, H; *F. darlingtonii* Britt., *F. smallii* Britt.—S.

4. *F. quadrangulata* Michaux, BLUE A. Flowers, fruits not seen. Rich or open woods over calcareous rock, local; CuP, HR.

5. *F. tomentosa* Michaux f. Credited to Alabama by Small (1933), and by Radford in Radford, Ahles and Bell (1968). *F. michauxii* Britt., *F. profunda* Bush—S.

4. *Ligustrum* L., PRIVET

1. Twigs glabrous .... 1. *L. japonicum*
1. Twigs pubescent .... 2. *L. sinense*

1. *L. japonicum* Thunberg. Spring; fall–winter. Occasional escape to fencerows, roadsides; CP, VR.

2. *L. sinense* Loureiro. Spring; fall–winter. Escaped to roadsides, fields and woods; throughout.

5. *Osmanthus* Loureiro

1. *O. americana* (L.) Gray. Spring; late summer–winter. Bluffs, mesic woods; CP and adjacent P. *Amarolea americana* (L.) Sm.—S; *O. americana* (L.) B. & H.—M, H.

65. LOGANIACEAE

1. Leaves serrate; plant a shrub .... 1. *Buddleja*
1. Leaves entire; plant a vine .... 2. *Gelsemium*

1. *Buddleja* L.

1. *B. lindleyana* Fortune. Summer–fall. Waste ground, rare; P.

2. *Gelsemium* Jussieu, YELLOW JASMINE

1. Calyx lobes acute; flowers odorless; capsule beak more than 2 mm long; seeds wingless .... 1. *G. rankinii*
1. Calyx lobes obtuse; flowers fragrant; capsule beak less than 2 mm long; seeds winged .... 2. *G. sempervirens*

1. *G. rankinii* Small. Spring; late summer–fall. Low, acidic ground, infrequent; OCP.

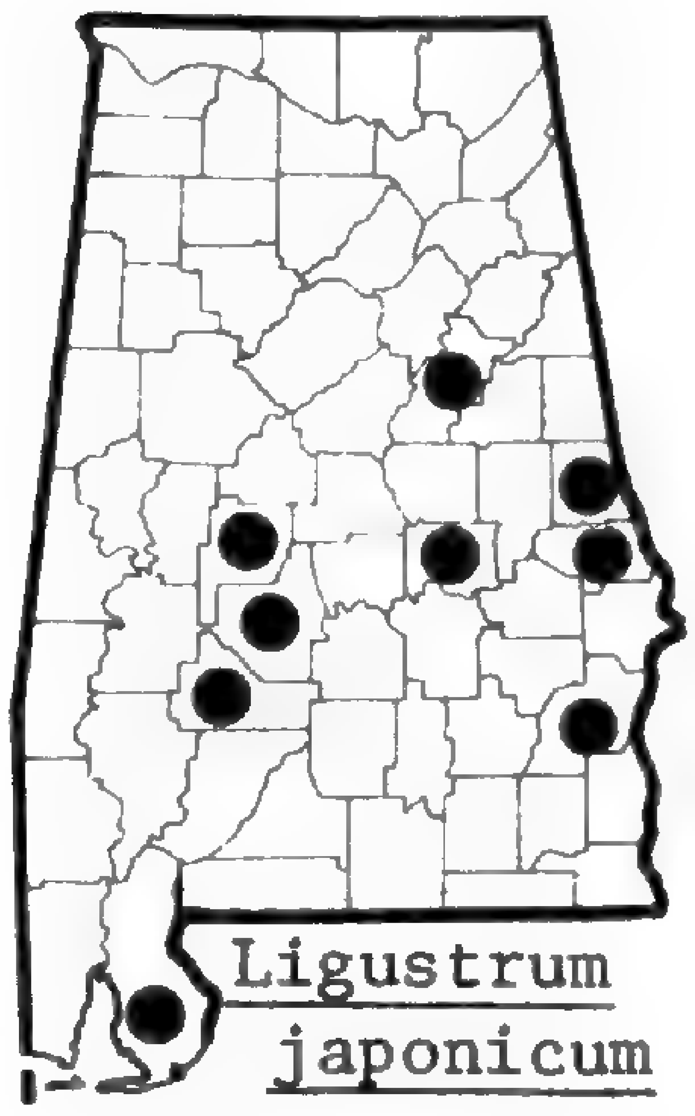
2. *G. sempervirens* (L.) Aiton f. Spring; late summer–fall. Roadsides, fencerows, openings in woods; CP, P, AM, VR (rare), CuP.

66. APOCYNACEAE

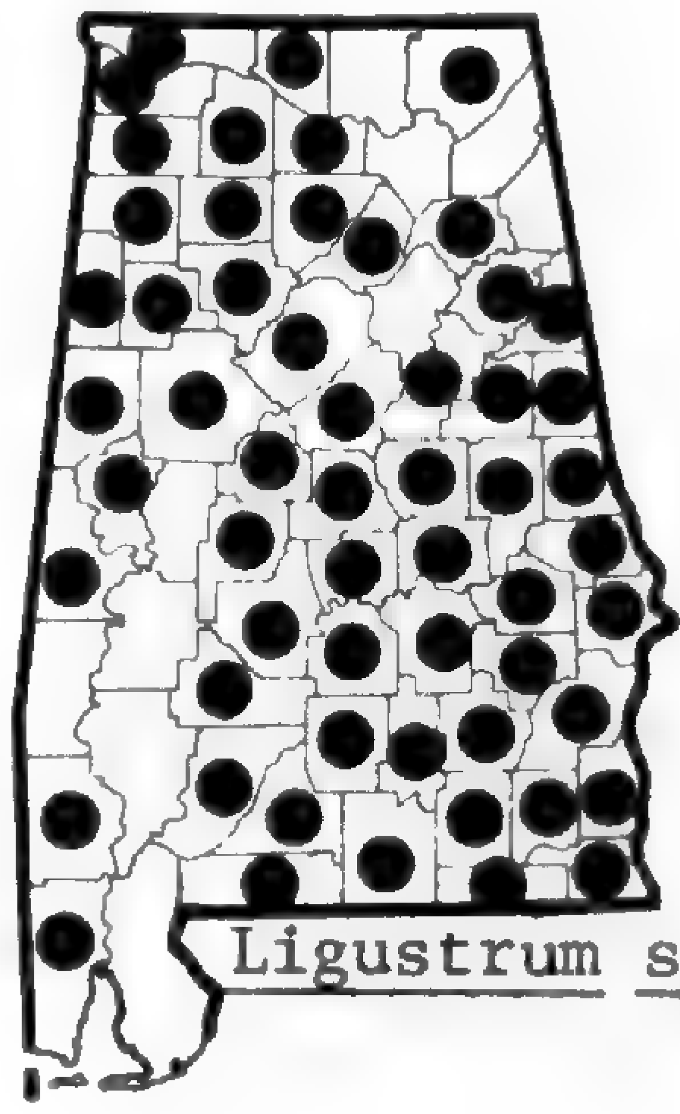
1. Leaves abruptly acuminate; corolla 10 mm or less long, less than 10 mm broad, yellow .... 1. *Trachelospermum*
1. Leaves obtuse to acute; corolla more than 10 mm broad and long, bluish or white .... 2. *Vinca*

1. *Trachelospermum* Lemaire

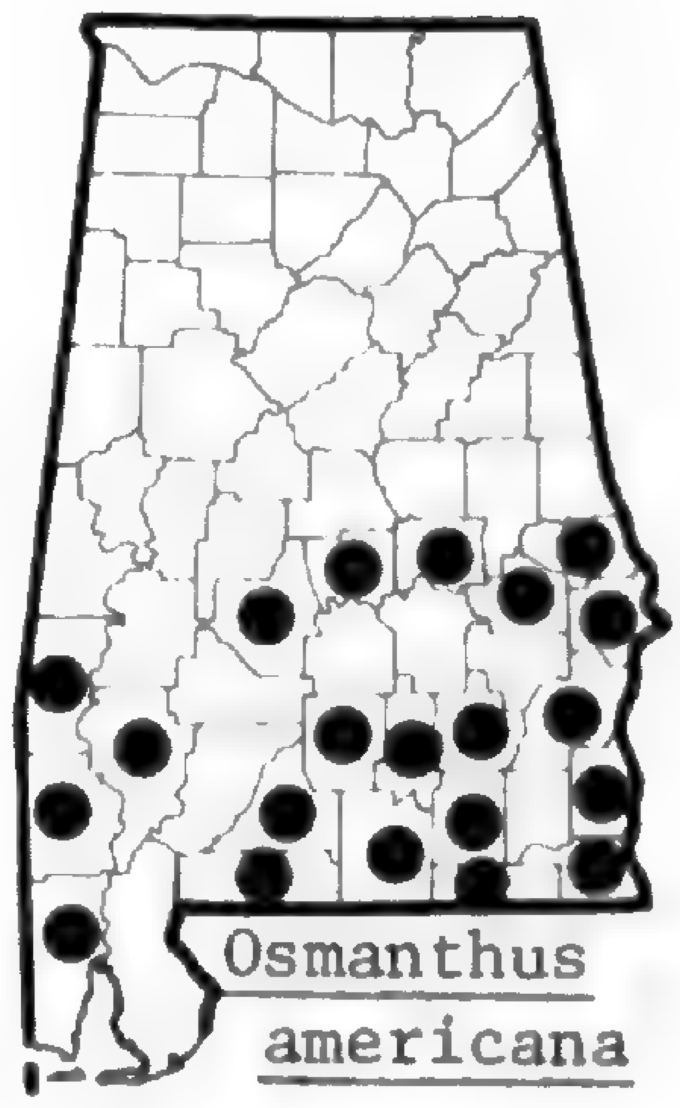
1. *T. difforme* (Walter) Gray. Late spring–early summer; late summer–fall. Swamps, low woods and thickets; CP, VR, CuP, HR.



Ligustrum japonicum



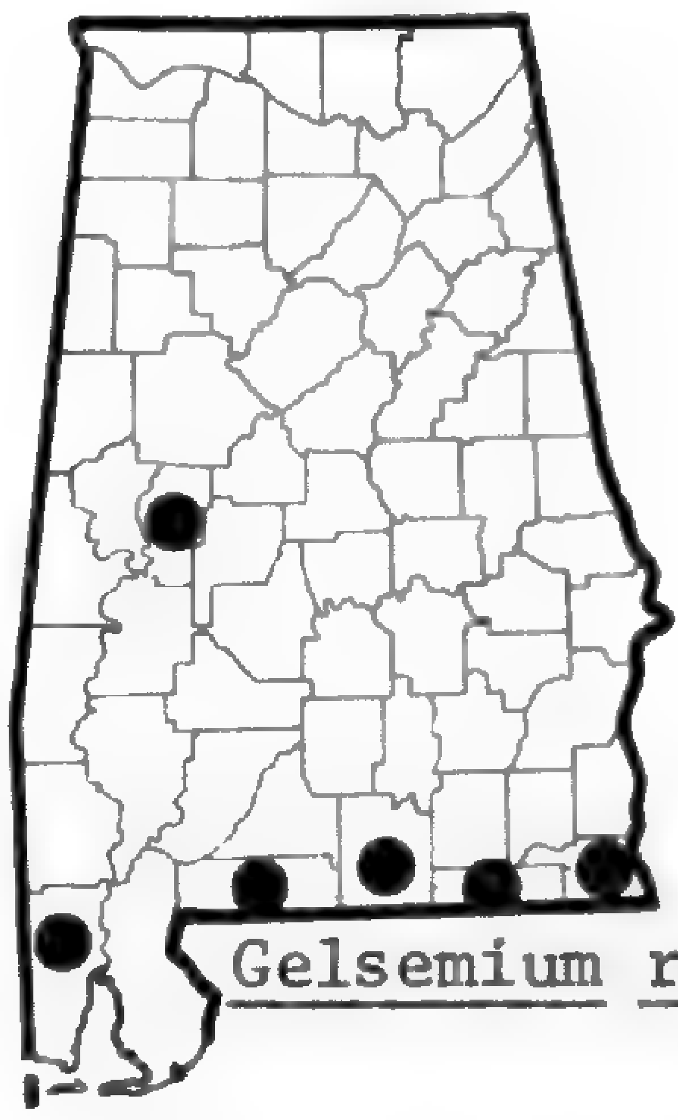
Ligustrum sinense



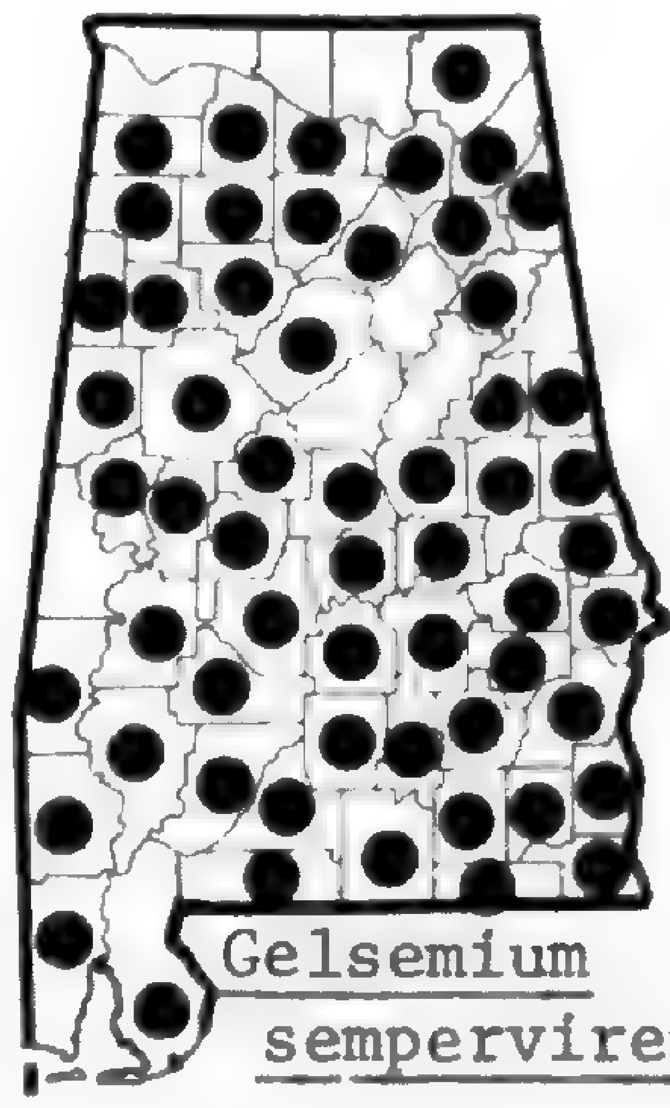
Osmanthus americana

65. LOGANIACEAE

Buddleja lindleyana

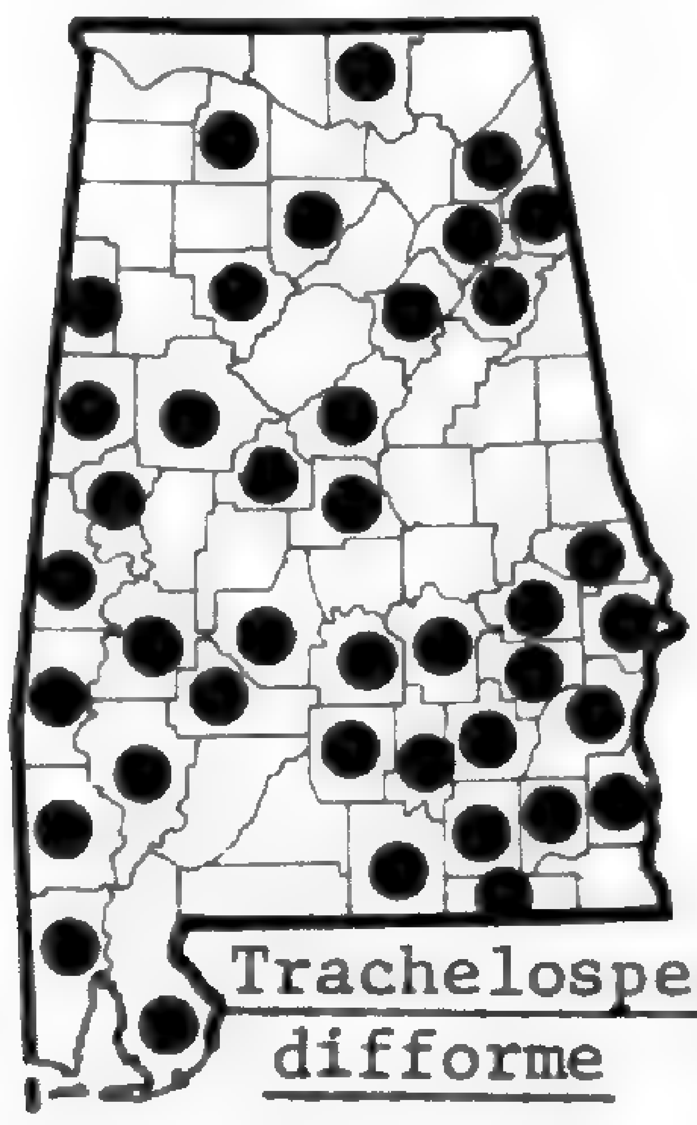


Gelsemium rankinii

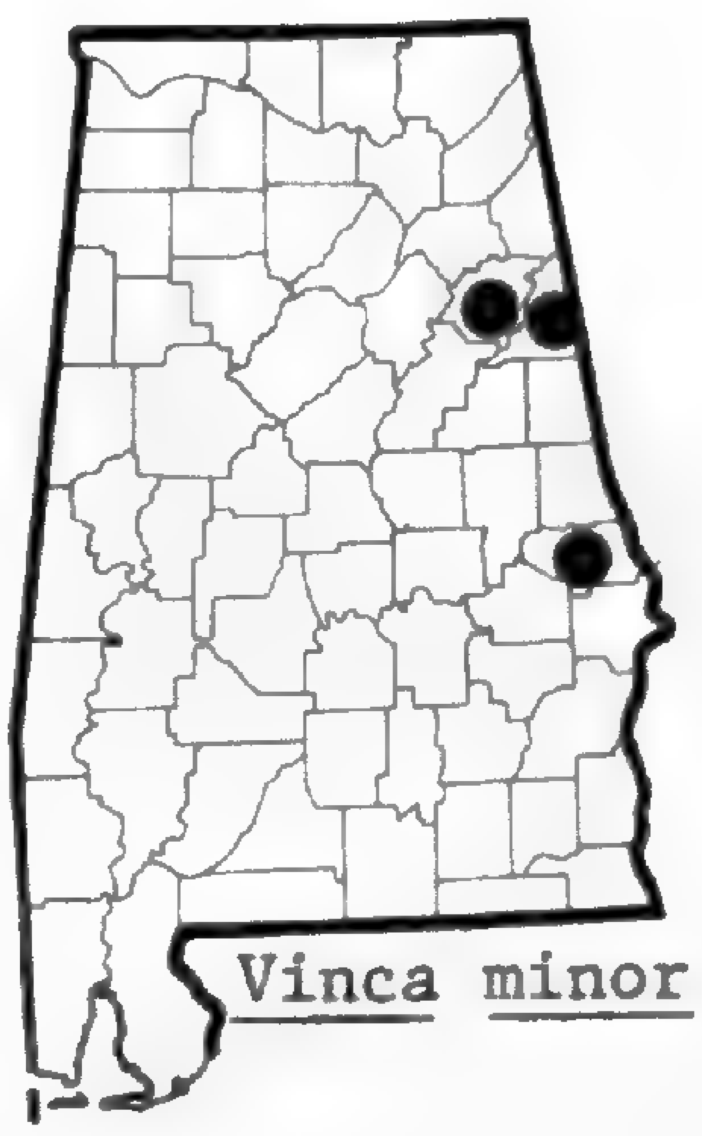


Gelsemium sempervirens

66. APOCYNACEAE

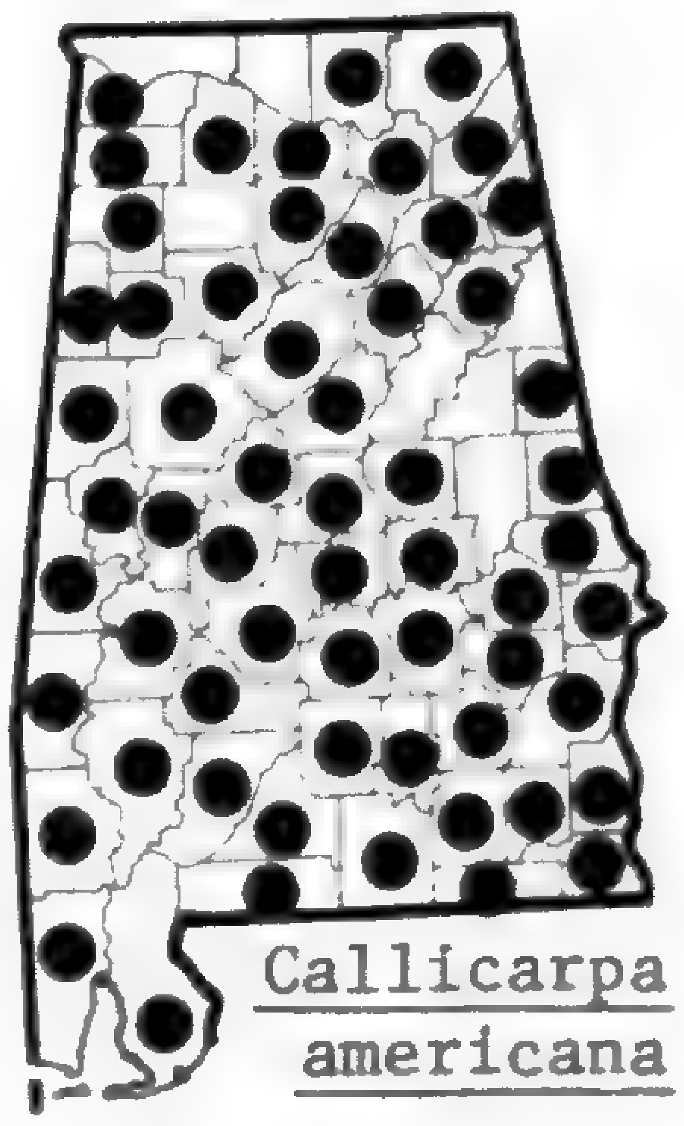


Trachelospermum difforme



Vinca minor

67. VERBENACEAE



Callicarpa americana

2. *Vinca* L., Periwinkle

1. *V. minor* L. Spring; summer. A rare escape to low woods; P, VR.

Nerium oleander L. is a doubtful OCP escape. It persists from cultivation.

67. Verbenaceae

1. Inflorescence spicate; fruit of nutlets enclosed by calyx .... 3. *Verbena*
1. Inflorescence racemose or corymbose; fruit fleshy, a drupe or berry 2
   2. Corolla orange, yellow or reddish; fruit a blue to black drupe .... 2. *Lantana*
   2. Corolla white, pink or lavender; fruit a lavender berry .... 1. *Callicarpa*

1. *Callicarpa* L., Beauty-Berry

1. *C. americana* L. Spring–summer; late summer–fall. Rocky or sandy woods, thickets; throughout.

2. *Lantana* L.

1. *L. camara* L. Spring–fall. Rare escape to roadsides and waste places; CP.

3. *Verbena* L.

1. *V. brasiliensis* Vellozo. Spring–fall. Fields, alluvial woods, waste places; principally CP.—This species is usually considered herbaceous, but stems become woody and persistent in Alabama. It was poorly collected during the field work for this study.

Clerodendron sp. has been reported as an escape by Dean (1961) and *Vitex agnus-castus* L. has been attributed to Alabama by Dean (1961) and by Bell in Radford, Ahles and Bell (1968). Verification of these as escaped awaits confirmation.

68. Lamiaceae

1. Leaves linear, densely hoary-canescent .... 1. *Conradina*
1. Leaves ovate to oblanceolate, not canescent .... 2. *Satureja*

1. *Conradina* Gray

1. *C. canescens* (Torrey & Gray) Gray. Summer–fall. Sandy woods; OCP.

2. *Satureja* L.

1. Corolla more than 2.5 cm long, scarlet; calyx 8 mm long or longer .... 1. *S. coccinea*
1. Corolla less than 2 cm long, white or purplish; calyx 6 mm long or shorter .... 2. *S. georgiana*

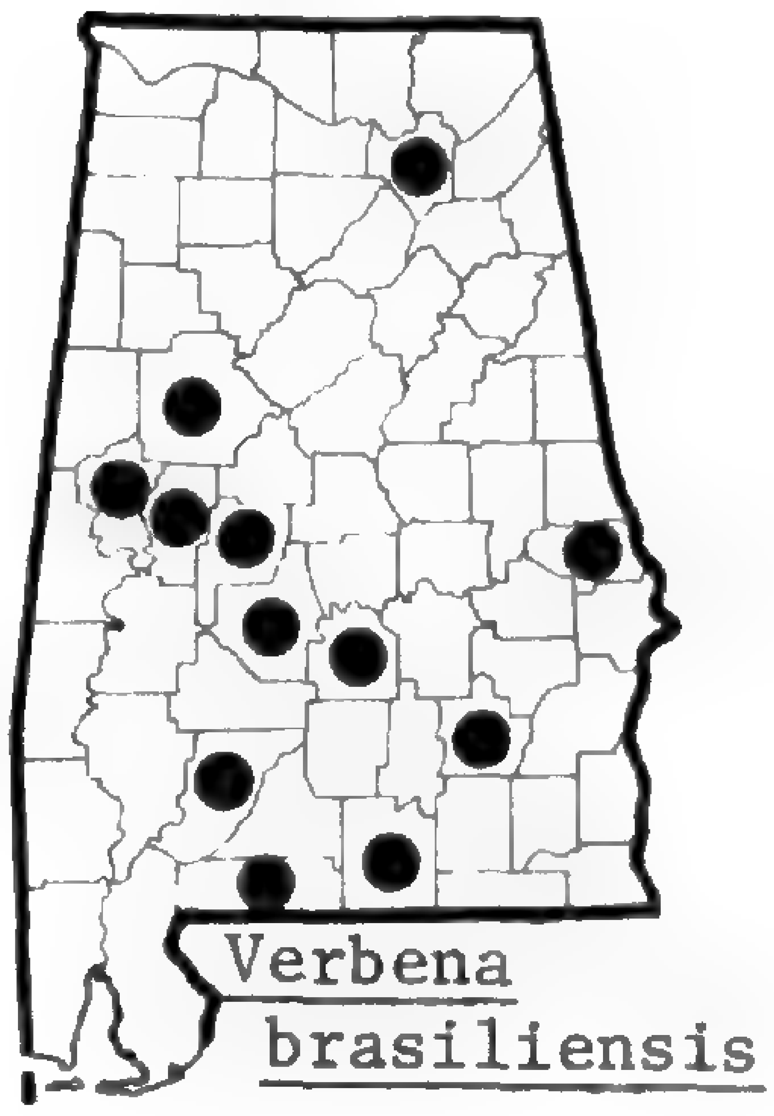
1. *S. coccinea* (Nuttall) Bentham. Late summer–fall. Dry woods, local; OCP. *Clinopodium coccineum* (Nutt.) Kuntze—M, H, S.

2. *S. georgiana* (Harper) Ahles. Summer–fall. Rocky or sandy woods, local; CP, CuP, AM. *Clinopodium carolinianum* (Walt.) Kuntze—M; *C. georgianum* Harper—H, S.

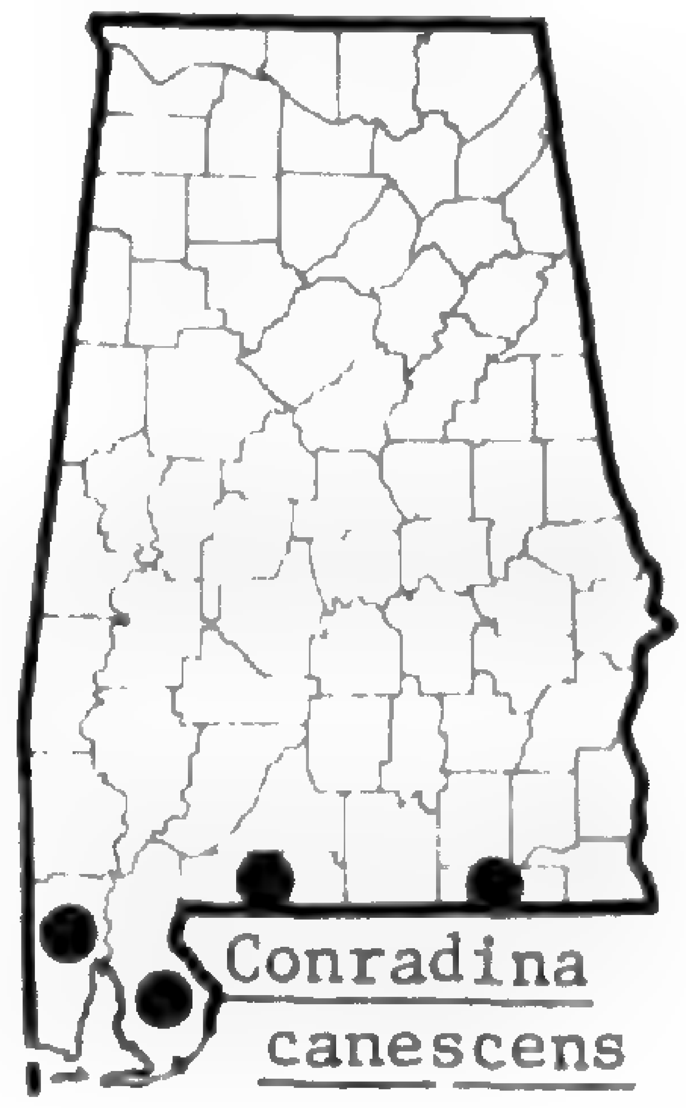
69. Solanaceae

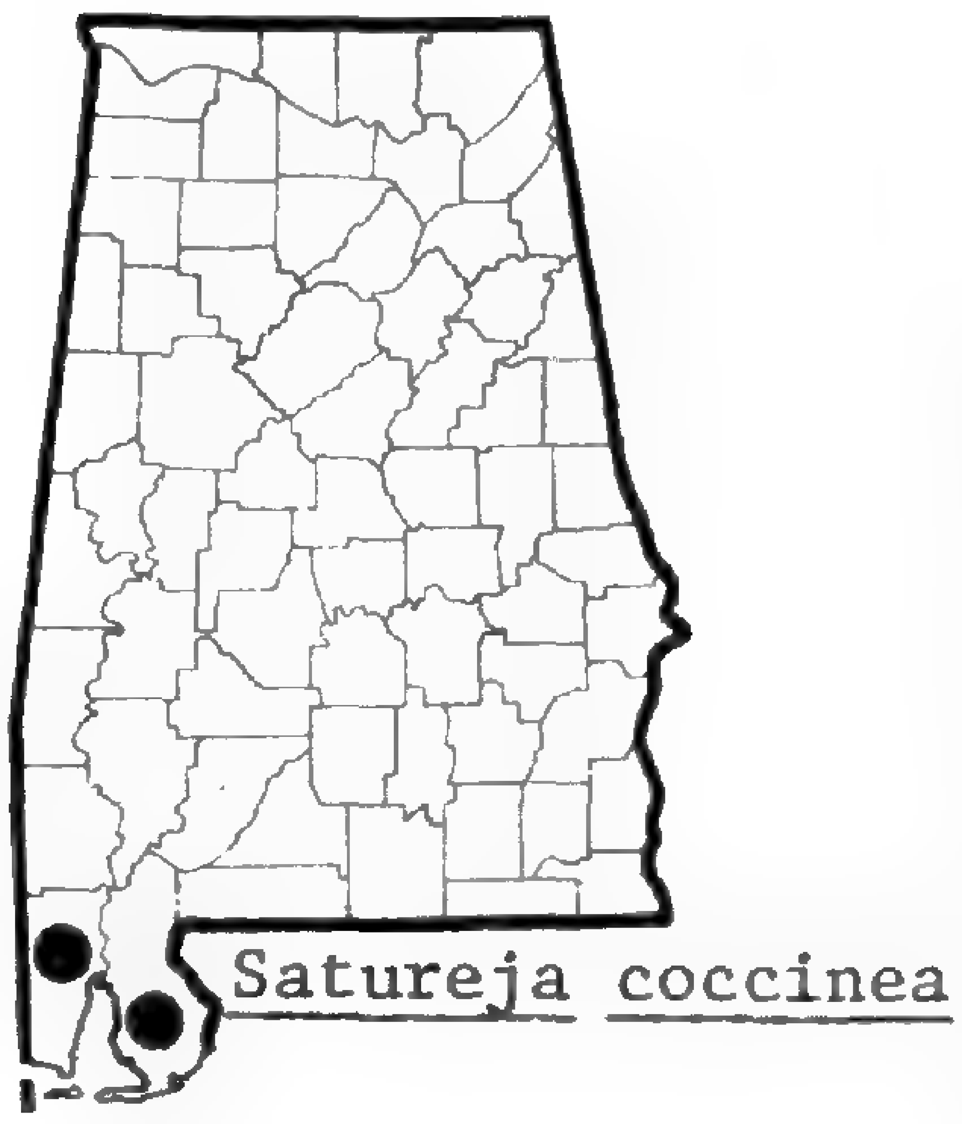
1. *Lycium* L.

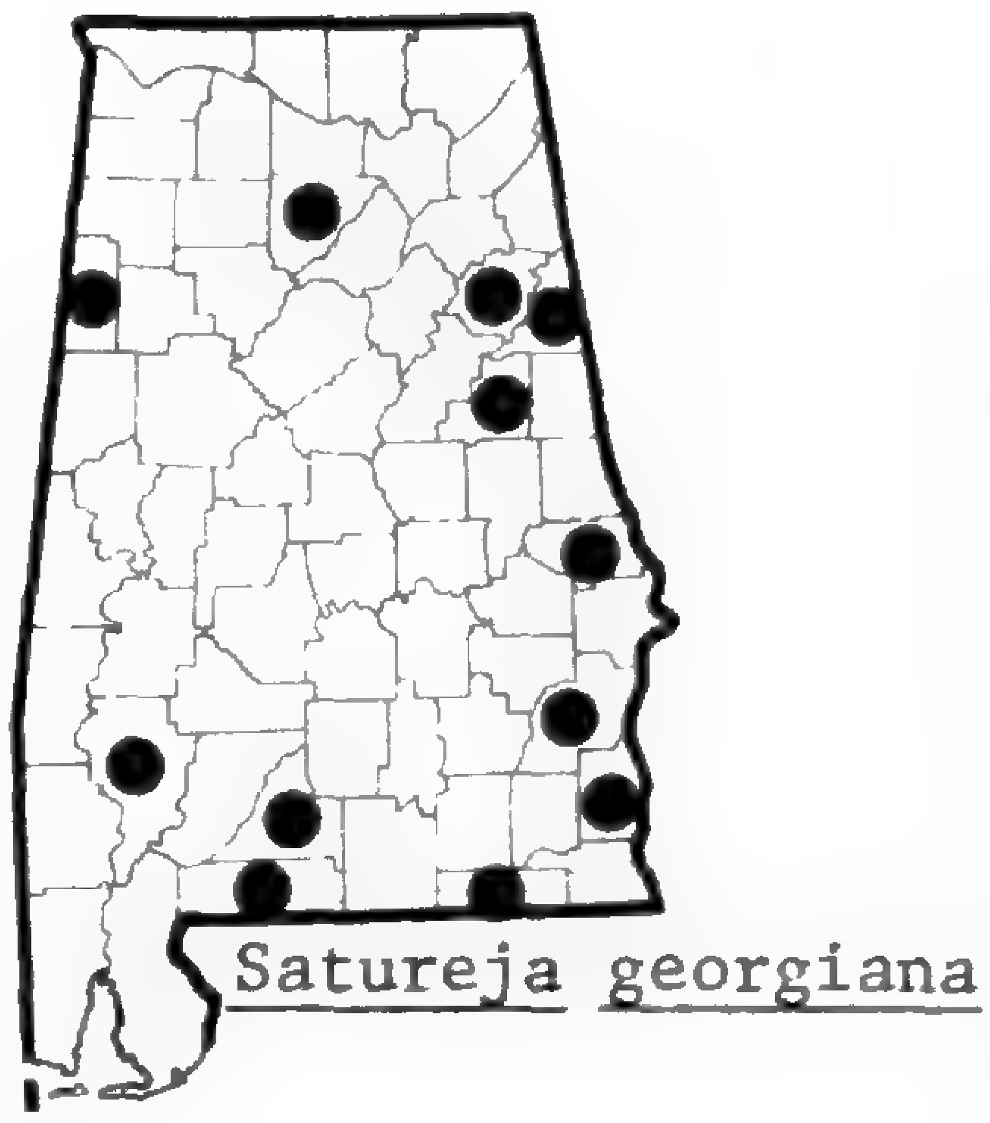
1. *L. carolinianum* Walter. Summer–fall. Reported from OCP by Mohr (1901).



68. LAMIACEAE

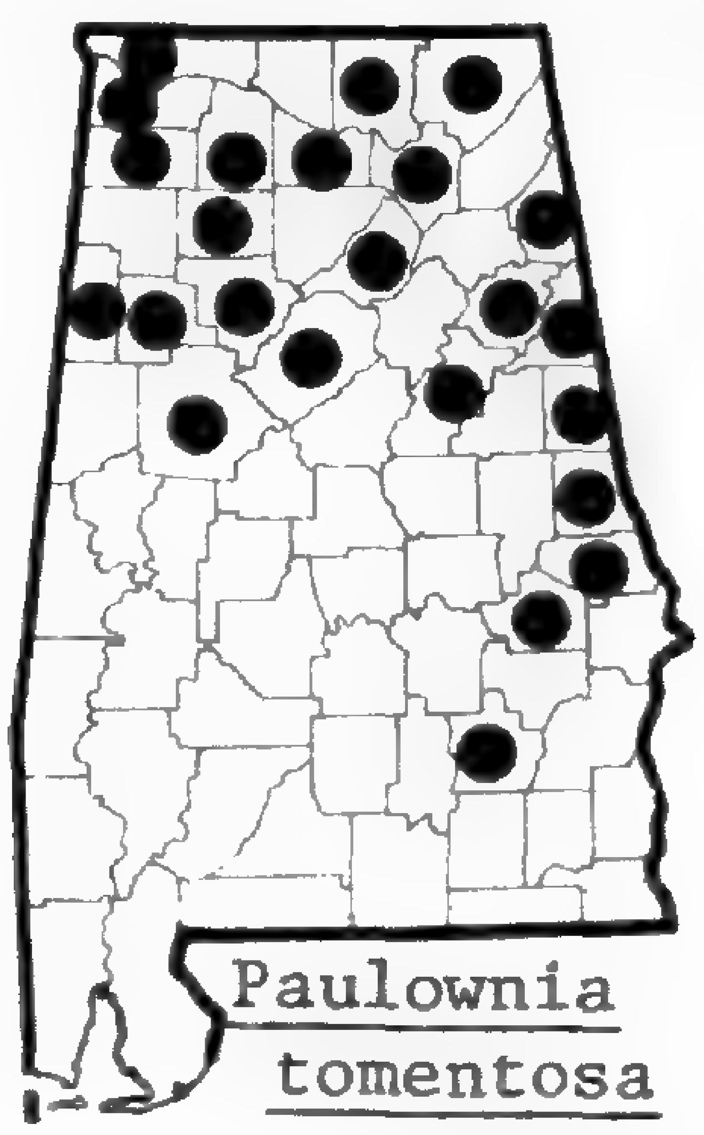




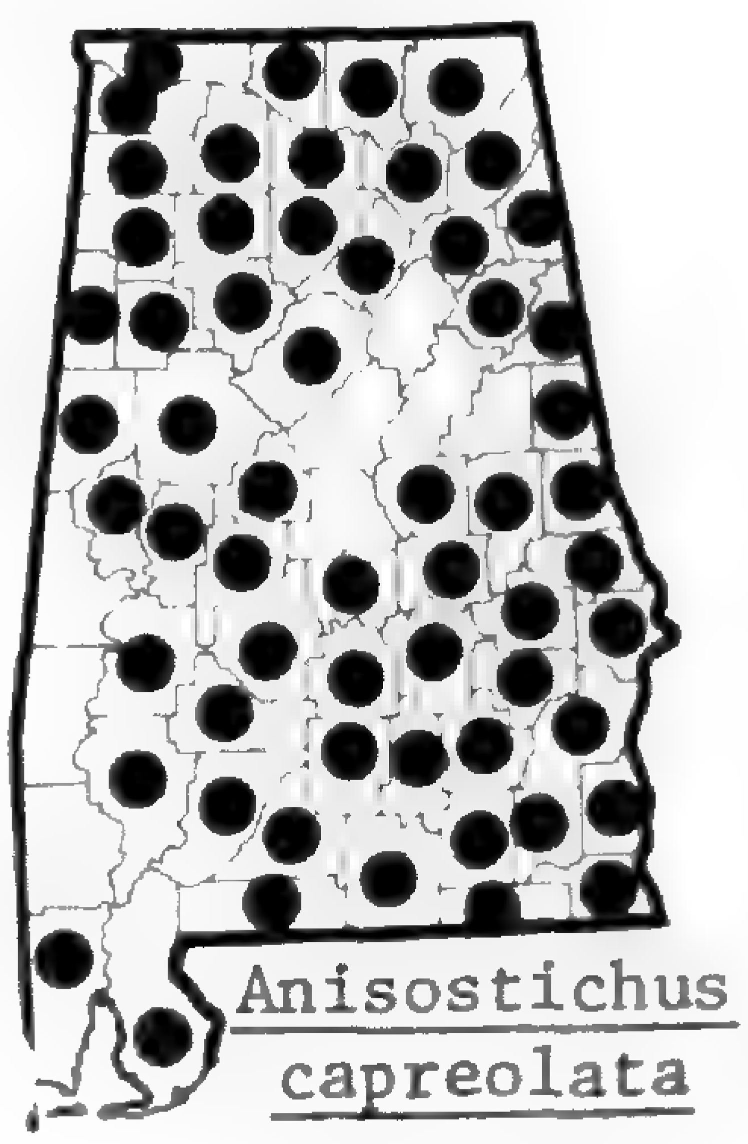


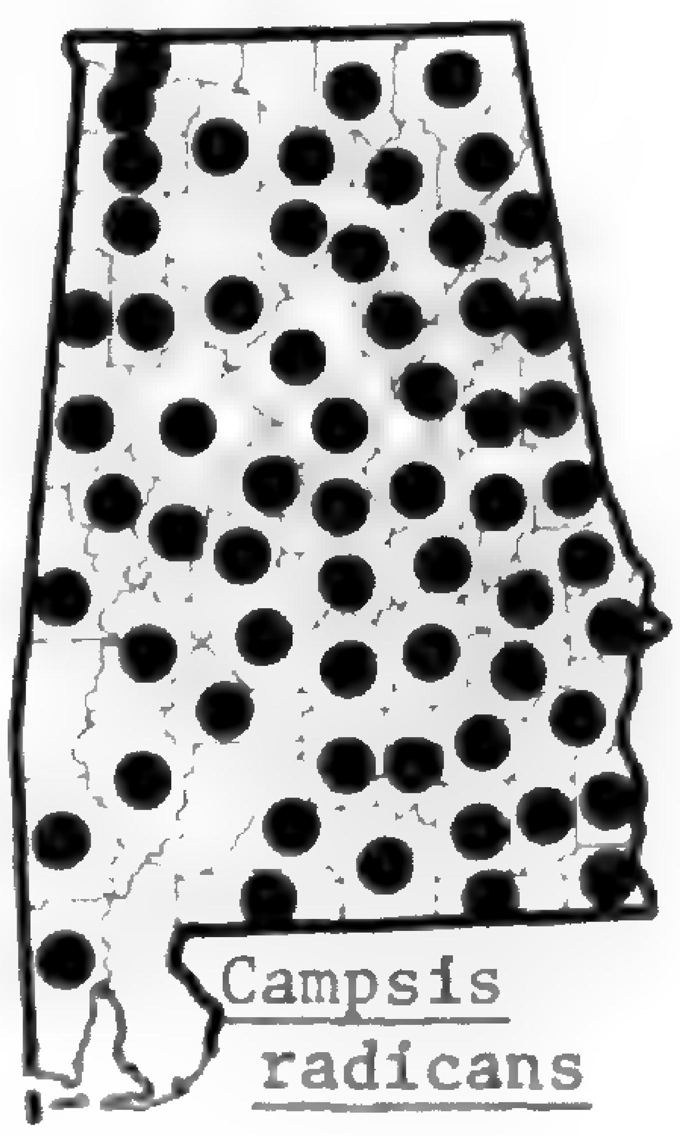
69. SOLANACEAE

70. SCROPHULARIACEAE



71. BIGNONIACEAE





70. SCROPHULARIACEAE

1. *Paulownia* Siebold & Zuccarini

1. *P. tomentosa* (Thunberg) Steudel. Spring; late summer–fall. Fencerows, waste places, escaped; throughout, but more common northward. *P. tomentosa* (Thunb.) Baill.—M.

71. BIGNONIACEAE

1. Leaves compound; plant a vine 2
  2. Leaflets 2, entire; leaf rachis terminated by a tendril .... 1. *Anisostichus*
  2. Leaflets 7 or more, serrate-dentate; leaf rachis terminated by a leaflet or leaflets .... 2. *Campsis*
1. Leaves simple; plant a tree .... 3. *Catalpa*

1. *Anisostichus* Bureau

1. *A. capreolata* (L.) Bureau, CROSS-VINE. Spring; summer. Woodlands, thickets; throughout. *Bignonia crucigera* L.—M, H; *A. crucigera* (L.) Bureau—S.

2. *Campsis* Loureiro

1. *C. radicans* (L.) Seemann, TRUMPET VINE, COW-ITCH. Late spring–summer; summer–fall. Fencerows, rights-of-way, thickets; throughout.

3. *Catalpa* L., INDIAN CIGAR TREE

1. *C. bignonioides* Walter, complex. Spring; late summer–fall. Fencerows, roadsides, swamp forests; throughout. *C. catalpa* (L.) Karst.—M; *C. speciosa* Warder *ex* Engelm. *in* Coult.—S, RAB.—This group is in need of biosystematic study.

72. RUBIACEAE

1. *Cephalanthus* L., BUTTONBUSH

1. *C. occidentalis* L. Late spring–early summer; summer–fall. Creek, swamp and pond margins, ditches; throughout.

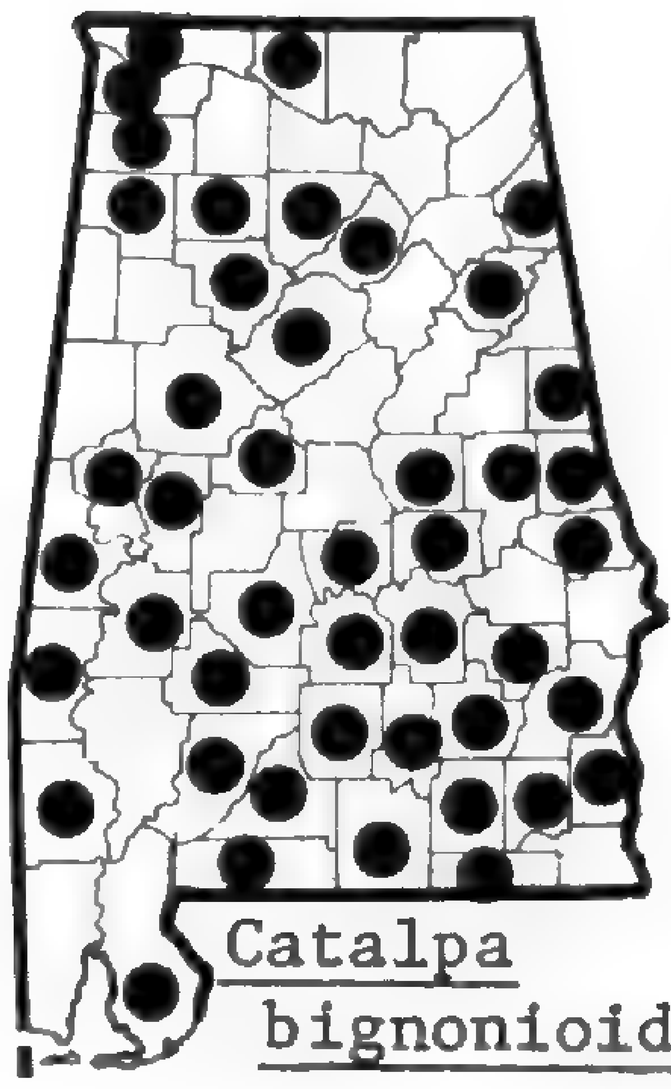
73. CAPRIFOLIACEAE

1. Leaves pinnately compound .... 3. *Sambucus*
1. Leaves simple 2
  2. Leaves subtending inflorescence connate-perfoliate; or plant a twining vine .... 2. *Lonicera*
  2. Leaves subtending inflorescence not connate-perfoliate; plant not a vine 3
    3. Inflorescences axillary .... 4. *Symphoricarpos*
    3. Inflorescences terminal 4
      4. Corolla funnelform; fruit a capsule .... 1. *Diervilla*
      4. Corolla rotate; fruit a drupe .... 5. *Viburnum*

1. *Diervilla* Miller

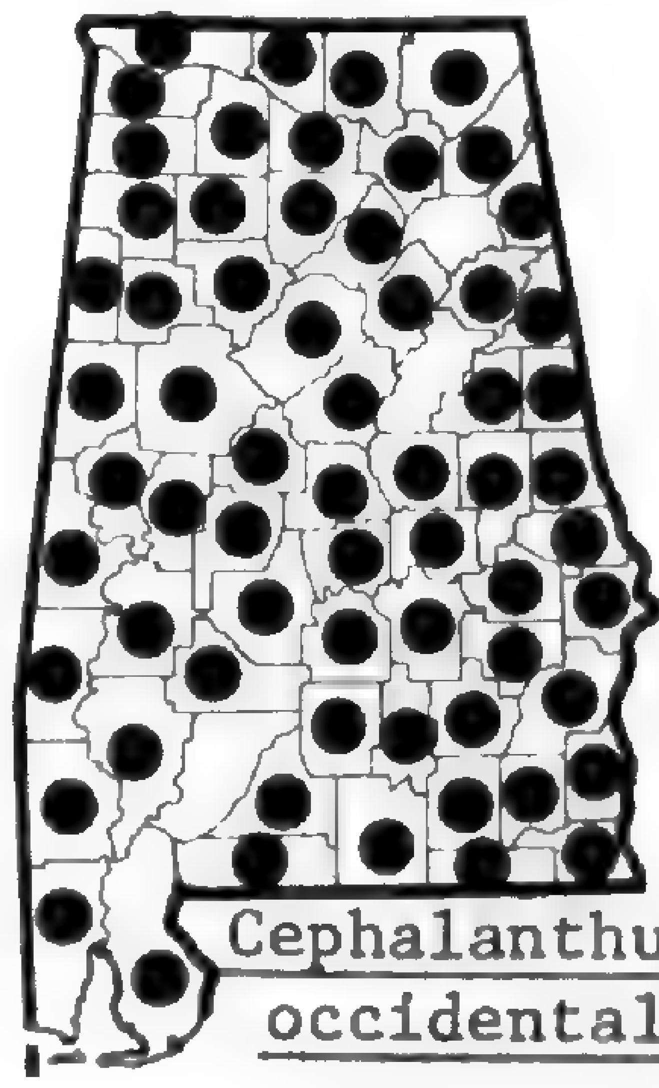
1. *D. sessilifolia* Buckley. Summer; late summer–fall.

1. Twigs glabrous, or pubescent in lines; calyx lobes more than 2 mm long .... 1. *D. sessilifolia* var. *sessilifolia*
1. Twigs densely pubescent over the entire circumference; calyx lobes 2 mm or less long .... 2. *D. sessilifolia* var. *rivularis*



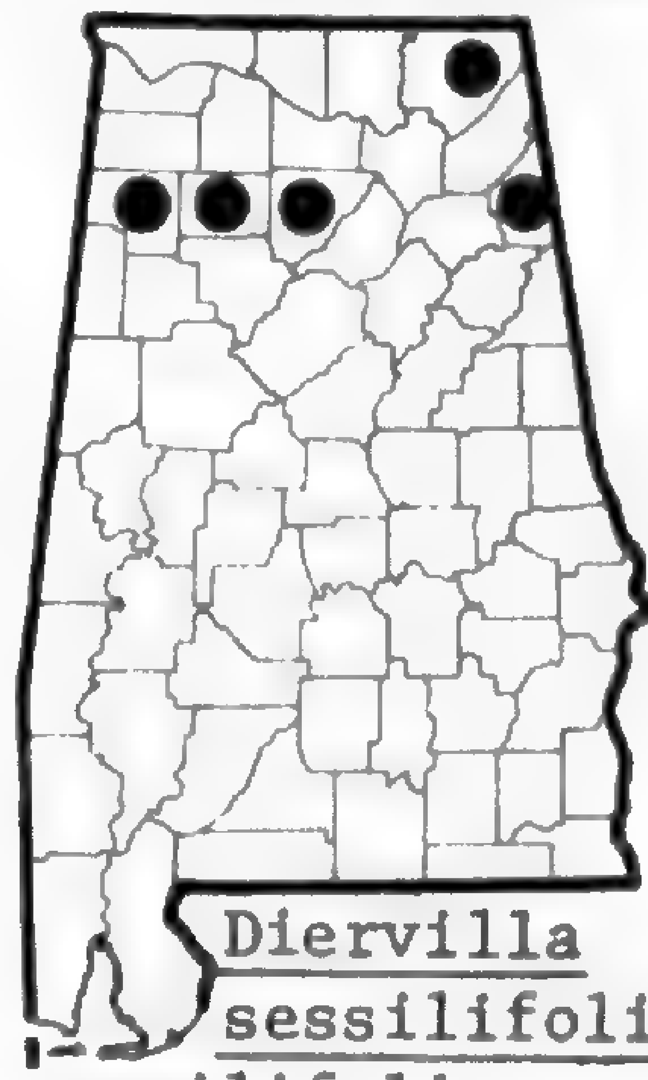
Catalpa bignonioides

72. RUBIACEAE



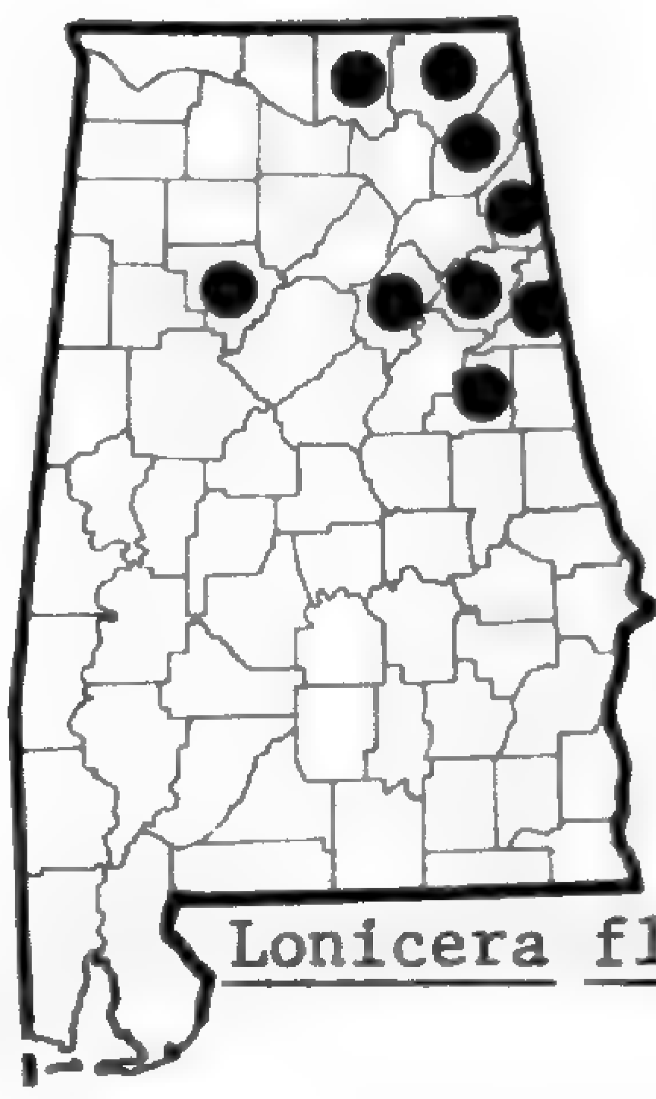
Cephalanthus occidentalis

73. CAPRIFOLIACEAE

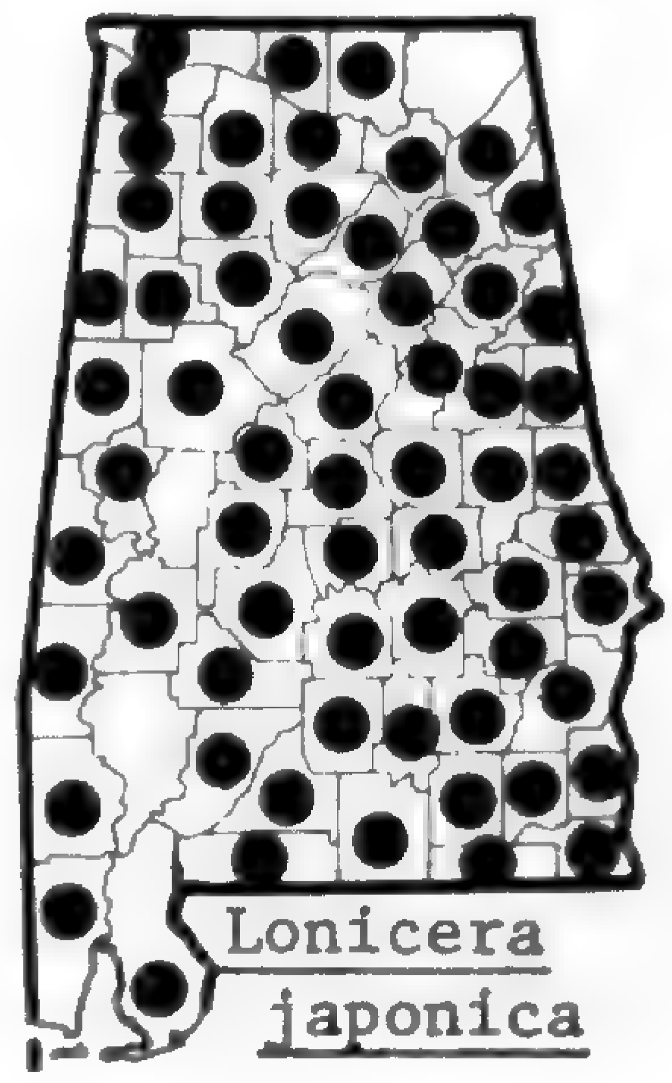


Diervilla sessilifolia var. *sessilifolia*

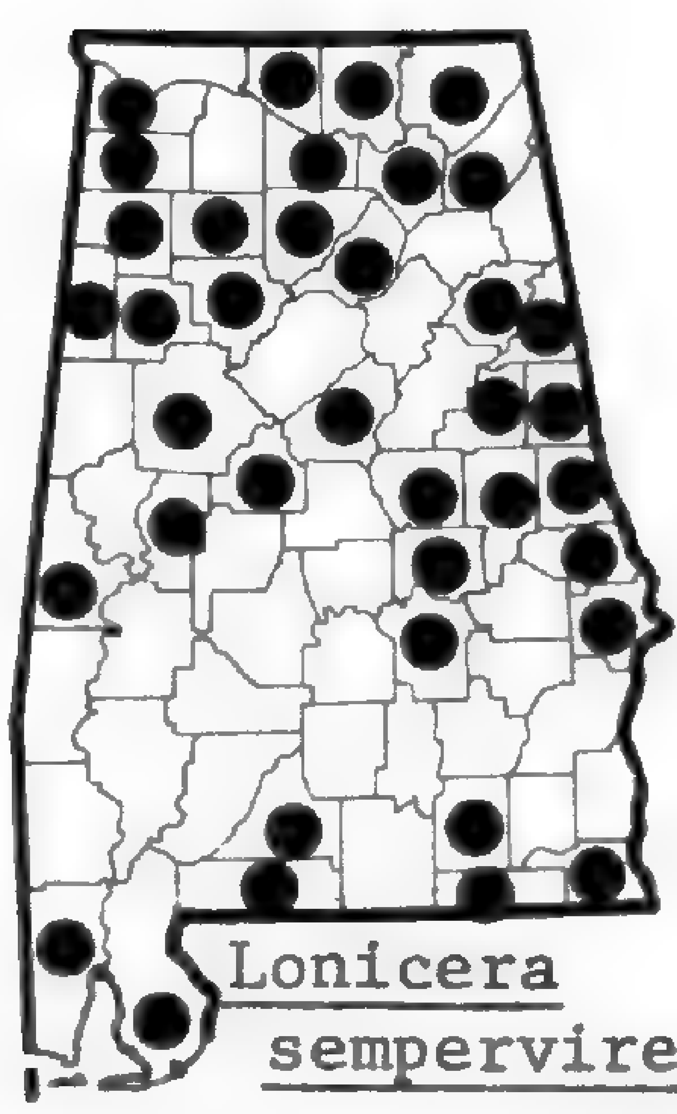
Diervilla sessilifolia var. *rivularis*



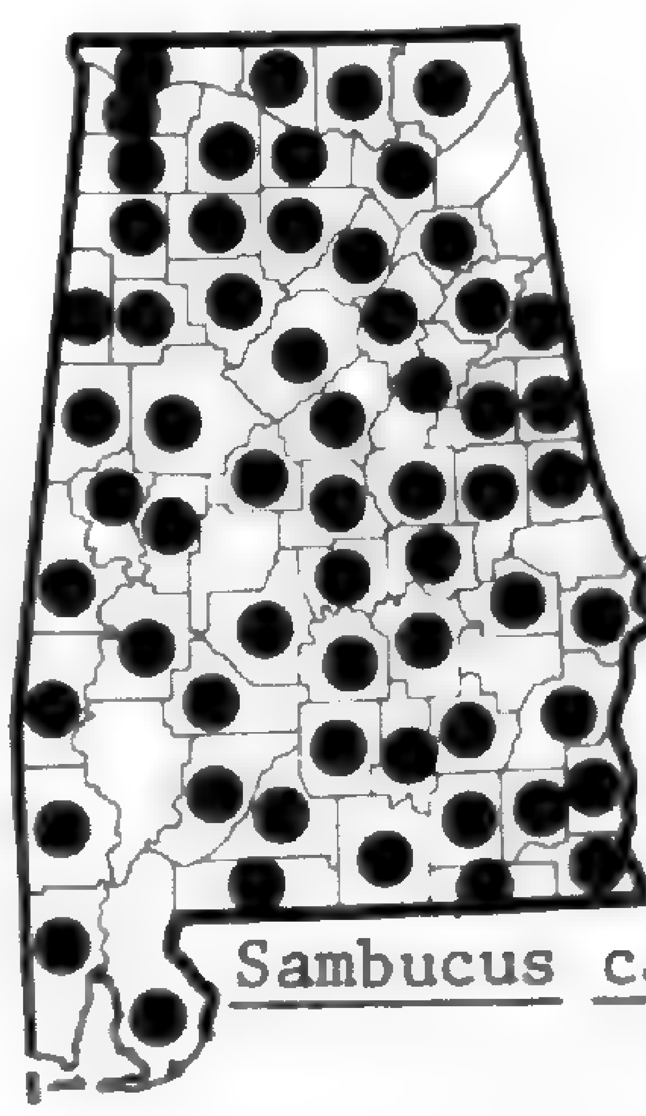
Lonicera flava



Lonicera japonica



Lonicera sempervirens



Sambucus canadensis

Symphoricarpos orbiculatus

D. sessilifolia Buckley var. *sessilifolia*. Open, rocky woods; CuP.

D. sessilifolia Buckley var. *rivularis* (Gattinger) Ahles. Open, rocky woods, northern CuP. *D. rivularis* Gatt.—M, H, S.

2. *Lonicera* L., HONEYSUCKLE

1. Inflorescence terminal; leaves subtending inflorescence connate-perfoliate 2
   2. Corolla yellow to golden, strongly bilabiate .... 1. *L. flava*
   2. Corolla red, its lobes subequal .... 3. *L. sempervirens*
1. Inflorescences axillary; leaves subtending inflorescences not connate-perfoliate 2. *L. japonica*

1. *L. flava* Sims, YELLOW H. Spring; summer. Open, rocky woods, rights-of-way; AM, VR, CuP.

2. *L. japonica* Thunberg, COMMON H. Summer; summer–fall. Thickets, roadsides, woodlands, a pesty escape; throughout.

3. *L. sempervirens* L., RED H. Spring–summer. Upland woods, thickets, fence-rows; throughout, but infrequent southward. *Phenianthus sempervirens* (L.) Raf.—S.

Lonicera longiflora (Sabine) DC. in Mohr (1901) is of uncertain status.

3. *Sambucus* L.

1. *S. canadensis* L., ELDERBERRY. Late spring–summer; summer. Open ditches, low woods, streambanks, pond margins; throughout. *S. simpsonii* Rehd.—S.

4. *Symphoricarpos* Duhamel

1. *S. orbiculatus* Moench. Summer; summer–fall. Alluvial or rich woods, in circumneutral soil; VR, CuP, HR. *S. symphoricarpos* (L.) MacM.—M, S.

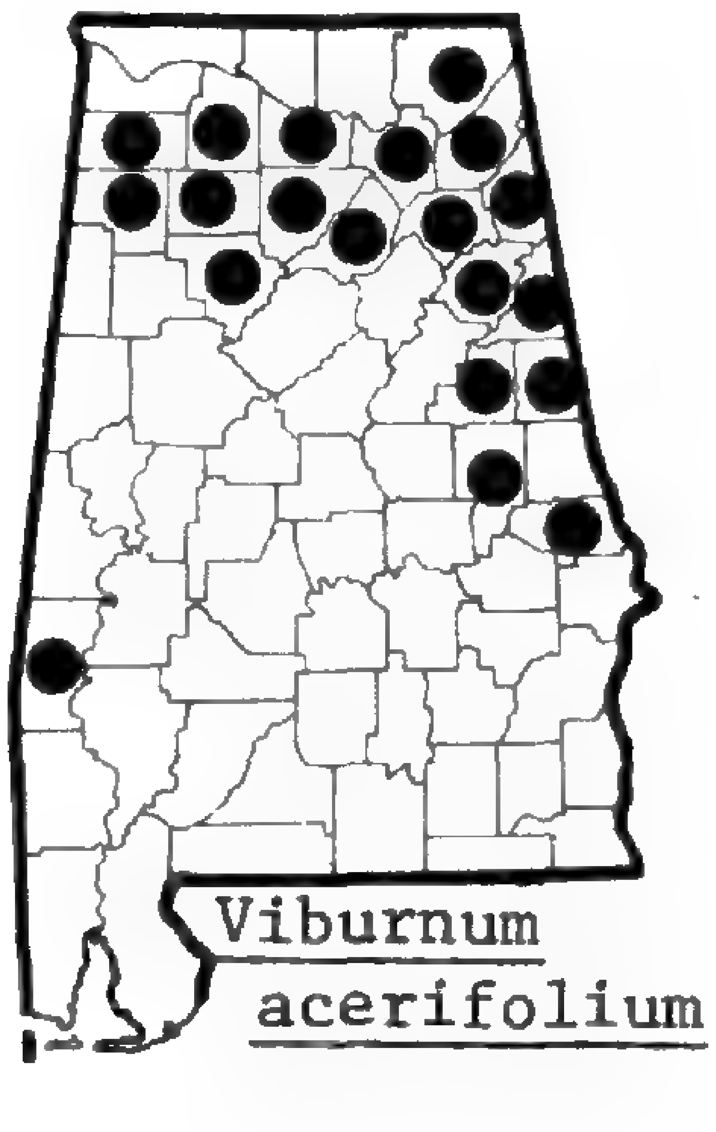
5. *Viburnum* L.

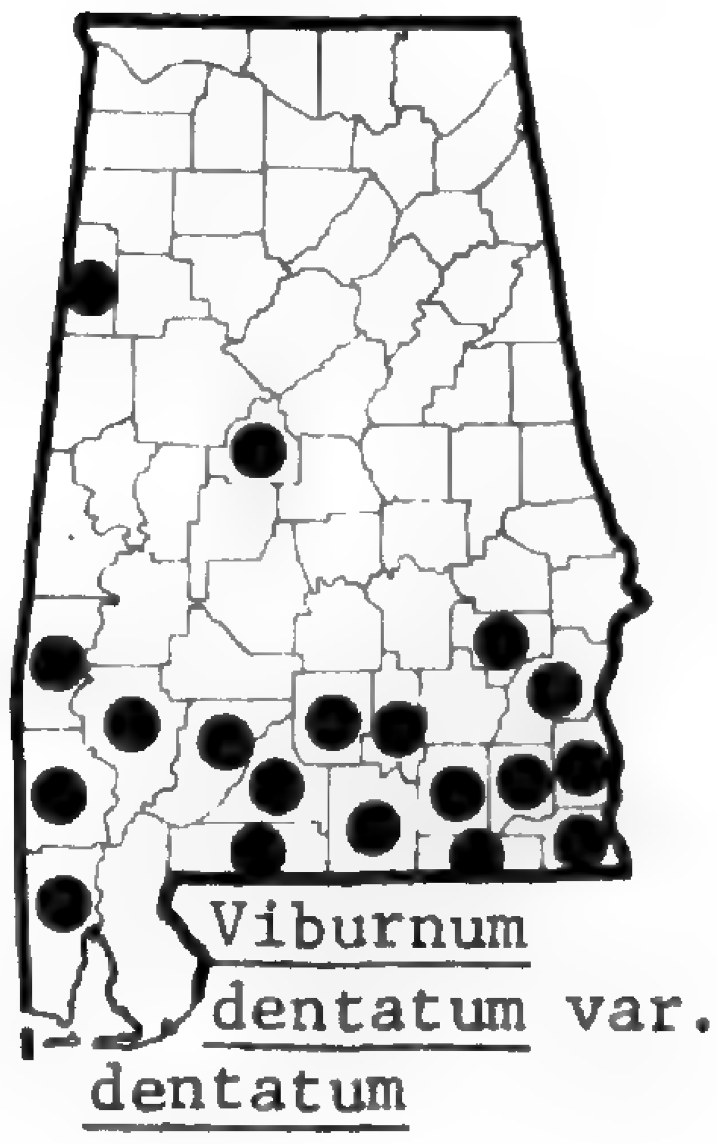
1. Leaves lobed .... 1. *V. acerifolium*
1. Leaves not lobed 2
   2. Leaves crenate, serrate or entire, or dentate and cuneate together 3
      3. Leaves spatulate to obovate, not acuminate .... 4. *V. obovatum*
      3. Leaves elliptic to ovate, usually acuminate 4
         4. Inflorescence sessile .... 5. *V. prunifolium*
         4. Inflorescence pedunculate 5
            5. Leaves glabrous beneath .... 3. *V. nudum*
            5. Leaves pubescent beneath, at least near the margins 6
               6. Leaf pubescence kinky, floccose, rufous, some trichomes stellate .... 7. *V. rufidulum*
               6. Leaf pubescence not kinky, floccose, rufous, or stellate .... 3. *V. nudum*
   2. Leaves dentate; rounded, truncate or cordate at base 7
      7. Petioles of upper leaves 5 mm long or less; stipules present .... 6. *V. rafinesquianum*
      7. Petioles of upper leaves more than 5 mm long; stipules usually absent .... 2. *V. dentatum*

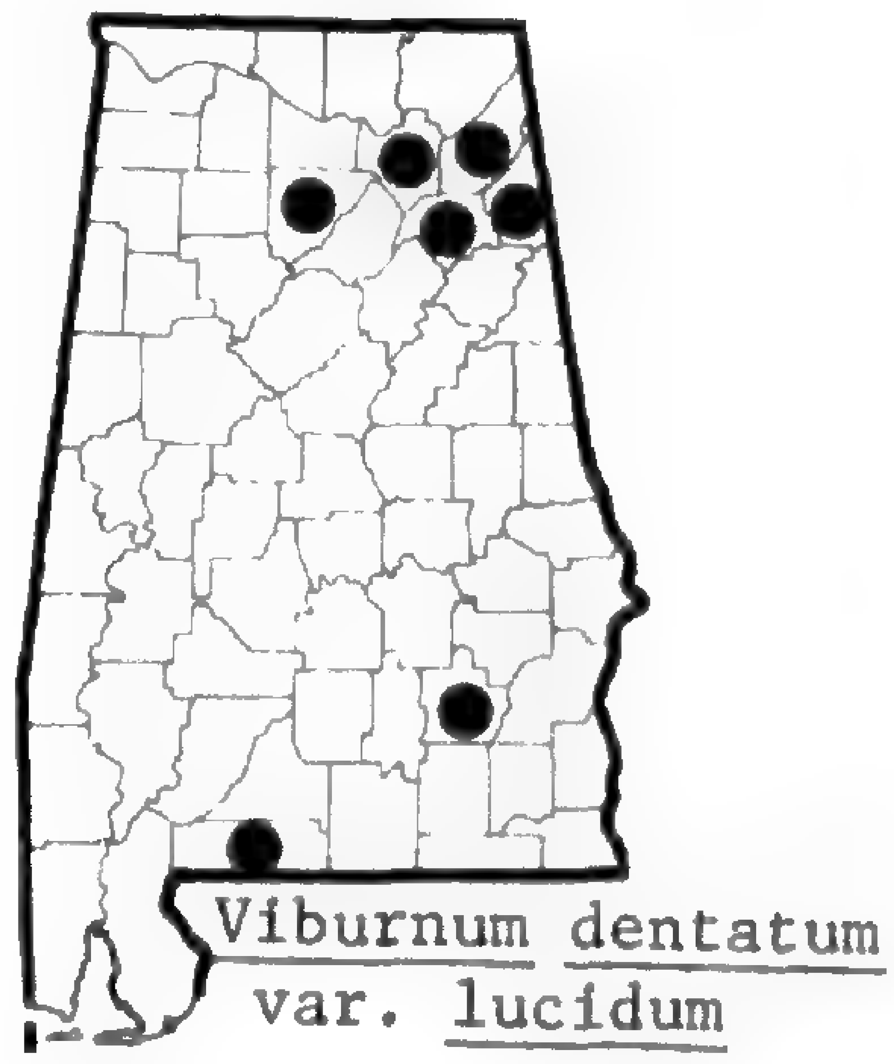
1. *V. acerifolium* L. Spring; late summer–fall. Rocky, rich or alluvial woods; CP (rare), AM, VR, CuP.

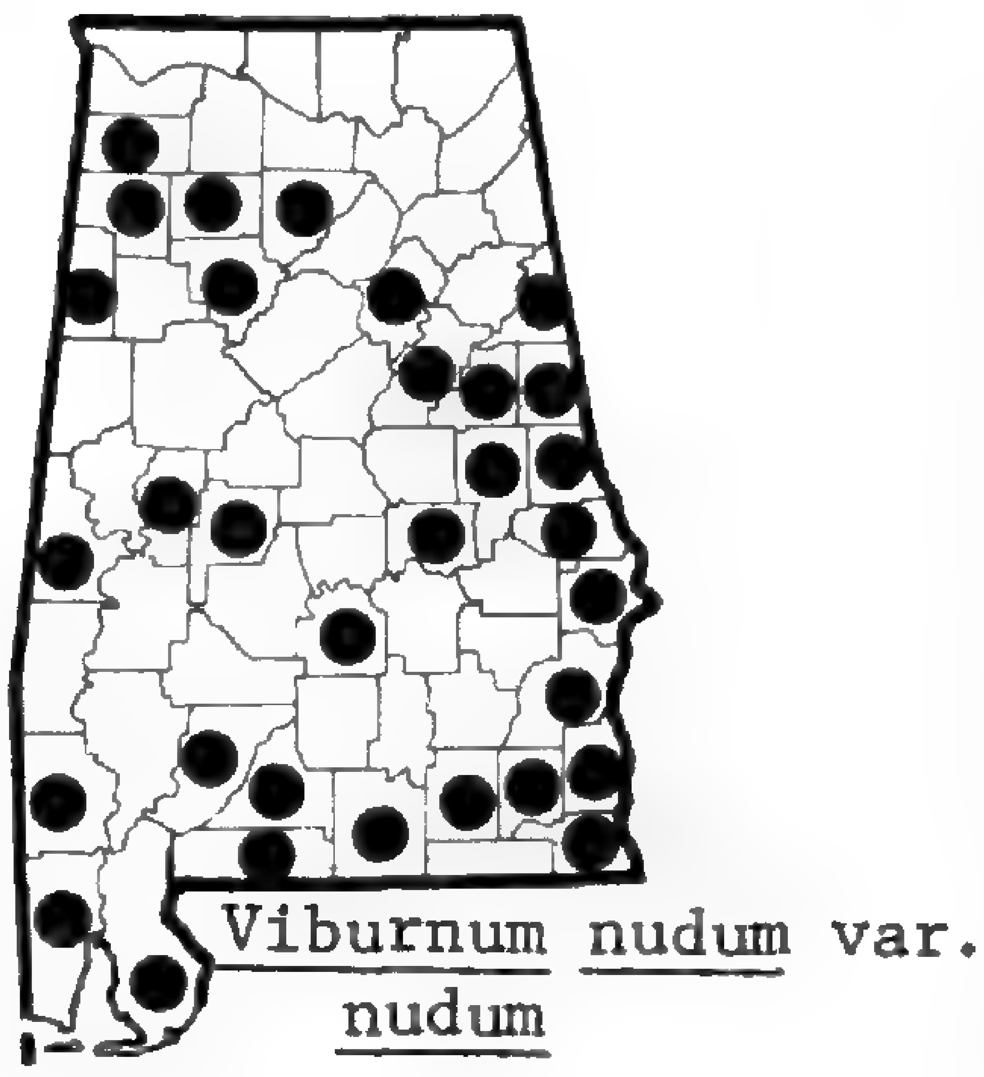
2. *V. dentatum* L. Spring; summer.

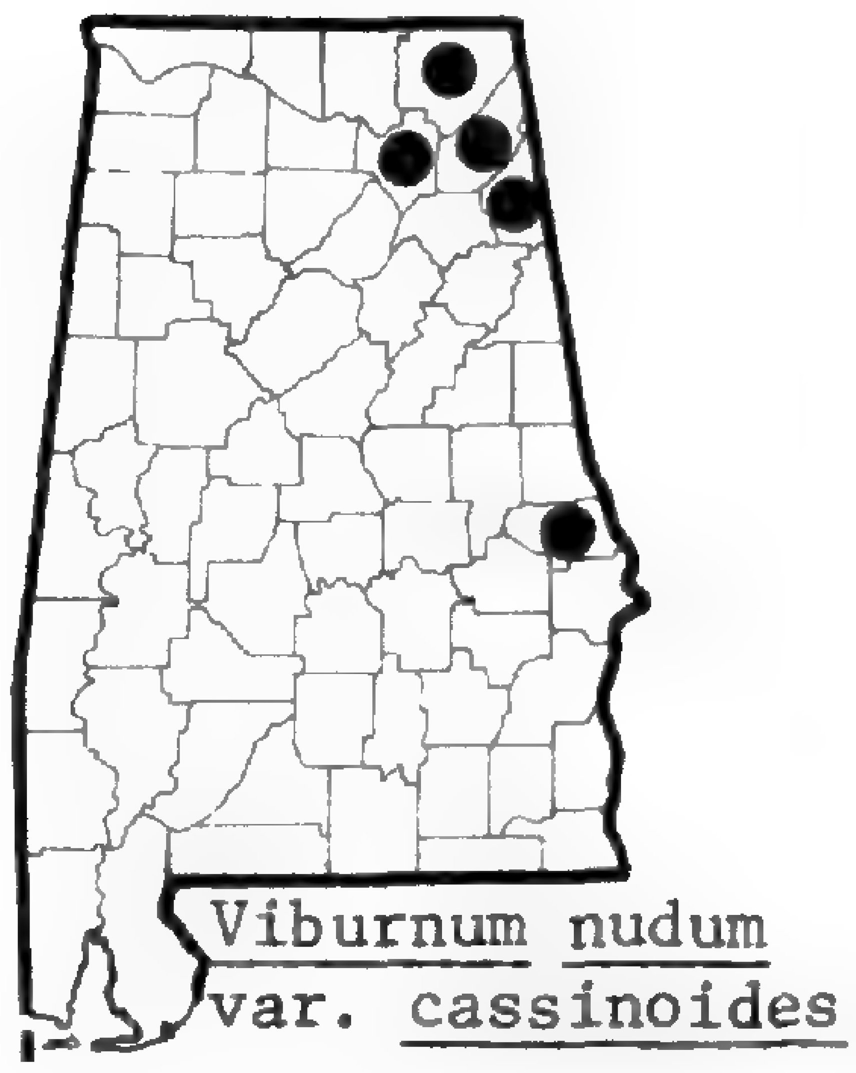
1. Leaves pubescent beneath .... *V. dentatum* var. *dentatum*
1. Leaves glabrous beneath, or pubescence confined to the principal veins and their axils .... *V. dentatum* var. *lucidum*

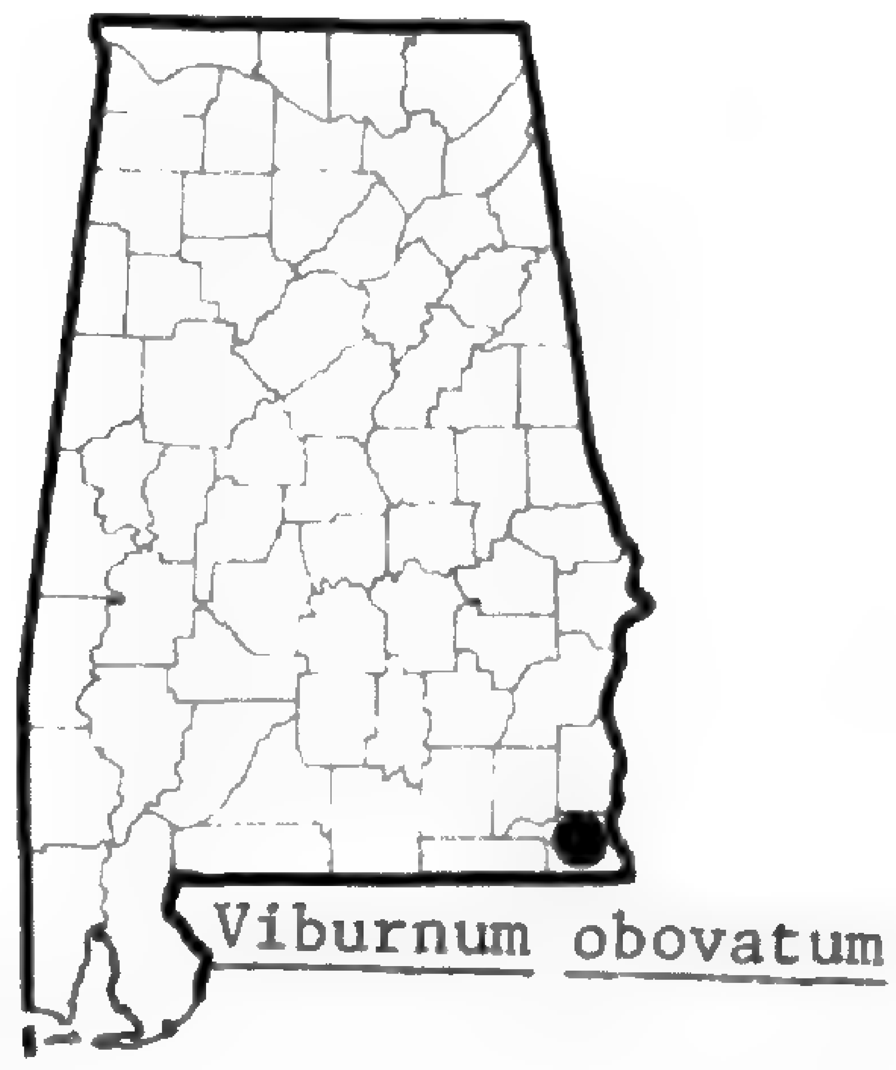

Viburnum
acerifolium

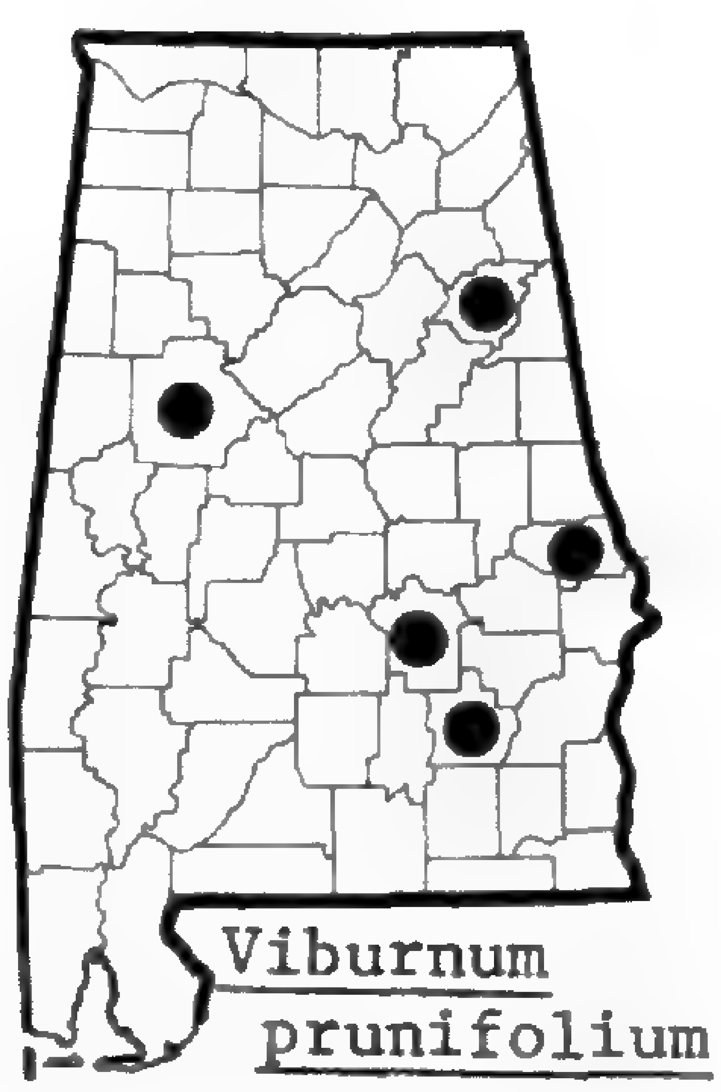

Viburnum
dentatum var.
dentatum


Viburnum dentatum
var. lucidum

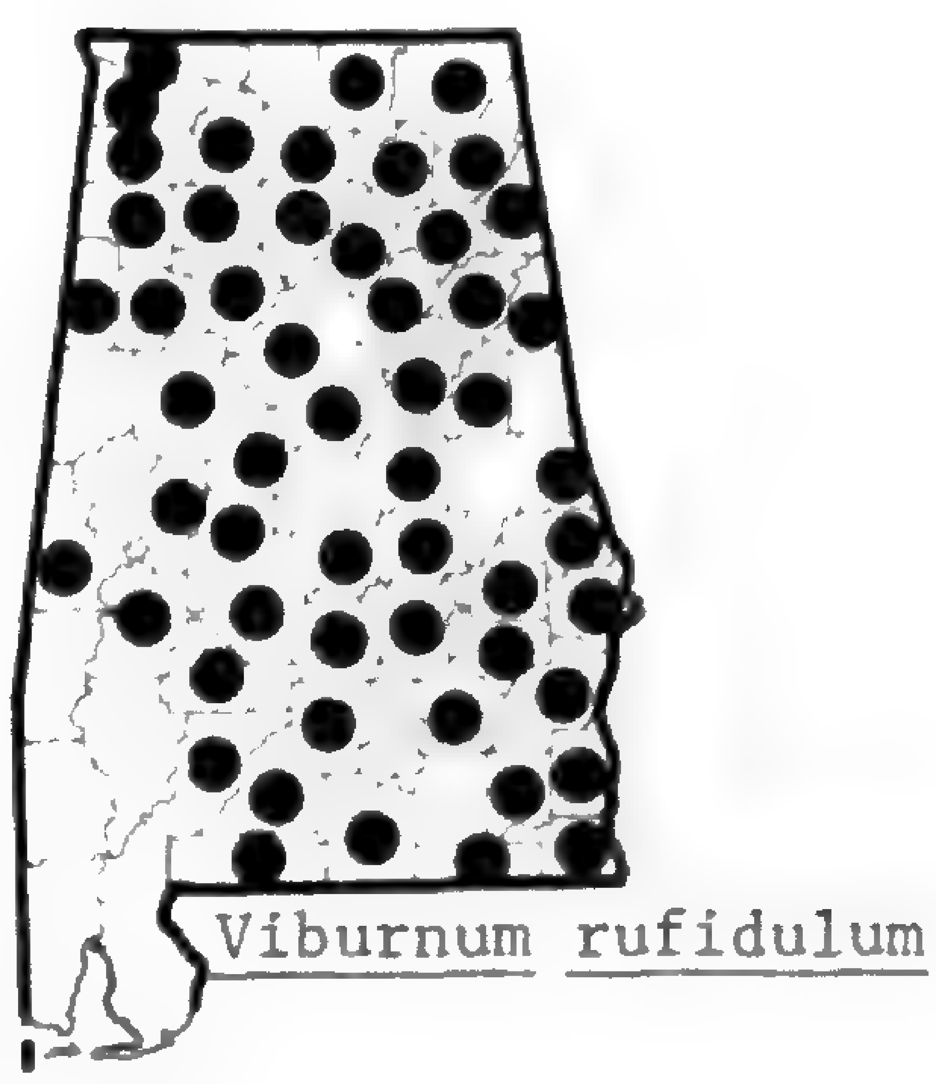

Viburnum nudum var.
nudum


Viburnum nudum
var. cassinoides


Viburnum obovatum


Viburnum
prunifolium


Viburnum
rafinesquianum


Viburnum rufidulum

V. dentatum L. var. *dentatum*. Alluvial woods, swamp forests, principally CP. *V. semitomentosum* (Michx.) Rehd., *V. bracteatum* Rehd.—S, H; *V. molle* Michx. —M.

V. dentatum L. var. *lucidum* Aiton. Low woods, alluvial woods; CP (rare), CuP. *V. dentatum* L.—S.

3. *V. nudum* L. Spring; summer–fall.

1. Leaves entire, sinuate or remotely serrate .... *V. nudum* var. *nudum*
1. Leaves, at least some, regularly serrate .... *V. nudum* var. *cassinoides*

V. nudum L. var. *nudum*. Seepages, bogs, swamps, low thickets; CP, P, AM, VR, CuP. *V. nitidum* Ait.—H, M.

V. nudum L. var. *cassinoides* Torrey & Gray. Rocky, moist woods, streambanks; P, northern CuP. *V. cassinoides* L.—M, H, S, RAB.

4. *V. obovatum* Walter. Spring. Alluvial woods, very rare; southeastern OCP.

5. *V. prunifolium* L. Spring; summer. Open, upland woods, very rare; CP, VR, southern CuP.

6. *V. rafinesquianum* Schultes. Known by a single collection from VR; very rare.

7. *V. rufidulum* Rafinesque. Spring; late summer–fall. Upland xeric or rich woods; throughout. *V. rufotomentosum* Sm.—M.

74. ASTERACEAE

1. Leaves opposite 2
   2. Ray flowers absent .... 3. *Iva*
   2. Ray flowers present .... 2. *Borrichia*
1. Leaves alternate 3
   3. Pappus absent .... 3. *Iva*
   3. Pappus present 4
      4. Flowers unisexual; staminate and pistillate flowers in separate heads .... 1. *Baccharis*
      4. Flowers bisexual .... 4. *Solidago*

1. *Baccharis* L.

1. Leaves linear, less than 5 mm wide .... 1. *B. angustifolia*
1. Leaves elliptic to ovate, more than 6 mm wide .... 2. *B. halimifolia*

1. *B. angustifolia* Michaux. Fall. Brackish marshes, rare; OCP.

2. *B. halimifolia* L., GROUNDSEL TREE. Fields, fencerows, brackish marshes, seepages; CP, AM (rare).—Much more common southeastward.

2. *Borrichia* Adanson, SEA OX-EYE

1. *B. frutescens* (L.) DC. Spring–fall. Brackish marshes, low dunes; OCP.

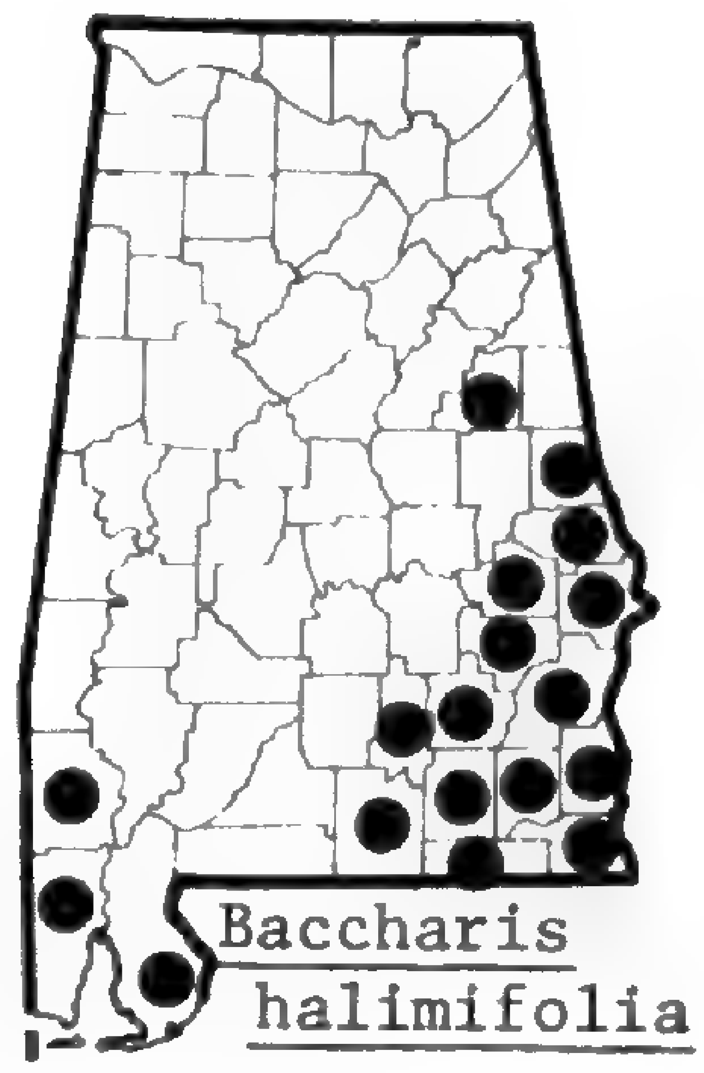
3. *Iva* L.

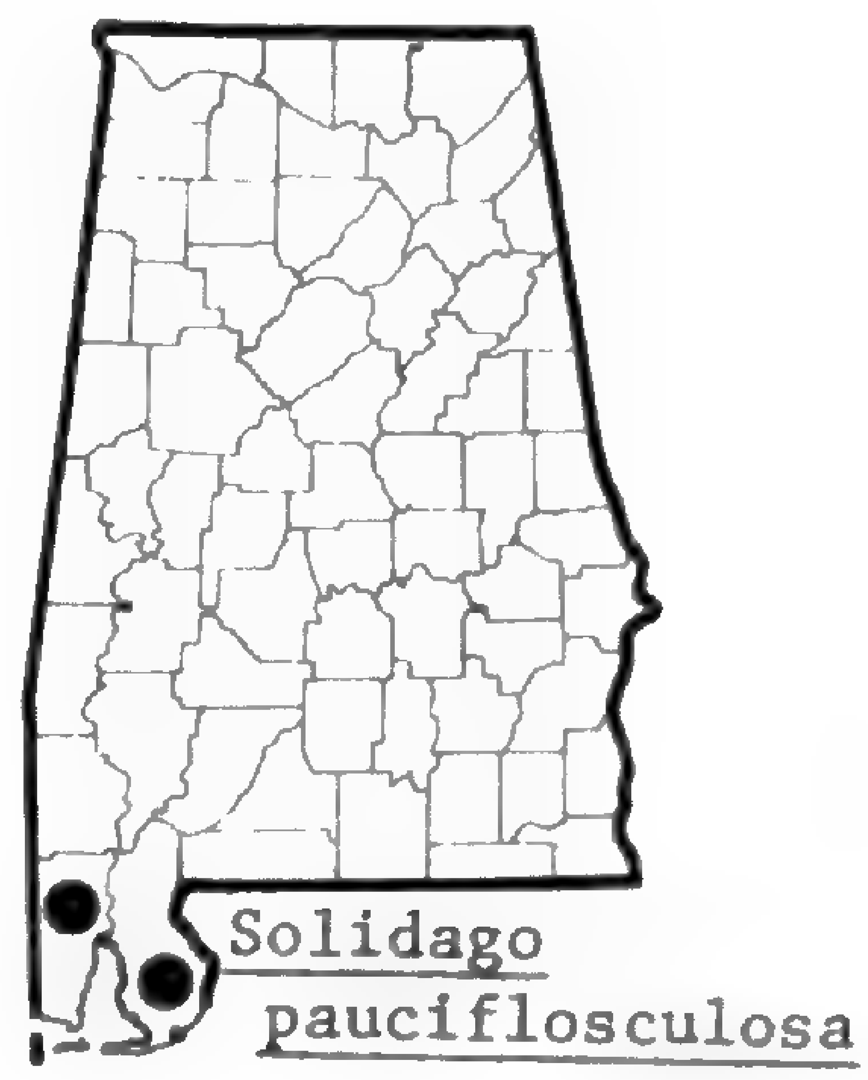
1. Stems and leaves appressed-pubescent .... 1. *I. frutescens*
1. Stems and leaves glabrous .... 2. *I. imbricata*

1. *I. frutescens* L. Summer–fall. Brackish marshes; OCP. Reported by Mohr (1901), Harper (1928), and Dean (1961).

2. *I. imbricata* Walter. Summer–fall. Dunes; OCP.

74. ASTERACEAE





4. *Solidago* L.

1. *S. pauciflosculosa* Michaux. Fall. Dunes; OCP. *Chrysoma pauciflosculosa* Greene—M, S; *C. pauciflosculosa* (Michx.) Greene—H.

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AN ADDITION AND NOMENCLATURAL CHANGE IN THE TRIBE PORANEAE (CONVOLVULACEAE)[1]

Daniel F. Austin[2]

Abstract

The New World members of *Calycobolus* are discussed in connection with *C. lanulosus* D. Austin, sp. nov., and *C. nutans* (Mociño & Sessé *ex* Choisy) D. Austin, comb. nov. Known ranges for the New World species are provided.

During my examination of the tribes in the Convolvulaceae, numerous collections of the family have come to me for determination (Austin, 1970*a*, 1970*b*, 1971; Steyermark & Austin, 1970). Among those collections were the following two members of the tribe Poraneae.

1. **Calycobolus lanulosus** D. Austin, sp. nov.

Species a *C. nutans* similibus, sed ramis dense lanulosis, tomento foliorum densiore, inflorescentiis cymosis axillaribus distincta est.

Lianas to 5 m; stems densely gray woolly pubescent with small soft trichomes. *Leaves* with petioles 5–10 mm long; blades ovate to ovate-elliptic, 5–8 cm long, 2.5–5 cm wide, coriaceous, base obtuse, apex mucronate, the secondary veins 5 or 6 pairs; densely pubescent above and below with woolly, white or yellowish trichomes. *Inflorescences* dense, axillary, cymose, peduncles 2–3 mm long, densely pubescent. *Flowers* with pedicels 2 mm long; two external sepals bracteose, 10–12 mm long, 9–10 mm wide, subdeltoid, base slightly auriculate, apex mucronate, with a dense cover of cream-white to yellowish indument, three internal sepals not bracteose, 4 mm long, 3–4 mm wide, ovate to lanceolate, apex acuminate, with indument as outer sepals; corolla funnelform, white, 8–9 mm long, lobes shallow, acuminate, erect; stamens included, filaments attached 2 mm from corolla base, subulate, 6 mm long, glabrous, anthers oblong, 1.7 mm long; ovary 1 mm long, 1 mm in diameter, apex pubescent with a beard 2 mm long, disc cupuliform, 5-lobed, styles fused for 2.5 mm with 2 free branches 1 mm long, stigmas capitate, subglobose. Immature *fruits* 2.5 mm long, 2 mm in diameter, 2-locular, septum complete, ovules 4.

Holotype: Brazil. bahia: Proximo a Jaguaquara, zona da mata, trepadeira em árvores de 5 m, corola branca, bracteas verde-creme, 22.I.1965, *Belem & Mendes 215* (US).

Although certain species [*Bonamia ferruginea* (Choisy) Hallier f., *B. maripoides*

[1] I wish to acknowledge support by the Air Force Office of Scientific Research (Contract No. F44620-67-C-0055, Walter H. Lewis, principal investigator), and grants from the Society of the Sigma Xi and the Florida Atlantic University Division of Sponsored Research. Thanks are due to the curators of herbaria (MO,US) for loans of plant specimens, and to Dr. Walter H. Lewis and Dr. Bernard Verdcourt who were kind enough to offer suggestions on the original manuscript.

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Ann. Missouri Bot. Gard. 58: 243–244.

Hallier f.] have been incorrectly placed in *Calycobolus*, their dehiscent fruits indicate affinities with the tribe Dicranostyleae *sensu* Hallier (1893). At present there appear to be five American species correctly referable to this genus. *Calycobolus nutans* (Choisy) D. Austin occurs in southern Mexico; *C. amazonicus* (Choisy) House, *C. glaber* (H.B.K.) House, and *C. sericeus* (H.B.K.) House in the upper Amazon basin; and *C. lanulosus* D. Austin along the Brazilian coast of Bahia State. The species in Bahia is a disjunct eastern range extension for the genus in the New World.

2. **Calycobolus nutans** (Mociño & Sessé *ex* Choisy) D. Austin, comb. nov.

Ipomoea nutans Mociño & Sessé *ex* Choisy *in* DC., Prodr. 9: 368. 1845.
Dufourea velutina Mart. & Gal., Bull. Acad. Roy. Sci. Bruxelles 12(2): 259. 1845.
Prevostea? (*Dufourea*?) *velutina* (Mart. & Gal.) Walpers, Repert. Bot. Syst. 6: 742. 1846.
Breweria mexicana Hemsl., Biol. Centr. Amer. Bot. 2: 400. 1882.
Porana velutina (Mart. & Gal.) Hallier f., Bot. Jahrb. Syst. 16: 538. 1893.
Calycobolus pringlei House, Bull. Torrey Bot. Club 34: 145. 1907.
Calycobolus velutinus (Mart. & Gal.) House, Bull. Torrey Bot. Club 34: 145. 1907.
Turbina velutina (Mart. & Gal.) Roberty, Candollea 14: 26. 1952.
Turbina mexicana (Hemsl.) Roberty, Candollea 14: 26. 1952.
Porana nutans (Choisy) O'Donell, Lilloa 30: 62. 1960.

Ipomoea nutans was based on an unpublished epithet and plate by Sessé and Mociño. I have not seen the plate in Geneva (G), but I have seen the copy of this plate at US.

Martens and Galeotti commented (1845: 278) that they received a copy of Choisy's (1845) treatment of the Convolvulaceae while their paper was in press. Because of this, Choisy's specific name has priority and must be used. O'Donell (1960), noting their comment, transferred the epithet to the African and south-eastern Asian genus *Porana* following Hallier (1893). Although both *Porana* and *Calycobolus* are badly in need of revision, they are distinct genera; flowering sepals are bracteose in *Calycobolus*, but in *Porana* they become bracteose only in fruit.

O'Donell (1960) put *Breweria mexicana* and *Calycobolus pringlei* in synonymy with *Porana nutans* (= *Calycobolus nutans*). This is probably correct, but the Mexican plants vary considerably in leaf shape, sepal shape, and pubescence density. There is perhaps more than one taxon involved, but more collections are needed to resolve the problem.

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O'DONELL, C. A. 1960. Notas sobre Convolvulaceas americanas. Lilloa 30: 39–69.

STEYERMARK, J. A. & D. F. AUSTIN. 1970 [1971]. A New Species of *Dicranostyles* from Venezuela. Ann. Missouri Bot. Gard. 57: 155–157.

SORGHUM PACHYTENE KARYOTYPES[1]

PHILIP BUSEY[2]

ABSTRACT

Sorghum [S. *bicolor* (L.) Moench] pachytene chromosomes show considerable detail in morphology. Previous reports have characterized karyotypes. In the present study, karyological observations covered a wide range of sorghum germplasm. Most collections were found unsatisfactory for karyotype analysis. Of those which were satisfactory, exhaustive simultaneous comparisons of chromosome lengths, arm ratios, and other morphology could not establish any complete karyotypes. Of the ten chromosome pairs, however, one nucleolar pair and one asymmetric pair were easily identified. A group of three longer pairs could be distinguished from five shorter pairs. Beyond this, it did not seem that complete karyotypes could ever be obtained, in view of the large length variation computed for the two identifiable chromosomes. This variation could not be entirely assigned to hypotheses of chromosome shortening or to any feature of the technique, though each step of the technique was analyzed for its reliability. The nonconformity of the present results from those of previous reports challenges the repeatability of the previous experiments. This, in line with statements by some sorghum workers, suggests that the basic karyology of sorghum is not well understood.

Sorghum bicolor (L.) Moench (Gramineae) includes the grain sorghums, cultivated widely in many of the world's developing regions—in much of Africa, and parts of India and China. Sorghum is thereby one of the six great staples in the human diet along with rice, wheat, cassava, maize, and the potato (Brown, 1963: 32).

I can think of two general purposes that speak for the application of cytology to cultivated plants. The first of these purposes is crop improvement; the second is the synthesis of new knowledge. One outgrowth of modern plant breeding has been the search for ways of applying cytology to selecting better crop varieties. Basic information on the chromosomes and their behavior has been sought for the major crops of the world. Admittedly, much of this information is yet to be of wide use. But the recent field of cytogenetics has provided the bases for the substitution of alien germplasm, techniques using autoploidization, and means of manipulating breeding systems to do much of the work of selection. These new tools already promise some amelioration of human life, in the face of expanding populations.

A further development of cytology in its application to cultivated plants is indirect knowledge of crop variation and origins. Anderson (1952: 72) said, "But quite as important as any of the specific information which it [cytology] contributes to the problem of the origin of cotton or the origin of tobacco, is the

[1] Derived from portions of a thesis submitted to the Graduate College of the University of Illinois in partial fulfillment of the requirements for the degree of Master of Science in Agronomy. Made possible by a Graduate Research Assistantship in Crop Science from the Agronomy Department of the University of Illinois Agricultural Experiment Station. I sincerely thank Mrs. Betty C. Busey, for making most of the pachytene chromosome measurements used in this study, and Dr. Jack R. Harlan, for encouragement and suggestions during the compilation of the observations. All collections were obtained from the herbarium of the Crop Evolution Laboratory of the Agronomy Department of the University of Illinois.

[2] Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.

ANN. MISSOURI BOT. GARD. 58: 245–257.

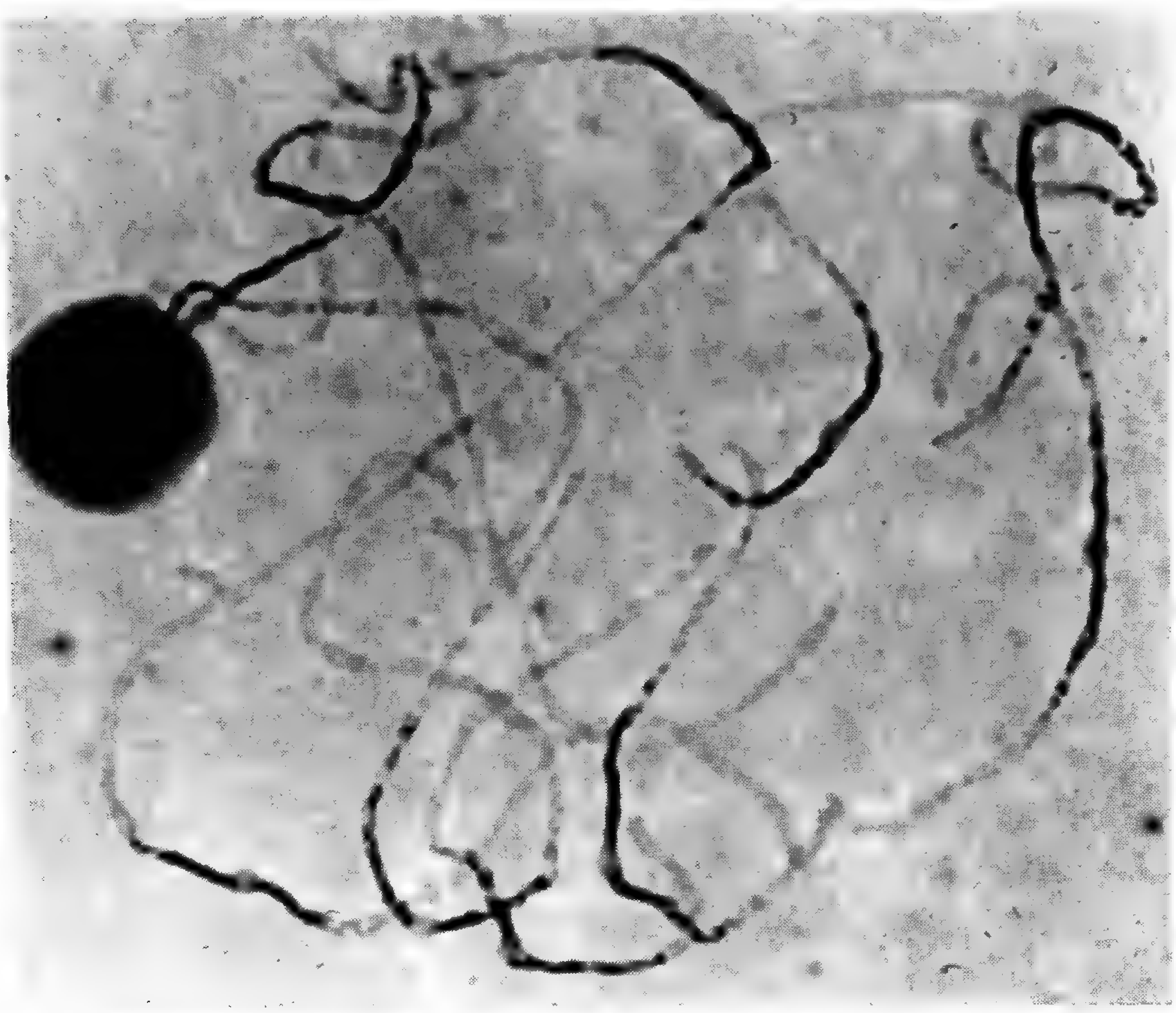

FIGURE 1. Pachytene chromosomes of *Sorghum bicolor* with 10 pairs separable (accession 2399), 1870 ×.

bearing of cytological evidence on the general problem of cultivated plants as a whole."

This "general problem" is one which has synthesized many fields and brought about new knowledge of man and his universe. Darwin (1868: 18) was one of the first to be aware of the ecological and evolutionary implications of domestication—"no limit exists to the number, singularity, and perfection of the contrivances and co-adaptations which may . . . be produced. An animal or a plant may thus slowly become related in its structure and habits in the most intricate manner to many other animals and plants, and to the physical conditions of its home." Other fields allied around the study of domestication include cytology, archeology, taxonomy, and history. With the new knowledge of domestication man may be seen as a connecting piece in the web of life; as a symbiote, he may be further comprehended in terms of the tie between his cultural evolution and the hereditary changes of his fellow travelers. And an intelligent view of the environment, and the successful use of it in the future, must also depend on the lessons from the past, that is, the history of man's recent biological advances.

For all this, of course, or even a part of it, we must obtain the best possible information. This paper reports a test of previous considerations of sorghum chromosomes—knowledge which has already been used to develop inferences concerning the evolution and genetic nature of *S. bicolor*.

Sorghum pachytene chromosomes show considerable detail, in the form of easily distinguishable centromeres and differentiation into dark- and light-staining regions (Fig. 1). A number of chromomeres of various sizes can often be distinguished near the margins of the median dark-staining regions. There is variation in the pachytene arm ratios, and one and only one chromosome pair (the longest of the complement) is consistently associated with the nucleolus.

Previous reports (Magoon & Ramanna, 1961; Magoon & Shambulingappa, 1960, 1961; Magoon, Shambulingappa & Ramanna, 1961; Venkateswarlu & Reddi, 1956, 1968) have established karyotypes for thirteen collections within the complex *S. bicolor.*[3] Reddi (1970*b*) has extended karyology to a $2n = 40$ *S. bicolor* and (1970*a*) to two other collections, one of which must also be classified as a $2n = 40$ *S. bicolor.*

A wide range of sorghum germplasm was available to me. This included types with wild, weedy, and cultivated adaptations, several of which were from remote regions of Africa. It was hoped that a study of pachytene in these materials, as well as several artificial hybrids, would help further characterize variation patterns in the group.

Materials and Methods

The materials studied (Table 1) were field grown from seed accessions or were field-grown hybrids. Inflorescences in the flag-leaf stage were collected from one plant for each material and fixed in 3:1 95% alcohol–acetic acid or in 3:1 absolute alcohol–propionic acid. No difference in the results from these two fixatives was noted. After at least 18 hours, the inflorescences were transferred to 70% alcohol and were stored in a refrigerator. Due to the attenuated nature of the pachytene chromatin, a more intense and yet standardized staining method was used than what is satisfactory for diakinesis-metaphase studies. Thus a system of mordanting the sporocyte tissue before staining (Swaminathan, Magoon & Mehra, 1954) was used successfully. Therein the propionic acid of the fixative is saturated with ferric acetate. Previously fixed materials were also successfully mordanted by placing them in such a mordant-fixative solution.

Meiotic anthers were stained and squashed in the standard way, except that a small steam bath was used in warming them. Barton (1950) suggested this procedure to avoid the violent heating of an alcohol lamp.

Good quality cells at pachytene were selected and their chromosomes were traced with a camera lucida apparatus. All cells were photographed before their slides were made permanent. Photographs were taken using an oil-emersion objective ($100 \times/1.3$ apertures) with a film holder set-up, such that the final magnification was $1870 \times$.

Measurements of the pachytene chromosomes were made from hand-traced $5 \times$ enlargements of the photographs. Separate measurements were made of each arm and of the total length for each traceable chromosome pair. Camera lucida drawings were not used for any measurements, but rather to solve problems of chromosome overlaps which could not be resolved from photographs.

A total of 329 fully traceable pachytene chromosomes were measured, in 79 cells of 6 accessions (1015, 1539, 1553, 1581, 1937, and 2399) and one artificial hybrid (S-69X-6). Of these, 17 cells were fully analyzable (each of the ten chromosome pairs could be traced from end to end). Another 9 cells were not fully analyzable, but in the latter the total chromosome length per cell was measured by pooling the segments of the chromosomes which could not be individually separated. Three accessions, 1539, 1581, and 2399, were particularly useful, based on the number of analyzable cells obtained from them, and the measurements of their chromosomes were submitted to several statistical analyses. The collections from which no fully traceable pachytene chromosomes were obtained were useful in studying qualitative variations.

Arm ratios were calculated by dividing the length of the short arm by that of the long arm,

[3] *Sorghum bicolor* includes diverse wild, weedy, and cultivated forms indigenous to all but the driest regions of Africa, and now found in every major habitable region of the world. Although once classified into 49 species (Snowden, 1936, 1955) the group is not recognized to have broad fertility barriers, discrete morphological isolates, or naturally occurring cytotypes. Therefore the conspecific treatment of this complex is used here to describe all $2n = 20$ forms within the section *Sorghum*.

TABLE 1. List of *Sorghum bicolor* materials studied. All materials were obtained from the Crop Evolution Laboratory of the Agronomy Department of the University of Illinois.

ORIGINAL COLLECTIONS

Accession number	Origin	Collector	Race[a]	Adaptation
1014	Guinea, Butu	Unknown	Arundinaceum	Wild
1015[b]	Rhodesia, Salisbury	Unknown	Bicolor	Cultivated
1016	South Africa, Kimberley	Unknown	Verticilliflorum	Wild
1018	Egypt, Cairo	*ex* U.S.S.R.	Virgatum	Weedy
1452	Java, Bogor	Unknown	Bicolor	Cultivated
1539[b]	Sudan, El Obeid	Harlan	Guinea-caudatum	Cultivated
1541	Sudan, El Obeid	Harlan	Guinea-caudatum	Cultivated
1553[b]	Sudan, Nuba Mountains	Harlan	Caudatum	Cultivated
1581[b]	Chad, Fort Lamy	Harlan	Caudatum	Cultivated
1930	South-West Africa, Okahandja	de Wet	Bicolor	Cultivated
1937[b]	South-West Africa, Omatoka River	de Wet	Verticilliflorum	Wild
2080	South Africa, Lobatsi	de Wet	Kafir	Cultivated
2399[b]	Sudan, Simsim	Harlan	Shattercane	Weedy
2577	Ethiopia, Awash	Harlan	Verticilliflorum	Wild

ARTIFICIAL HYBRIDS[c]

Number	Parents	Racial designation of parents
S-68X-24	1015 × 1021	Bicolor × Shattercane
S-68X-27	1015 × 1014	Bicolor × Arundinaceum
S-68X-31	1021 × 1020	Shattercane × Shattercane
S-69X-6[b]	1016 × 1452	Verticilliflorum × Bicolor
S-69X-7	1026 × 1018	Aethiopicum × Virgatum
S-69X-12	1016 × (1014 × 1016)	Verticilliflorum × (Arundinaceum × Verticilliflorum)

[a] Racial designations are based on a descriptive classification of variation within *S. bicolor.* See pp. 2–4 *in* P. Busey, "Meiosis and karyotypes in *Sorghum bicolor* (L.) Moench." M.S. thesis, University of Illinois.

[b] These seven materials were used for pachytene chromosome measurements.

[c] The artificial hybrids were made by E. G. Price.

thus giving values not greater than 1.0. Relative lengths were also computed, and these are a percentage of the sum of the chromosome lengths in the cell. In the statistical analyses, the figure "±" following a number indicates the standard deviation. "N" represents the sample size, in contrast to "*n*," the haploid number of chromosomes.

RESULTS AND DISCUSSION

Only seven of the twenty accessions or hybrids were found suitable for pachytene chromosome measurements. The determining factor lay in the completeness of separation between chromosome pairs. It is necessary to discuss some of the theory which must go into karyotype comparisons.

It is assumed that there is a degree of consistency in chromosome characteristics between different pachytene cells of the same material. An intensive study of the chromosomes should reveal repeatable defining patterns, called the "karyotype." A reasonable approach accepts that cell-to-cell differences are superimposed on differences between chromosomes. Thus in the intensive comparisons, cellular variations must be accounted for. The procedure here was to consider relative lengths for each chromosome (as a proportion of the sum of the chromo-

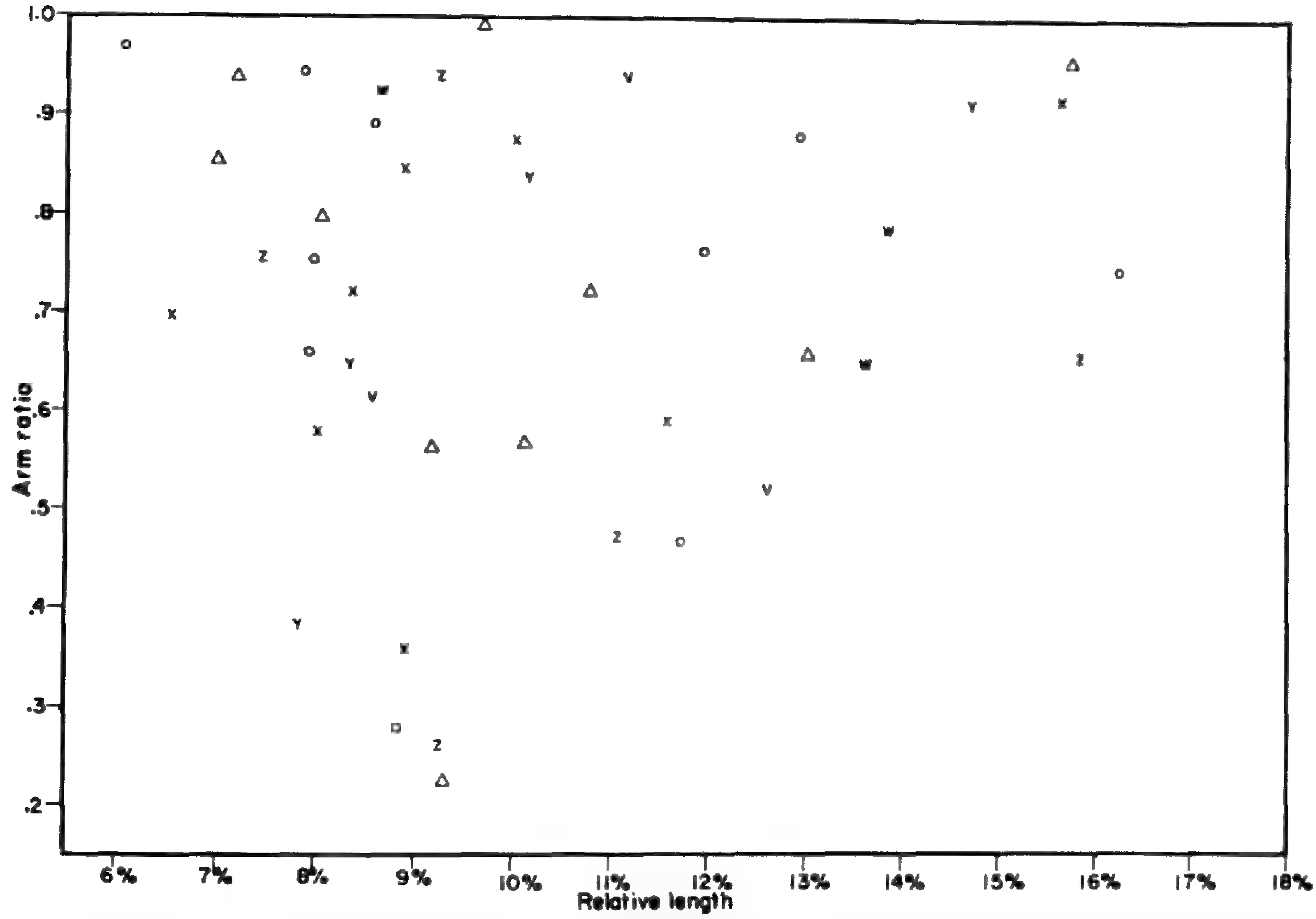

FIGURE 2. A plot of the chromosome measurements from accession 1539. Each different symbol locates the chromosomes in a single cell. Letter symbols refer to cells which were not fully analyzable.

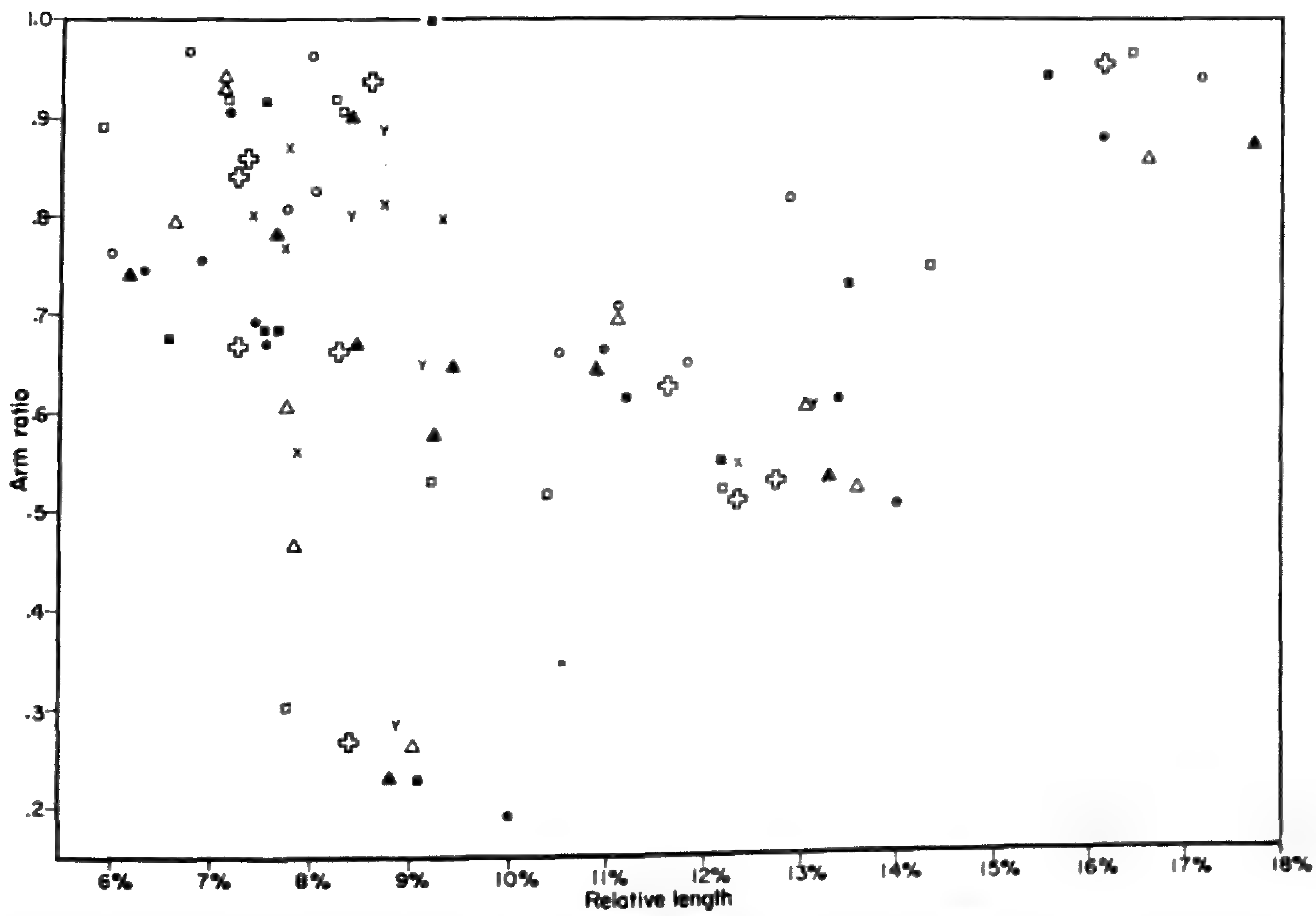

FIGURE 3. A plot of the chromosome measurements from accession 1581. Each different symbol locates the chromosomes in a single cell. Letter symbols refer to cells which were not fully analyzable.

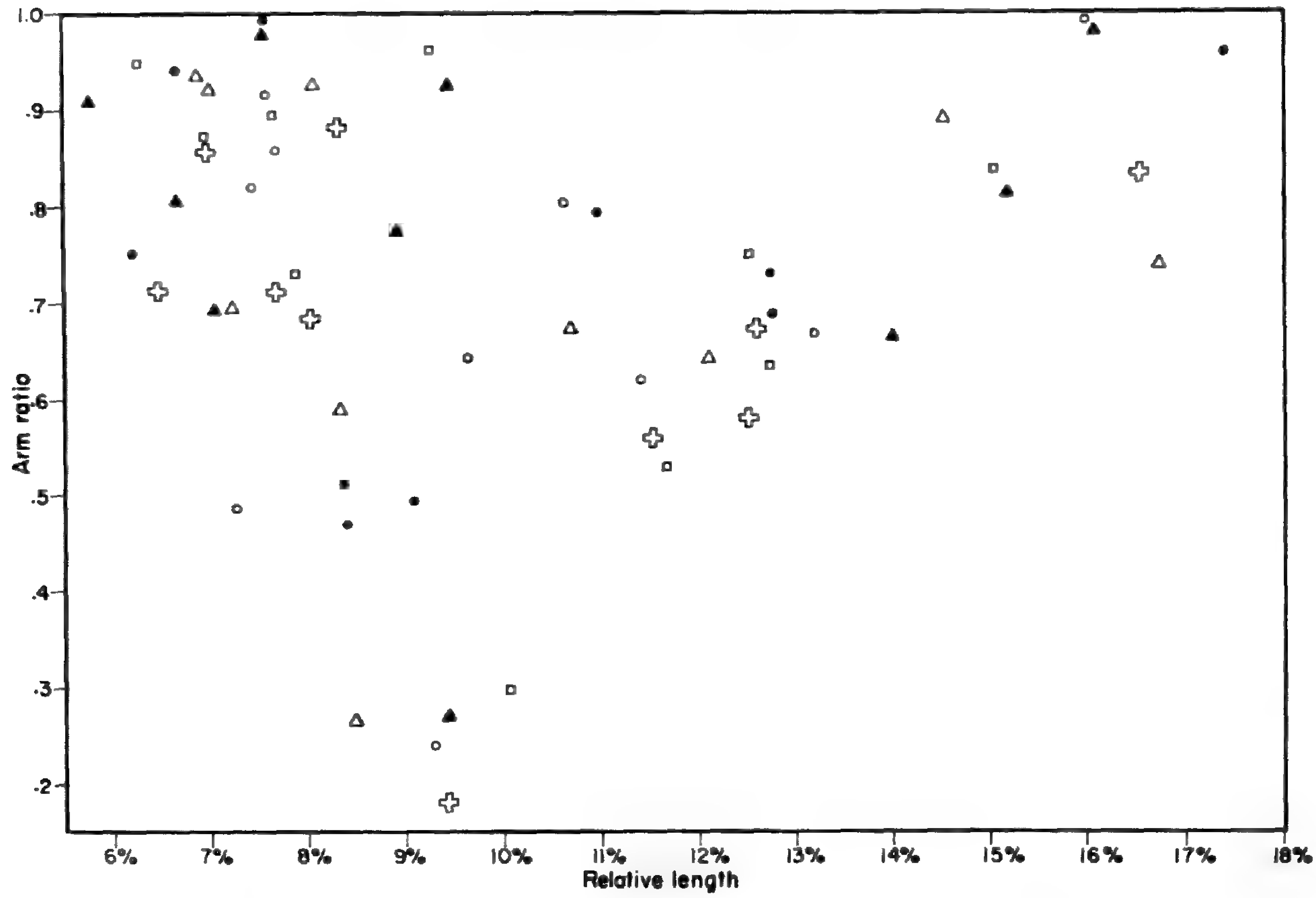

FIGURE 4. A plot of the chromosome measurements from accession 2399. Each different symbol locates the chromosomes in a single cell.

some lengths in the cell) in comparing the lengths of chromosomes in different cells. I will later show that this was a useful tool in reducing the variations between homologous chromosome pairs in different cells.

The mean lengths, in microns, for cell totals (the sum of chromosome lengths for each cell) were: 389.3 for accession 1539 (N = 7); 350.0 for 1553 (N = 3); 323.1 for 1581 (N = 9); 475.8 for 2399 (N = 6); and 340.5 for hybrid S-69X-6 (N = 1). Individual chromosomes varied from 6–18% of the cell totals, for all collections. The actual values for chromosome lengths ranged between 15 and 90 μ.

By means of plotting arm ratios and relative lengths on the same graph, as used by Essad and Najcevska (1969) for the mitotic chromosomes of *Festuca pratensis* Huds., several comparisons may be made in one operation. This has been done for accessions 1539, 1581, and 2399 in Figures 2–4.

A general pattern is consistent between collections, and this is summarized in Figure 5. In all pachytene cells ten chromosome pairs are observed. In all cells studied, one and only one pachytene pair is consistently associated with the nucleolus, and in all cells for which measurements were obtained, this nucleolar pair is the longest of the complement. Most commonly (18 times out of 25), the short arm is attached to the nucleolus. In nearly every cell, one and only one asymmetric pair is present, and this is regularly number five or six in terms of its rank—based on length—with the other pairs in the cell. In each material for which pachytene measurements were obtained, there is a clear indication that

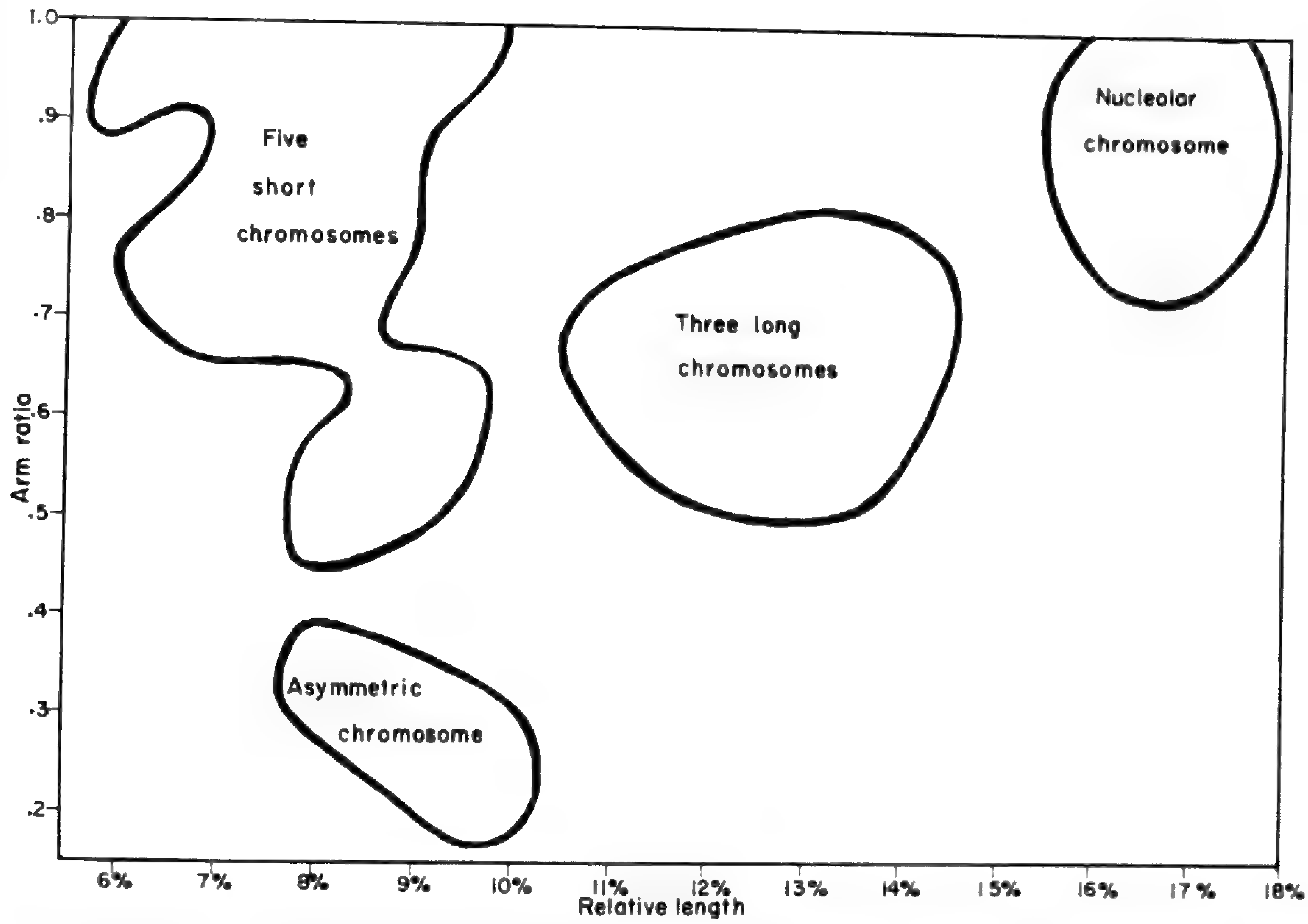

FIGURE 5. A plot summarizing the chromosome measurements from accessions 1539, 1581, and 2399. Of 185 chromosomes 90.3% fit within the distributions shown.

three relatively long and five shorter pairs are definable. It seems that finer distinctions than these cannot be established, to say nothing of complete karyotypes. I will devote the rest of this paper to discussing this conclusion.

Exhaustive comparisons had been made between chromosomes. In addition to comparisons based on arm ratios and relative lengths, absolute lengths were worked with, and variations in morphology (dark-staining regions and chromomeres) were studied. Many possible homologies were observed, but too many contradictions appeared to establish complete karyotypes. It was realized that variability attributable to the techniques and/or to the chromosomes could be present. In addition, the size of the sample could have been too small, though for accession 1581 it involved seven fully analyzable cells and a total of 82 individual chromosomes.

ANALYSIS OF CHROMOSOME LENGTH VARIATION

The suggestion (Maguire, 1962) that most of the length variation in homologous chromosomes is attributable to cellular variation (and not to variation between slides or plants), and that this variation is based on a pattern of uniform shortening differences between cells, had been accepted. Uniform shortening differences are here defined as the effect of an equal shortening per chromosome length throughout the complement. This variation would be totally eliminated by the use of relative chromosome lengths to compare homologs in different cells. Continuous-but-nonuniform shortening variation could also exist, being based on

TABLE 2. Coefficients of variability of the two identifiable chromosomes, using absolute lengths *versus* relative lengths.

Chromosome	1539 (N = 4)		1581 (N = 6)		2399 (N = 5)	
	Absolute	Relative	Absolute	Relative	Absolute	Relative
Nucleolar	12.7%	4.2%	5.6%	4.4%	9.6%	4.1%
Asymmetric	12.1%	7.2%	10.0%	8.6%	6.8%	6.1%

different rates of contraction for different chromosomes. A qualification for both of these shortening patterns is that the chromosomes must consistently shorten in the same pattern from cell to cell. Discontinuous variation is here defined as that which cannot be related to a systematic shortening of the chromosomes.

A comparison of the use of absolute *versus* relative lengths for the two identifiable chromosomes was made (Table 2). In purely pragmatic terms it is clear that a fractional reduction in coefficients of variability is obtained by using relative lengths instead of absolute lengths. Despite the small sample sizes, the validity of this comparison must be considered in terms of its consistency between different collections and between different chromosomes. To test the question of continuous variation (whether uniform or nonuniform) statistically, simple and multiple correlation tests were performed (Table 3). For multiple correlation, the absolute lengths of the two identified chromosomes of accession 1581 were compared to the total absolute lengths of the eight unidentified chromosomes. The lengths from accession 1539 and 2399 were treated similarly, but by a means which pooled their variances to give a combined sample 1539-2399. (Pooling was justified because the total variances for 1539 and 2399 were similar.)

Based on the determinable variation, from multiple correlation of the two identified chromosomes with the sum of the eight unidentified chromosomes, the non-determined, or unaccountable, variation of the two identified chromosomes can be estimated. This is shown in Table 3, and the weighted averages of coefficients of variability are 4.58% for the nucleolar chromosome, and 7.92% for the asymmetric chromosome. (These values reflect standard deviations per chromosome of 3.09 μ and 3.00 μ, respectively.) These values are our best estimates of chromosome length variation not determinable by a continuous, linear shortening process, whether or not that shortening was uniform for different chromosomes.[4] This non-determined variation is, according to our definitions, discontinuous. If this non-determined variation were present in a similar magnitude in the eight unidentified chromosomes, it could seriously hamper karyotype analysis.

ANALYSIS OF TECHNIQUE

Because a non-determined chromosome length variation seems to have hampered karyotype analysis, it is important to decide whether the major source of

[4] Curvilinear shortening might at first seem plausible, but it must be remembered that linearity or curvilinearity pertains here not to any absolute standard, such as time, but rather to the comparisons of shortening between chromosomes. Furthermore, it becomes less likely that curvilinear effects would manifest themselves as a variation for samples of this size.

TABLE 3. Statistics from simple correlation, and from the multiple correlation of lengths of the nucleolar chromosome (X_1), and the asymmetric chromosome (X_2) against the sum (X_3) of the 8 unidentified chromosomes.

Parameter	1581 (N = 6)	1539-2399 (N = 9)	
Simple correlation			
$r_{1 \cdot 2}$	.170	.690[a]	
$r_{1 \cdot 3}$	.545	.897[b]	
$r_{2 \cdot 3}$	.272	.731[a]	
Partial correlation			
$r_{31 \cdot 2}$	.525	.794[a]	
$r_{32 \cdot 1}$	.217	.349	
Multiple correlation, R	.574	.910[b]	
Determinability of X_3 variation	33.0%	82.8%	Weighted
Coefficient of non-determined variability			average
X_1	3.86%	4.66%	4.58%
X_2	8.82%	7.41%	7.92%

[a] Significant at the 5% level.
[b] Significant at the 1% level.

this variation was in the technique. I will discuss the technique from five angles: 1) Variations in measurements from the photographs, 2) variations from photography, 3) variation in the vertical placement of chromosomes within the slides, 4) random variations between slides, and 5) uniform variations related to preparation.

The chromosomes from two photographs of the same cell were each drawn and measured twice, on different days. In this replicated experiment, a standard deviation of .33 μ per chromosome was obtained (with 20 degrees of freedom). This cannot account for more than 3% of the unaccountable variance of either accession 1581 or accessions 1539-2399 combined. This estimated measurement variance includes variation in identifying the chromosome ends, in tracing out the 5 × enlargements, and in the use of the map measurer. It does not include mistakes due to the improper solution of overlapping chromosomes. These mistakes were definitely reduced by the use of camera lucida drawings for the direct solution of overlaps and are probably best represented by the 9.7% scatter of chromosomes not fitting the general distribution pattern (Fig. 5). That improper solutions were of little importance is shown by the fact that the two identified chromosomes maintained their approximate ranks with the other chromosomes of the cells.

The optical steps were expectably precise. Photographs of a ruled grid showed no measurable distortions, even when enlarged in the regular manner. The same microscope setting was consistently used, in order to obtain the same magnification. Photographs of a ruled grid were taken on seven different occasions, at an exact same setting as had been used for photographing pachytene cells. The results show that the magnification produced in the photographs of the cells was 1870.1 ± 6.5 ×.

No abrupt variations in plane of focus for the chromosomes were observed. By separate focusings, and the use of a calibrated focusing knob, the region of sharp focus for all the chromatin in seven cells from a permanent slide was estimated to be $1.23 \pm .28\ \mu$. This represents a slight, barely visible slope across the cell; no abrupt, vertical wiggles were seen in the chromosomes. On this basis, no hypothesis of vertical displacements could account for a considerable part of the length variations observed.

Variations probably exist between slides, and these are likely to reflect different stages of contraction in the anthers from which the slides are made. Slide variations should not be a major factor here in the chromosome length variations; out of the fifteen cells which went into these calculations, eleven came from only one slide for each material. Of the four which did not, the cell totals of two of these cells were within the range of cell totals for the principal slide of the material.

Slide preparation was done as cautiously as possible, by methods standard for many meiotic materials, some of which (*e.g.* maize) have been used extensively in karyotype analysis. Barton's steam bath was used, as previously described. Thus in this respect the results from this study would not be expected to differ from those of other studies.

A HYPOTHETICAL MODEL

Let us illustrate some of the concepts used in interpreting chromosome length variations. Consider yourself an observer in an unusual race, analogous to the "shortening of the chromosomes." Each of the ten vehicles (chromosomes) is approaching (shortening toward) a goal. Unfortunately you cannot readily identify more than two vehicles, but you can try to identify the other eight. But all you have to go on is a set of photographs, presumably all from the same race. (If we have presumed wrong, that is, if the chromosomes in different cells do not synchronize their shortening similarly, as though they were repeating the same race, then these vehicles cannot be identified by observation alone.) Your object is to match the vehicles in the photographs by being able to show their position from one photograph to another, relative to the two identifiable vehicles and relative to each other. Now you had hoped that all ten travel at the same rate (uniform shortening). Unfortunately, they do not. Your next hope is that the ten vehicles travel at a continuous speed throughout the race. You do find that this hypothesis can explain, in one case, over 80% of the variation in locations of the two "marked cars," in relation to the other eight. Yet the remaining, "discontinuous" variation is considerable—sufficient, it seems to hamper identification. In other words, the vehicle locations fluctuate too widely, for unexplained reasons, to follow their locations from one photo to another. And far from identifying the "unmarked cars," we are left to explain the cause for discontinuous variation.

Throughout the present study there has been the realization that pachytene chromosomes are in the midst of a process, that of contraction. Could some special aspect of contraction be responsible for this discontinuous length variation? Yes, I suggest, there could be, and it might come out of the coiling hypothesis of the nature of chromomeres. Brown (1949) suggested that the chromomeres of tomato are formed in light-staining regions and move medianly during pachytene. In the present study, the median dark-staining regions often appeared as groups of fused chromomeres. Eventually the entire chromosomes become dark-staining, perhaps through an accumulation of many chromomeres. Thus I suggest that the chromomeres are temporary knots of chromatin, the formation of which permits the chromosomes to contract and become dark-staining. These knots might be expected naturally as differential coilings within the helical, tightly paired chromosomes. If the suggestion were true, then it is quite likely that the formation of these knots of chromatin would involve abrupt, quantum changes of length during chromosome contraction. This would create some variation residual from a linear correlation test, which would be assigned to discontinuous sources.

Conclusion

The results from the present study have not yielded complete karyotypes. This is in contrast to the report by Magoon and Ramanna (1961: 398) that the pachytene chromosomes of sorghum are "capable of easy identification." It is very difficult to resolve this point. Because the earlier workers have not mentioned the several problems encountered in the present study (availability of high-quality material, chromosome overlaps, and chromosome length variation), it is not possible to assess the relative importance of these problems.[5] It is even possible that unreported differences in technique existed.

In the present study at most seven fully analyzable cells were used for one collection (1581), in contrast to the report of ten fully analyzable cells for each of the earlier studies, with the exception of Venkateswarlu and Reddi (1968), who used eight fully analyzable cells, but at least ten representatives of each chromosome. Yet this does not account for the degree of contrast between the present study and the others. For here there has been no indication that certain chromosomes could ever be reliably separated, or that the number and location of chromomeres had any value in separating the unidentified chromosomes.

In addition, other workers have reported difficulties in working with *Sorghum* chromosomes (Garber, 1948; Hanna & Schertz, 1971; Harpstead, Ross & Franzke, 1954; Lin & Ross, 1969; Schertz, 1966, 1970). Admittedly, most of these workers have been studying aberrations, but Hanna and Schertz (1971: 105) say with some sureness, "No satisfactory karyotype analysis is available in sorghum. . . ."

The general need for repeatability in karyotype analysis has been discussed by Torres (1968: 582), "Often, however, karyotypic data and comparisons based on them are largely subjective and non-operational in the sense that the logical steps which yielded the evidence and led to the interpretations are not indicated and therefore are not repeatable." It would be interesting, then, to know from the data of Magoon and Ramanna (1961), who report some statistically significant differences, what manner of variation was observed in the identified chromosomes. Were these variations uniform between different chromosomes, and

[5] Reddi (1970*a*, *b*) did report difficulty in identifying all chromosomes in $2n = 40$ collections of *Sorghum*.

perhaps correlated with a pattern of shortening; how did they relate to the chromomere pattern?

In any case, difficulties in chromosome identification and problems with the repeatability of results seem to seriously limit full realization of the taxonomically great significance of the "pachytene karyomorphological meioty" (expression by Magoon & Ramanna, 1961: 307).

As an afterword, Schertz (1970) has recently made a great advance in sorghum chromosome identification by the development of a complete set of translocation stocks. This accomplishment will permit many of the practical applications which would be obtainable from accurate and repeatable methods for karyotype analysis. Furthermore, we are nearer to a demonstration as to what, if any, feature of the chromosomes of *S. bicolor* hampers their simple measurement.

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ADDITIONAL PANAMANIAN BRYOPHYTES

Marshall R. Crosby[1]

Abstract

Twenty-seven mosses and one liverwort are reported from Panamá for the first time.

In a recent survey of the mosses recorded from Panamá, 213 species and seven varieties were listed (Crosby, 1969). Breen and Reese (1971) added 21 species, and Crosby (1971*a*) described *Squamidium chiriquense* from western Panamá. The 27 additional records listed herein are based mainly on collections I made in 1965 and 1969. I am grateful to various members of the staff of the Missouri Botanical Garden for taking time to collect mosses while engaged in work for the *Flora of Panama* and other projects. Specimens of all taxa listed are in MO, and duplicates of most are in DUKE.

Hepaticae

Micropterygium trachyphyllum Reim. COLÓN: Santa Rita Ridge, *Crosby 4444*. COCLÉ: N of El Valle de Antón, base of Cerro Pilón, *Crosby 4395*. PANAMÁ: Cerro Campana, *Crosby 4495*; Cerro Jefe, *Crosby 4535*, *Lewis & Dressler 7603*. — According to Fulford (1966) the genus *Micropterygium* is not known from Central America. Fulford recognizes 18 species, many of which occur in Venezuela and Colombia. *Micropterygium trachyphyllum* is common on tree trunks in moist localities in Panamá. This species has a wide distribution, ranging from Cuba and Jamaica through the Lesser Antilles and across northern South America.[2]

Musci

Acrocryphaea gardneri (Mitt.) Jaeg. CHIRIQUÍ: Boquete, *Cornman 3168*.

Adelothecium bogotense (Hampe) Mitt. CHIRIQUÍ: N of Cerro Punta, *Croat 10534D*.

Aongstroemia jamaicensis C. Müll. CHIRIQUÍ: N of Cerro Punta, *Croat 10453, 10462B*; N of El Hato del Volcán, *Croat 10663*.

Calymperes lonchophyllum Schwaegr. COLÓN: Santa Rita Ridge, *Crosby 4461*. VERAGUAS: Mouth of Río Concepcion, *Lewis et al. 2802A*.

Calymperes venezuelanum (Mitt.) Reese. PANAMÁ: Cerro Jefe, *Crosby 4531*.

Campylopus harrisii (C. Müll.) Par. PANAMÁ: Cerro Jefe, *Lewis & Dressler 7604, 7605*. — Previously known from Cuba, Jamaica, and Surinam.

Daltonia longifolia Tayl. COCLÉ: N of El Valle de Antón, base of Cerro Pilón, *Crosby 4392B*.

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[1] Cryptogamic Herbarium, Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.

[2] I thank Dr. Margaret Fulford, University of Cincinnati, for confirming my initial determinations of this species.

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Eustichia spruceana (C. Müll.) Par. CHIRIQUÍ: S of Boquete, *Crosby 3965.*

Heterophyllium nemorosum (Brid.) Kindb. CHIRIQUÍ: Las Cumbres near Cerro Punta, *Croat 13751C.*

Holomitrium arboreum Mitt. CHIRIQUÍ: S of Cerro Horqueta Peak, N of Boquete, *Crosby 4004.* PANAMÁ: Cerro Campana, *Stimson 5392A.*

Hypnella pilifera (Hook. & Wils.) Jaeg. CHIRIQUÍ: Holcomb Trail, N of Boquete, *Crosby 4068B, 4071, 4079.*

Hypnum polypterum (Mitt.) Broth. CHIRIQUÍ: N of Cerro Punat, *Croat 10463*; Las Cumbres near Cerro Punta, *Croat 13749B, 13751F.*

Isodrepanium lentulum (Wils.) Britt. CHIRIQUÍ: S of Cerro Horqueta Peak, N of Boquete, *Crosby 3994.* COCLÉ: N of El Valle de Antón, base of Cerro Pilón, *Crosby 4387, 4417.* PANAMÁ: Cerro Campana, *Crosby 4480.*

Leptodontium cirrhifolium Mitt. CHIRIQUÍ: Boquete, *Cornman 3079*; above Cerro Punta, *D'Arcy 5377.*

Leptodontium valerianum Bartr. CHIRIQUÍ: S of Boquete, *Crosby 3964.*

Leptotheca costaricensis Card. & Thér. CHIRIQUÍ: Holcomb Trail, N of Boquete, *Crosby 4067.* — This species is also known from Colombia, Costa Rica, Jamaica, and Venezuela. See Crosby (1971*b*).

Leskeodon longipilus (Besch.) Bartr. PANAMÁ: Cerro Campana, *Crosby 4498.*

Macromitrium standleyi Bartr. CHIRIQUÍ: Holcomb Trail, N of Boquete, *Crosby 4049.* — A distinctive species with very long, undulate leaves. Previously known only from Costa Rica.

Meteorium undulifolium Broth. & Thér. CHIRIQUÍ: N of Cerro Punta, *Croat 10534B*; Río Chiriquí Viejo, near Nueva California, *D'Arcy 4245B.*

Neohypnella diversifolia (Mitt.) Welch & Crum. CHIRIQUÍ: Holcomb Trail, N of Boquete, *Crosby 4023B, 4046A, 4052, 4063, 4074.*

Octoblepharum cocuiense Mitt. COCLÉ: N of El Valle de Anton, base of Cerro Pilón, *Crosby 4393.* PANAMÁ: Cerro Jefe, *Crosby 4518.* — Previously known from Brazil, Colombia, Gayana, and Surinam.

Phyllodrepanium falcifolium (Schwaegr.) Crosby. PANAMÁ: Along road above Goofy Lake, *Crosby 4343.* — See Crosby (1970) for notes on this species.

Stenodictyon sericeum Bartr. CHIRIQUÍ: Holcomb Trail, N of Boquete, *Crosby 4010.* — Bartram (1929) based this species on a sterile collection from Costa Rica. The present collection is fertile, and the peristome confirms its placement in *Stenodictyon.* The seta, slightly roughened at the apex and smooth below, is 2–2.5 cm long, intermediate in length between that of *S. nitidum* (Mitt.) Jaeg. (5 cm), Ecuador and Panamá, and that of *S. pallidum* Crum & Steere (0.8–1.4 cm), Greater Antilles.

Stereophyllum subobtusum Ren. & Card. CHIRIQUÍ: S of Boquete, *Crosby 3959B.*

Streptopogon calymperes C. Müll. *ex* Geh. CHIRIQUÍ: About 4 km from Cerro Punta, *Correa 1219.*

Tayloria moritziana C. Müll. CHIRIQUÍ: Holcomb Trail, N of Boquete, *Crosby 4019, 4076.*

Zygodon reinwardtii (Hornsch.) B.S.G. CHIRIQUÍ: S of Cerro Horqueta Peak, N of Boquete, *Crosby 3987D.*

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NOTES

A NEW COMBINATION IN *ZANTHOXYLUM* (RUTACEAE)

The following new combination results from a study of the family Rutaceae for the *Flora of Panama.* A photograph is included (Fig. 1, p. 262), as this species has never been illustrated.

Zanthoxylum tripetalum (Standley) D. M. Porter, comb. nov.

BASIONYM: *Amyris tripetala* Standley, Field Mus. Nat. Hist. Publ., Bot. Ser. 22: 84. 1940. [PANAMA. CHIRIQUÍ: "Boquete. 3800 ft. Tree, 10–20 ft. Flower creamy-white." 12 May 1938. *M. E. Davidson 621* (F, holotype; GH, MO, US, isotypes)]

Examination of the above-cited type material, plus a more recent collection [PANAMA. CHIRIQUÍ: "Denuded premontane rain forest between Pinola and Quebrada Seco on the Chiriquicito-Caldera Trail. Tree 20 cm diameter; apparently armed with conical corky spines, or unarmed." 21 April 1968. *Kirkbride & Duke 1024* (MO)], shows this taxon to fall within the generic limits of *Zanthoxylum.* Following his type description, Standley indicated that, "In its trimerous flowers the tree is perhaps anomylous in the genus *Amyris,* to which it seems best referred."—*Duncan M. Porter, Missouri Botanical Garden.*

TWO NEW SPECIES OF *PROTIUM* (BURSERACEAE) FROM CENTRAL AMERICA

Protium is the largest New World genus of the Burseraceae, with probably more than 100 species. By far the largest number of species occur in the vast Amazon basin of South America. Perhaps 15 or 20 species are to be found in Mexico and Central America. The latter appear to form a group of closely-related species, with only *Protium tenufolium* subsp. *mcleodii* (Johnston) Porter and *P. tenuifolium* subsp. *sessiliflorum* (Rose) Porter having definite affinities with South American taxa. The two new species from Costa Rica and Panama described below both fall into this pattern, their affinities being with other Middle American species. Both are named for their respective collectors. Unfortunately, each is known only from a single collection.

Protium correae D. M. Porter, sp. nov.

Protio tenuifolio subsp. *mcleodio* (Johnston) Porter primo adspectu maxime simile, sed floribus tetrameris rufis-tomentosis et pedicellatis.

Tree, the branchlets reddish-tomentose and minutely puberulent, soon glabrate and somewhat glaucous. *Leaves* alternate, odd-pinnate, 7.5–13.5 cm long; petioles canaliculate, 1.5–3 cm long, they and the petiolules swollen apically and basally,

Figure 1. Isotype (US) of *Zantroxylum tripetalum* (Standley) D. M. Porter.

they, the petiolules, and the rachises minutely puberulent and somewhat reddish-tomentose, becoming glabrate; leaflets 3–5, elliptic to slightly ovate or obovate, abruptly acuminate apically, cuneate and slightly inequilateral basally, subcoriaceous, the margins entire, reddish-tomentose and minutely puberulent, especially on the veins, the blades of the laterals 3.7–6.5 cm long and 1.7–3.4 cm wide, the blades of the terminals 5–8.5 cm long and 2–4.5 cm wide. *Carpellate inflorescences* axillary, panticulate, few-branched from the base, reddish-tomentose and minutely puberulent throughout, to 5 cm long. *Carpellate flowers* beige, 4-merous; pedicels reddish-tomentose and minutely puberulent, 1–2 mm long; calyx cupuliform, 1.5 mm high, reddish-tomentose, fleshy, 4-lobed, the lobes broadly triangular, shorter than the tube; petals 4, lanceolate, recurved and inflexed-apiculate apically, reddish-tomentose on both surfaces, fleshy, ca. 3 mm long and 1 mm wide; stamens 8, inserted at the base of the disc, 1.5 mm high, the filaments subulate, widened basally, the anthers less than 1 mm in diameter, sterile; disc fleshy, thick, glabrous, surrounding the base of the ovary; ovary ovoid, reddish-tomentose, tapering into the style, ca. 1 mm high, the style reddish-tomentose basally, glabrous apically, the stigma 4-lobed. *Fruits* unknown.

Type. PANAMA. PANAMÁ: "Beyond Cerro Jefe near La Eneida. New road just before La Eneida, along new trail which begins exactly beside Lopez House. Large tree on ground. Flowers beige." 20 February 1968. *Mireya D. Correa A. 723* (MO, holotype).—Fig. 1.

This species superficially resembles *Protium tenuifolium* subsp. *mcleodii*, which is endemic to Panama and known from the islands of the Archipielago de las Perlas and from one locality in Darién province. The latter differs, however, in having minutely puberulent branchlets, leaves, and inflorescences; leaves 17.5–38.5 cm long; leaflets 7–11; flowers 5-merous and sessile or subsessile; calyx minutely puberulent; petals glabrous and not reflexed; disc tomentulose; and ovary tomentulose. Despite the superficial resemblance, the two do not appear to be closely related.

In my key to *Protium* for the *Flora of Panama* (Ann. Missouri Bot. Gard. 57: 11. 1970 [1971].), specimens of *P. correae* would be determined as *P. costaricense*, a species known from the Canal Zone and the Costa Rican provinces of Alajuela and Puntarenas. *Protium costaricense* differs from *P. correae* in having brownish-hirtellous branchlets, leaves, and inflorescences; leaves 13–44 cm long; leaflets (3–) 5–7 (–9); flowers sparsely puberulent; and ovary pubescent. The two obviously are closely related.

Protium ravenii D. M. Porter, sp. nov.

Differt a *Protio panamensi* (Rose) Johnston foliis adpressis-puberulis, inflorescentiis frugiferis adpressis-puberulis et 15–19.5 cm longis, fructibus adpressis-puberulis et longis-stipitatis.

Tree, 50 feet high, the branchlets brownish, dotted with paler brown lenticels, appressed-puberulent, becoming glabrate. *Leaves* alternate, odd-pinnate, to 30 cm long and 26 cm wide; petioles canaliculate, 5–6.5 cm long, they and the petiolules swollen apically and basally, they, the petiolules and the rachises dotted with pale brown lenticels and appressed-puberulent, becoming glabrate; leaflets 3–5, ovate to elliptic or obovate, abruptly acuminate apically, cuneate and inequalataral basally, coriaceous, the margins entire, sparsely appressed-puberulent, more so on the midveins, the blades 12.5–25.5 cm long and 5–8.5 cm

FIGURES 1–2. Two new species of *Protium* from Central America.—1. Holotype of *P. correae* D. M. Porter (*Correa 723*).—2. Holotype of *P. ravenii* D. M. Porter (*Raven 21611*).

wide. *Carpellate inflorescences* appressed-puberulent, sparsely branched, 15–19.5 cm long in fruit. *Flowers* apparently 4-merous, unknown. *Fruits* ellipsoid, more or less angled when dry, sparsely appressed-puberulent to glabrate, dotted with pale brown lenticels, 34–36 mm long and 10–15 mm in diameter, apiculate and long-stipitate, the apiculum 2–3 mm long, the stipe 5–6 mm long.

Type. COSTA RICA. PUNTARENAS: "Deep forest near the airport area, 4 miles west of Rincon de Osa, Osa Peninsula. 100 ft. elevation. Tree 50 ft. tall with milky resinous sap." 8 August 1967. *Peter H. Raven 21611* (MO, holotype; F, isotype).—Fig. 2.

Of the Central American species of *Protium*, *P. ravenii* most closely approaches *P. panamense* in its morphology. The latter is known only from Panama, where it is widespread in low, wet forests on the Caribbean side of the Continental Divide. *Protium panamense* differs from *P. ravenii* in having leaves glabrous; inflorescences glabrous and to 10 cm long in fruit; and fruits glabrous, short-stipitate, and 17–26 mm long. *Protium ravenii* is not likely to be confused with any other species of the genus known to occur in Costa Rica.—*Duncan M. Porter, Missouri Botanical Garden.*

EDITOR'S NOTE

The illustration on the cover of this issue of the ANNALS is from Asa Gray's note "*Neviusia*, a new genus of Rosaceae" (Mem. Amer. Acad. Arts, n. s. **6**: 373–376. 1859). The original engraving by Isaac Sprague occupied an entire quarto page and depicted flowering and fruiting branches as well as details of floral morphology. Only a portion of "a branch in fruit" is reproduced here.

The plant was discovered near Tuscaloosa, Alabama, by Rev. R. D. Nevius in 1857. Upon learning that it represented an undescribed genus, Nevius suggested that it be called *Tuomeya* in memory of Michael Tuomey (1805–1857), Alabama's first State geologist. However, William Henry Harvey (*Nereis Boreali-Americana* 3: 64. 1857 [1858]) had already used this name for a fresh-water floridean alga which Tuomey had collected. So Gray latinized the discoverer's name "in an unclassical, but not wholly unprecedented manner," and the plant is known as *Neviusia alabamensis*.—*Editor*.

The previous issue of the ANNALS OF THE MISSOURI BOTANICAL GARDEN, Vol. 58, No. 1, pp. 1–98, was published on 14 July 1971.

PREPARATION OF MANUSCRIPT

The ANNALS publishes original manuscripts in systematic botany and related fields. There is a charge of $25 per printed page to help defray costs of publication. Authors are asked to follow the suggestions below in order to expedite editing and publication. If an author feels that his manuscript presents special problems, he should write the editor concerning the best way to handle these before submitting the manuscript.

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Acknowledgements to granting agencies, herbaria, illustrators, and technical assistants may be conveniently placed as a footnote on page one. The author's full mailing address should appear as a second footnote.

An abstract must accompany each paper other than "Notes." The abstract should succinctly summarize the findings and conclusions of the paper and should be completely comprehensible itself.

A brief Latin diagnosis for each new taxon is preferred to a complete Latin description. A complete description should be given in English.

The citation of specimens should be concise. Geographic names are put in order of decreasing political magnitude. Only the barest essential data concerning each specific locality should be given. Collectors are cited by family name and collection number. If there is no collection number, the year of collection should be given. Herbaria are designated according to the current edition of *Index Herbariorum*.

Abbreviations should be checked for consistency and to make sure they are unambiguous. Periods are used after all abbreviations except metric measures, compass directions, and herbarium designations.

All illustrative material should be mounted on stiff cardboard. If the originals are too large to be conveniently mailed, photographic reductions should be submitted. The maximum size of a printed illustration is 5 × 7¾ in., and therefore, the height of an illustration must not exceed about 1.5 its width. Figures are numbered consecutively, since they are not printed as "plates." Numbering must be done with a mechanical device or with dry-transfer lettering and never by hand. The amount of reduction should be noted on the back of each illustration, together with the figure numbers, author's name and title of the paper. Photographs should be sharp, glossy prints. Numbering should be applied directly to the surface of the photograph. Several photographs may be assembled to form a composite block, and each photograph should be numbered separately. The individual photographs should be mounted with the interior edges flush. Line drawings are prepared with India ink and must never be placed in the same block with photographs. Authors wishing to have original illustrations returned must notify the editor when proofs are returned.

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CONTENTS

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The ANNALS contains papers, primarily in systematic botany, contributed from the Missouri Botanical Garden and the Department of Biology of Washington University. Papers originating outside the Garden or University will also be accepted. For information on preparation of manuscripts, see the inside back cover.

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 111. RHAMNACEAE

JOAN W. NOWICKE[2]

Trees, shrubs, or woody vines, rarely herbs, deciduous or evergreen, armed with spines or unarmed. *Leaves* alternate or opposite, simple, pinnately-nerved or 3-nerved from the base, petiolate and usually stipulate, the stipules mostly minute and deciduous, sometimes modified to spines. *Inflorescences* umbelloid or corymboid cymes and axillary, or sometimes reduced to a single flower, or racemose or spicate thyrses and axillary or terminal. *Flowers* small, actinomorphic, bisexual or polygamous; floral tube obconic to campanulate, generally persistent in fruit; calyx-lobes 4–5(–6–8); petals 4–5(–6–8), mostly cucullate and often clawed; stamens 4–5(–6–8), opposite the petals and often enfolded by them, functional or smaller and sterile in carpellate flowers, the anthers 2-locular, longitudinally dehiscent; nectariferous disc intrastaminal, annular or lobed, rarely absent; ovary perigynous to epigynous, 2–3(–4)-carpellate, syncarpous, functional or rudimentary in staminate flowers, the ovules 2–3(–4), the style 1 or 2–3-parted, the stigmas (1–)2–3(–4). *Fruit* a drupe with 2–3(–4) pyrenes or rarely a winged (or unwinged) schizocarp; seeds 2–3(–4), smooth and convex on the abaxial side.

A family of 50–60 genera and 550–900 species with an almost cosmopolitan distribution. Six genera are found in Panama.

a. Plants climbing by tendrils; fruit a 3-winged schizocarp .... 6. *Gouania*
aa. Plants erect shrubs or small trees; fruit a fleshy or leathery drupe, sometimes 3-lobed but not winged.
    b. Leaves opposite .... 4. *Rhamnidium*
    bb. Leaves alternate.

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[1] Assisted by National Science Foundation Grant GB-27713 (Duncan M. Porter, principal investigator).

[2] Missouri Botanical Garden and Department of Biology, Washington University, St. Louis, Missouri.

ANN. MISSOURI BOT. GARD. 58: 267–283. 1971.

c. Stipules small spines; leaves 3-nerved almost to the apex .... 5. *Ziziphus*
cc. Stipules generally not spinose; leaves mostly penninerved.
 d. Fruits fleshy, ovoid, subtended basally by a more or less flat remnant of the floral tube; inflorescences few-flowered .... 1. *Rhamnus*
 dd. Fruits dry, 3-lobed, adnate basally to a cup-like floral tube; inflorescences few- to many-flowered.
  e. Leaves densely tomentose beneath; inflorescences racemose, many-flowered; fruit distinctly 3-lobed, crested on the ridges .... 2. *Ceanothus*
  ee. Leaves generally glabrous, or if pubescent, not densely tomentose; inflorescences few-flowered axillary thyrses; fruit subspherical .... 3. *Colubrina*

1. RHAMNUS

Rhamnus L., Sp. Pl. 193. 1753.

Trees or shrubs, rarely woody vines, mostly unarmed, deciduous, the buds scaly or naked. *Leaves* alternate, rarely opposite, pinnately-veined, entire or toothed, mostly petiolate. *Inflorescences* umbellate cymes, sometimes reduced to a single flower, sessile or pedunculate. *Flowers* bisexual or polygamo-dioecious, small, perigynous; floral tube cupulate to campanulate; calyx lobes 4–5, ovate to deltoid, deciduous separately or with the circumscissile upper part of the floral tube after anthesis; petals 4–5, shorter than the calyx-lobes, ovate to obovate, concave, hooded or flat, often clawed, the margin entire or bilobed apically, inserted at the margin of the floral tube; stamens 4–5, functional or sterile and rudimentary in carpellate flowers, about as long or longer than the petals, inserted at the upper margin of the floral tube; nectariferous disc lining the wall of the floral tube, sometimes thickened near its margin; ovary superior, 2–3-carpellate, ± 2–3-locular, the ovules 2–3, the style simple or 2–3-lobed, the stigma 2–3-lobed. *Fruit* a drupe, subglobose, dark red to black, containing 2–3 pyrenes; seeds 2–3, lenticular or wedge-shaped.

A genus of about 150 species in the temperate and tropical regions of both hemispheres, but most abundant in eastern Asia and southwestern North America.

Useful reference:

Wolf, C. B. The North American Species of *Rhamnus.* Rancho Santa Ana Bot. Gard. Monogr., Bot. Ser. 1. 136 pp. 1938.

a. Umbels with a distinct peduncle ca. 1–2 cm long; leaves serrate .... 1. *R. pubescens*
aa. Umbels sessile; leaves entire .... 2. *R. capraeafolia*

1. **Rhamnus pubescens** (Ruiz & Pavon) Tr. & Planch., Ann. Sci. Nat. Bot., Sér. 5. 16: 379. 1872.—Fig. 1.

Ceanothus pubescens Ruiz & Pavon, Fl. Peru. 3: 6, *pl, 228.* 1802.

Trees, to 20 m high, or shrubs 3–5 m high, the younger stems pubescent, the trichomes brown and appressed. *Leaves* alternate, lanceolate-elliptic to slightly ovate, acuminate, serrate, the teeth mostly glandular-tipped, obtuse to slightly rounded basally, to 15 cm long and 4 cm wide, brown-pubescent on both surfaces, firmly membranaceous; petioles 8–20 mm long, slender, pubescent,

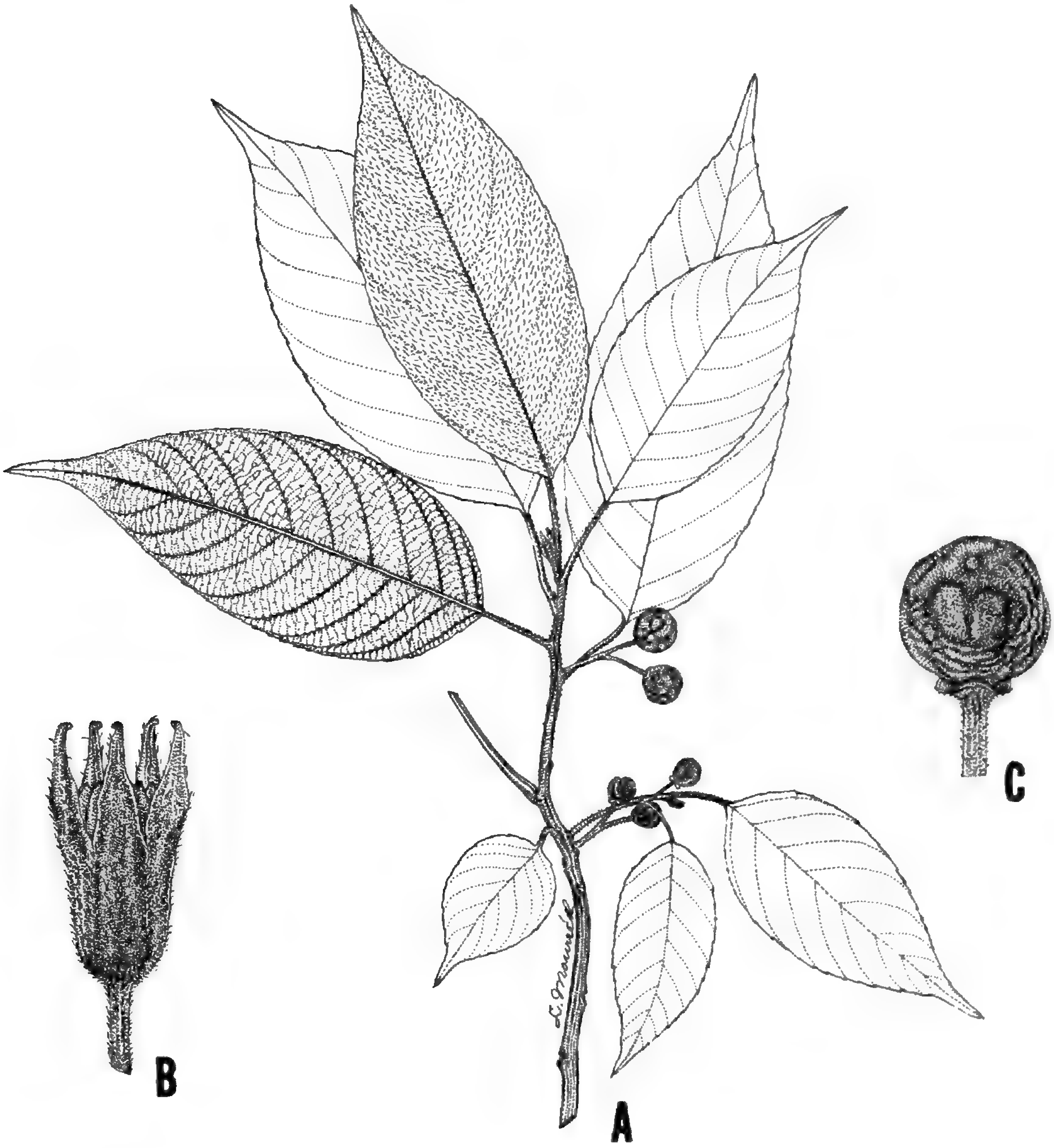

FIGURE 1. *Rhamnus pubescens* (Ruiz & Pavon) Tr. & Planch.—A. Habit (× 0.8).—B. Flower (× 7.7).—C. Fruit (× 3.1). [A–C, after *White 204* (MO); B, after *Woodson & Schery 209* (MO).]

the stipules small, pubescent, and deciduous. *Inflorescences* umbellate, axillary, 8–12-flowered, pedunculate, the peduncles ca. 1–2 cm long. *Flowers* bisexual, the pedicels 3–6 mm long, pubescent; floral tube cupulate; calyx lobes deltoid, ca. 2 mm long, keeled on the inner surface; petals 5, short-clawed, hooded, notched apically, ca. 1 mm long, inserted at the rim of the disc, embracing the stamens; stamens 5, inserted at the margin of the disc, slightly shorter than the petals, the anthers ca. 0.5–0.6 mm long; ovary more or less spherical, the style simple, short, ca. 1 mm long, the stigma 2-lobed. *Drupe* ovoid, dark red, ca. 5–6 mm in diameter, with 3 pyrenes.

Northern South America and Panama.

CHIRIQUÍ: Boquete, *Davidson 804, 1066* (both MO). Vicinity of Finca Lerida, *Allen 4737, Woodson & Schery 209, 492* (all MO). Río Chiriquí Viejo Valley near El Volcán, *White 204* (MO). 3 mi. N of El Volcán, *Tyson 5722, 5725* (both MO).

2. **Rhamnus capreaefolia** Schlecht., Linnaea 15: 464. 1841.—FIG. 2.

Trees or shrubs, to 10 m high, the younger stems pubescent, the trichomes brown and appressed. *Leaves* alternate, ovate to elliptic, acuminate, entire or sometimes serrulate, more or less rounded to weakly obtuse basally, to 14 cm long and 6.5 cm wide, slightly coriaceous, glabrous to sparsely pubescent above, densely pubescent beneath; petioles ca. 1.5–2.5 cm long, softly pubescent, the stipules minute, pubescent, deciduous. *Inflorescences* umbellate, sessile, axillary, 10–15-flowered. *Flowers* bisexual, the pedicels 3–5 mm long (to 11 mm in fruit), pubescent; floral tube more or less campanulate, the tube ca. 1.5–2 mm long, the lobes deltoid, ca. 1.2–1.5 mm long, densely pubescent; petals short-clawed, hooded, notched apically, ca. 1 mm long; inserted at the rim of the disc; stamens 5, inserted at the rim of the disc, the anthers ca. 0.6 mm long; ovary more or less pubescent, the style ca. 0.4 mm long, the stigma 3-lobed. *Drupe* ovoid, green and red, more or less pubescent, ca. 6–7 mm in diameter, with 1–3 pyrenes.

Mexico and occasionally in Central America.

CHIRIQUÍ: Vicinity of Boquete, *Stern et al. 1145* (GH, MO). Finca Collins, *Blum & Dwyer 2532A* (MO). Vicinity of Cerro Punta, *Allen 1566* (MO). 1 mi. S of Cerro Punta, *Tyson 5771, 5791* (both MO).

The Panamanian material was in early flower or fruit stages, and parts of the floral description were completed from a Mexican collection, *Purpus 2061* (MO), which Wolf (*op. cit.*, p. 117) cited as this species.

2. CEANOTHUS

Ceanothus L., Sp. Pl. 195. 1753.

Shrubs, rarely small trees, unarmed or spinescent, deciduous or evergreen. *Leaves* alternate or opposite, 3-nerved from the base or pinnately-veined, the margins entire or dentate; stipules small and deciduous or corky and persistent. *Inflorescences* racemes or panicles, or flowers solitary, terminal and/or axillary, pedunculate. *Flowers* bisexual, floral tube cupulate; sepals 5(–6–8), pelatoid, adnate basally to the floral tube; petals 5(–6–8), clawed and hooded, longer than the sepals; stamens 5(–6–8), exserted; disc nectariferous, surrounding the ovary; ovary semi-inferior, 3-locular, the style 1, the stigmata 3. *Fruit* a drupe, mostly 3-lobed, adnate basally to the floral tube, separating at maturity into 3 pyrenes; seeds 3, smooth, wedge-shaped.

A genus of 55 species confined to the continent of North America. One species ranges as far south as Panama.

Useful reference:

Van Rensselaer, M. & H. McMinn. Ceanothus. Santa Barbara Botanic Garden, Santa Barbara, Calif. 1942.

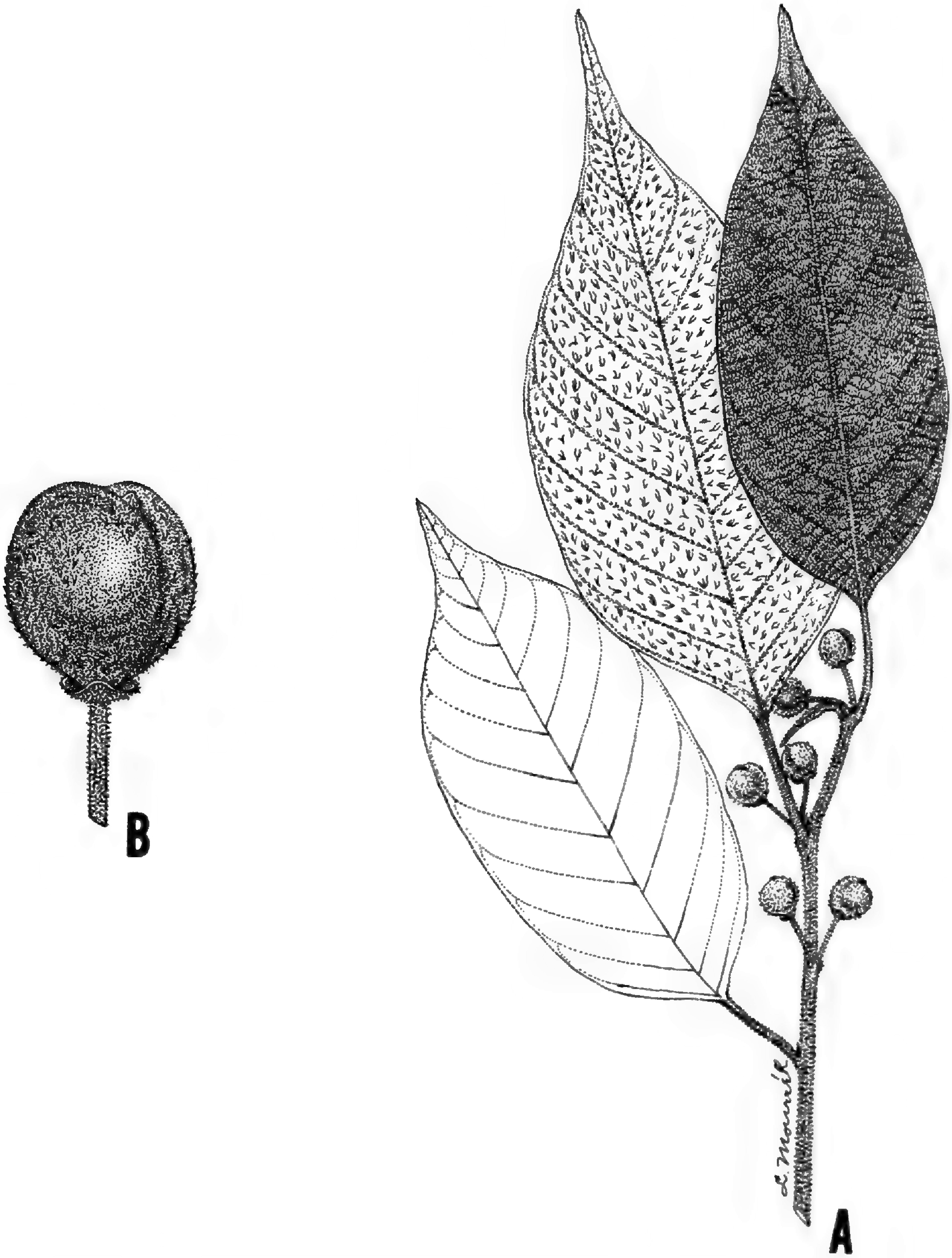

FIGURE 2. *Rhamnus capreaefolia* Schlecht.—A. Habit (× 0.7).—B. Fruit (× 3.6). [After *Stern et al. 1145* (MO).]

Figure 3. *Ceanothus caeruleus* Lag.—A. Habit (× 0.3).—B. Flower (× 9.4).—C. Fruit (× 5.4). [After *Davidson 917* (F).]

1. **Ceanothus caeruleus** Lag., Gen. Sp. Nov. 11. 1816.—Fig. 3.

Shrubs, erect, 3–5 m high, unarmed, the younger branches brown-tomentose. *Leaves* alternate, ovate-lanceolate, acute, serrulate, slightly rounded basally, 2–3(–4) cm long and 1–1.5 cm wide, pubescent above, densely pale brown tomentose beneath; petioles 2–4 mm long, tomentose, the stipules caducous, 2–4 mm long, elongate-deltoid and keeled, fimbriolate. *Inflorescences* racemose or paniculate, terminal ca. 4–8 cm long. *Flowers* with the pedicels ca. 4–7 mm long, pubescent; sepals broadly ovate, becoming notched apically, ca. 1 mm long; petals pale blue, long-clawed; stamens exserted, the filaments ca. 1 mm long, the anthers ca. 0.4 mm long; style ca. 1 mm long, the stigma branches 0.2 mm long. *Drupes* 3-lobed, slightly crested on the ridges, dark brown, ca. 3–4 mm broad; seeds ca. 2 mm long.

Mexico, Guatemala, El Salvador, and Panama.

chiriquí: Volcán de Chiriquí, *Davidson 917* (A, F, MO).

In his key to species, McMinn (*op. cit.*, pp. 164–165) treats *Ceanothus caeruleus* as having leaves with three main veins from the base and white flowers, neither of which characterizes the Panamanian collection. However, in his description of the species (*op. cit.*, p. 202) he includes the possibilities of only a single vein from the base and blue, lavender, or white flowers.

3. COLUBRINA

Colubrina L. Rich. *ex* Brong., Mém. Fam. Rhamn. 61. 1826, *nom. cons.*

Shrubs, or small trees, evergreen or deciduous, with or without spines. *Leaves* alternate or opposite, pinnately-nerved or 3-nerved from the base, entire or finely dentate, with or without small glands on the lower surface, and/or 1 or 2 glands at the base of the blade; mostly petiolate, the stipules minute, free, caducous, or rarely connate and persistant. *Inflorescences* cymes or thyrses, small, sessile or shortly-peduncled, axillary, few-flowered, rarely reduced to a single flower. *Flowers* bisexual; floral tube cupulate; calyx 5-lobed, the lobes triangular-ovate, spreading, with a fleshy keel on the inner surface, deciduous; petals 5, greenish-yellow, yellow, or white, more or less ovate and concave, sessile or with a short stalk; stamens 5, enclosed by the petals, the anthers ovate; disc large, fleshy, filling the floral tube, adnate to the lower half of the ovary; ovary semi-inferior, 3-carpellate, ovules 3, the style slender, 3-lobed, the stigmas 3, small. *Fruit* capsular, slightly 3-lobed, dehiscent; seeds 3, obovate, brown to black, the testa lustrus.

A pantropical genus of 30 species.

Useful reference:

Johnston, M. C. Revision of *Colubrina* (Rhamnaceae). Brittonia 23: 2–53. 1971.

a. Plants armed with spines; leaves mostly less than 6 cm long .... 1. *C. heteroneura*
aa. Plants unarmed; at least some leaves more than 8 cm long.
  b. Leaves subopposite, coriaceous, lustrous above .... 2. *C. glandulosa*
  bb. Leaves alternate, membranaceous, dull above.
    c. Leaf glands restricted to margin near the base of the petiole .... 3. *C. spinosa*
    cc. Leaf glands scattered over the undersurface .... 4. *C. arborescens*

1. **Colubrina heteroneura** (Griseb.) Standley, Jour. Washington Acad. Sci. 15: 285. 1925.—Fig. 4.

Zizyphus heteroneurus Griseb., Bonplandia 6: 3. 1858.

Shrubs, or trees, to 7 m high, armed with spines 7–25(–35) mm long, the younger stems pubescent, the trichomes brown. *Leaves* alternate, ovate to obovate, retuse, entire to slightly undulate, obtuse basally, to 7(–8) cm long and 5(–6) cm wide, glandular at the base of the midribs, without glands on the lower surface, firmly membranaceous, glabrous to sparsely pubescent on the veins beneath; petioles 5–10 mm long. *Inflorescences* cymes, sessile, brown-pubescent. *Flowers* with the slender pedicels to ca. 12 mm long; calyx-lobes ca. 1 mm long, brown-pubescent on the outer surface; petals more or less ovate,

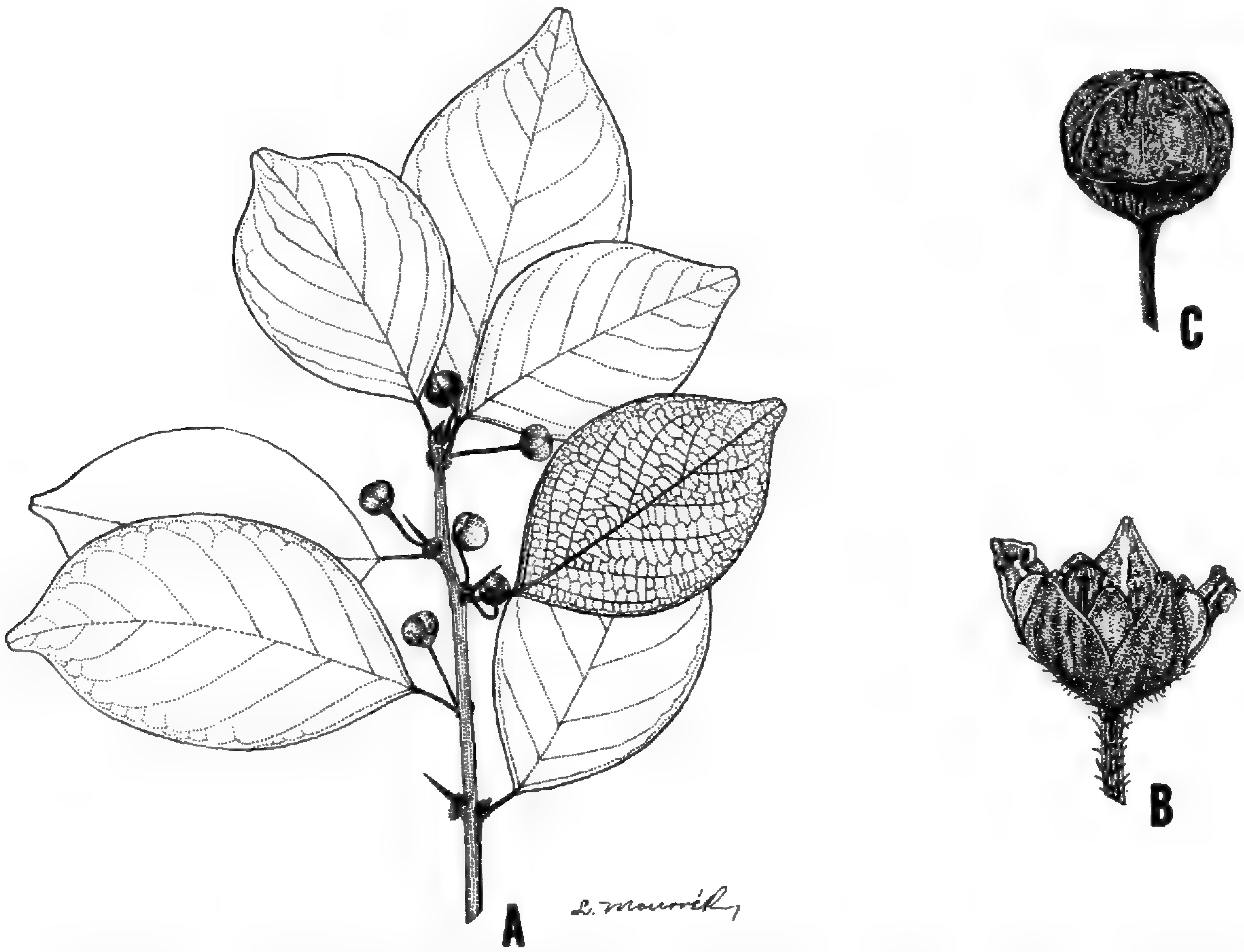

FIGURE 4. *Colubrina heteroneura* (Griseb.) Standley.—A. Habit (× 0.7).—B. Flower (× 8.0).—C. Fruit (× 2.7). [A–C, after *Standley 28894* (A); B, after *Dwyer 7219* (GH).]

somewhat keeled and notched apically, less than 1 mm long, inserted at the margin of the disc, subsessile, enclosing the stamens; stamens slightly longer than the petals, the anthers ca. 0.3 mm long; disc lining the cup, more or less 10-lobed; style ca. 0.4 mm long, the lobes 0.1–0.2 mm long. *Capsules* subspherical, weakly 3-lobed, the floral tube adhering to the lower third, ca. 6–8 mm in diameter; mature seeds unknown.

Mexico, Central America, and northern Colombia.

CANAL ZONE: Chiva-chiva Trail, *Piper 5732* (F, US), *5770* (US). Cocolí Road to Contractors Hill, *Dwyer 7219* (GH). Around Culebra, *Pittier 4774* (US). Farfan Beach, *Lewis et al. 53* (MO), *Tyson & Blum 2602* (MO). Along road K-9, *C. E. Smith Jr. & H. M. Smith 3269* (US). Madden Dam, *Lewis 19* (MO). Miraflores Lake, *Tyson & Blum 3558* (MO), *G. White 189* (GH, MO). Around El Paraiso, *Pittier 2580* (US). Sosa Hill, *Standley 25242* (US). PANAMÁ: Near Matías Hernández, *Standley 28894* (A, US). Between Matías Hernández and Juan Diaz, *Standley 32061* (US). Vicinity of Pacora, *Allen 1120* (GH, US). Swamp E of Rio Tocumen, *Standley 26617* (US). PROVINCE UNKNOWN: *Williams 356* (US).

2. **Colubrina glandulosa** Perkins var. **glandulosa** Bot. Jahrb. Syst. 45: 465. 1911.—FIG. 5.

C. rufa var. *glandulosa* (Perkins) M. C. Johnston, Wrightia 3: 91. 1963.

Trees, to 15 m high, without spines, the bark lenticellate. *Leaves* subopposite, ovate, acute, entire or slightly undulate near the apex, shallowly cordate basally,

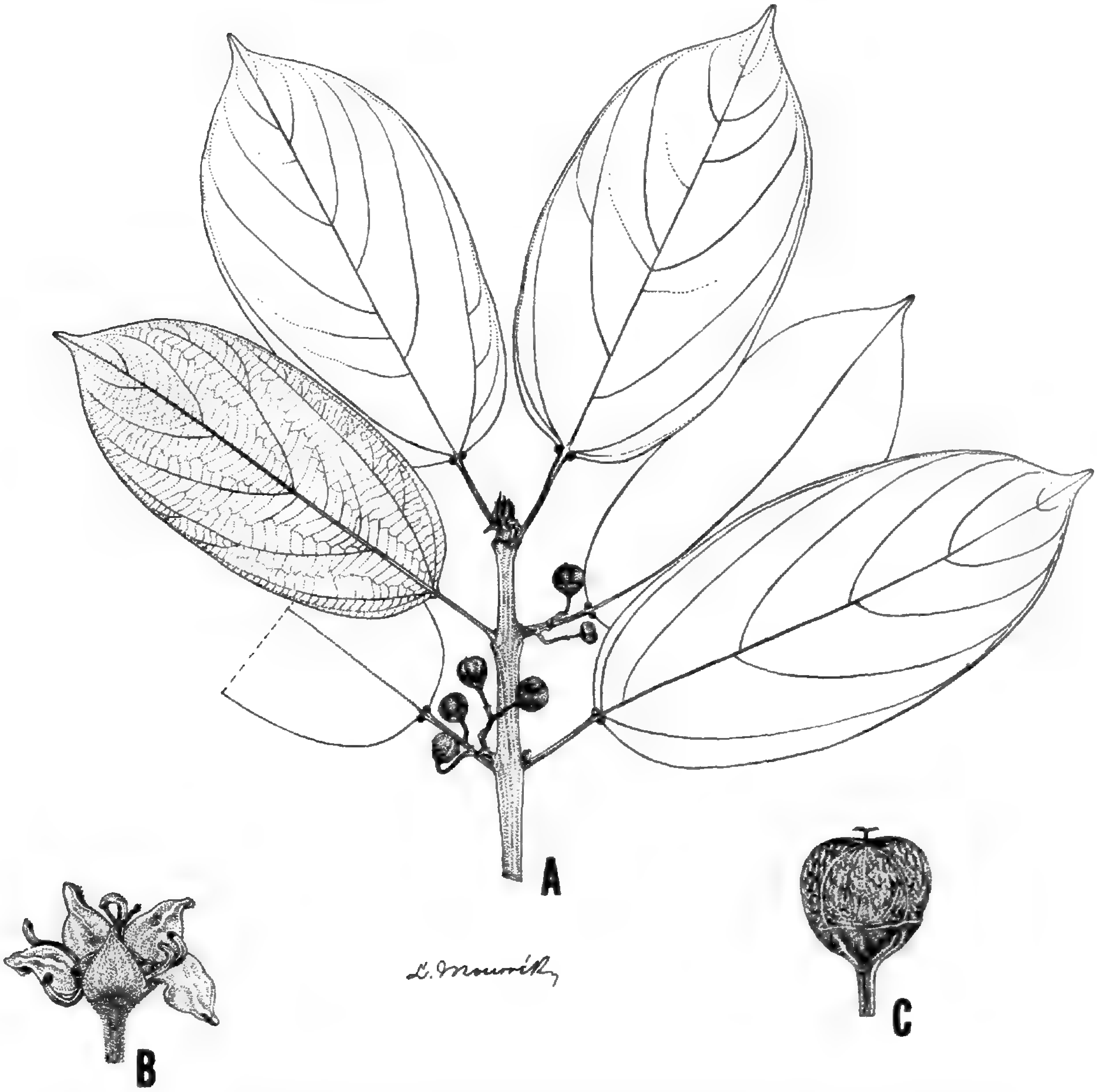

FIGURE 5. *Colubrina glandulosa* Perkins.—A. Habit (× 0.5).—B. Flower (× 6.7).—C. Fruit (× 2.0). [A–C, after *Johnston 1363* (GH); B, after *Johnston 1018* (GH).]

to 20 cm long and 10 cm wide, the glands at the base of the blade prominent, without glands on the lower surface, subcoriaceous, more or less glabrous to slightly pubescent on the veins beneath, lustrous above; petioles ca. 1–2.5 cm long, glabrous to pubescent, the stipules caducous. *Inflorescences* cymose, the peduncles less than 1 cm long, brown-pubescent. *Flowers* shortly pedicellate; calyx-lobes ca. 1.5 mm long, brown-pubescent on the outer surface; petals narrowly-ovate, ca. 1.2 mm long, inserted at the margin of the disc, subsessile; stamens slightly longer than the petals, the anthers ca. 0.3–0.4 mm long; disc fleshy and somewhat lobed; ovary almost covered by the disc, the style ca. 0.7–0.8 mm long, 3-lobed, the lobes ca. 0.4 mm long. *Capsules* subspherical, slightly 3-lobed, the floral tube adhering to the lower third, ca. 6–8 mm in diameter; mature seeds unknown.

Panama and northern South America.

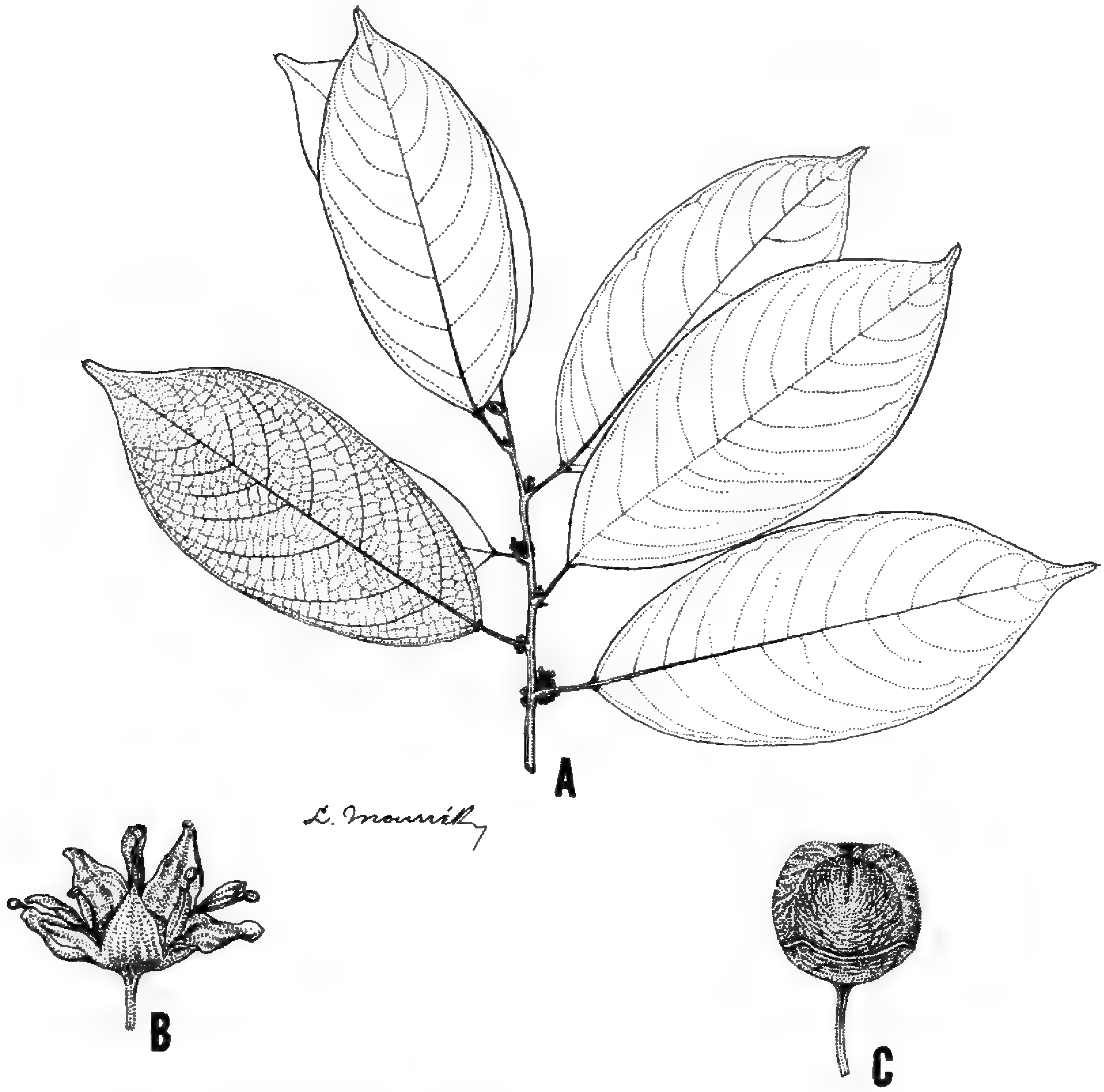

FIGURE 6. *Colubrina spinosa* Donn. Sm.—A. Habit (× 0.5).—B. Flower (× 9.9).—C. Fruit (× 2.8). [A–B, after *von Wedel 1231* (GH); C, after *Cooper 365* (A).]

CANAL ZONE: Barro Colorado Island, *Croat 7349* (MO), *Shattuck 709* (F, MO), *Wetmore & Abbe 165* (F, GH, MO), *540* (A, F), *588* (A, F), *Woodworth & Vestal 540*, *588* (both MO). PANAMÁ: Between France Field and Cativai, *Standley 30276* (A). Río Tapía, *Standley 30677* (A). San José Island, *Johnston 742* (GH), *1018*, *1363* (both GH, MO).

3. **Colubrina spinosa** Donn. Sm. var. **spinosa**, Bot. Gaz. (Crawfordsville) 23: 4. 1897.—FIG. 6.

C. panamensis Standley, Publ. Field Columbian Mus., Bot. Ser. 4: 225. 1929.

Trees, to 10 m high, the stems to 3 cm in diameter, without spines, the bark lenticellate, the younger stems pubescent. *Leaves* alternate, elliptic to ovate-elliptic, acuminate, entire, obtuse to slightly rounded basally, to 22 cm long and 8 cm wide, membranaceous, glabrous to sparsely pubescent on the veins beneath, the glands prominent at the base of the blade, without glands on the lower surface; petioles to 2 cm long, sparsely brown-pubescent, the stipules caducous.

Inflorescences cymose, sessile, brown-pubescent. *Flowers* with the pedicels 3–5 mm long at anthesis; calyx-lobes ca. 1 mm long, brown-pubescent on the outer surface; petals narrowly ovate, notched apically, ca. 1 mm long, subsessile; stamens slightly longer than the petals, the anthers ca. 0.25 mm long; ovary half-inferior, the disc not conspicuously lobed, the style ca. 0.4 mm long, the stigma ca. 0.1 mm long. *Capsules* subspherical, slightly 3-lobed, the floral tube adhering to the lower third, 5–6 mm in diameter; seeds 3, wedge-shaped, 3–4 mm long, the testa brown.

Nicaragua, Costa Rica, and Panama.

BOCAS DEL TORO: Almirante region, *Cooper 365* (A, GH, MO, US), *411* (F, holotype of *C. panamensis*; GH, MO, isotypes). Vicinity Chiriquí Lagoon, *von Wedel 1231* (GH, US), *1550* (GH, MO).

4. **Colubrina arborescens** (Mill.) Sarg., Trees & Shrubs 2: 167. 1911.

Ceanothus arborescens Mill., Gard. Dict. ed. 8. 1768.

Trees, to 20 m (in Panama). *Leaves* alternate, oblong-ovate, shortly acuminate, entire, the bases rounded, to 16 cm long and 8 cm wide, glabrous above, sparsely pubescent on the veins beneath, dark glands scattered on the undersurface; petioles 10–12 mm long, sparsely pubescent, stipules not apparent. *Flowers* and *fruit* unknown for Panama.

Southern Mexico, Central America, and the West Indies.

BOCAS DEL TORO: Region of Almirante, *Cooper 564* (US).

The single Panamanian collection is sterile, and I rely on M. C. Johnston's determination and the fact that he includes (apparently) this collection in his treatment of *C. arborescens* (Brittonia 23: 12–13. 1971).

4. RHAMNIDIUM

Rhamnidium Reissek *in* Mart., Fl. Bras. 11(1): 94. 1894.

Shrubs or trees, the lenticels conspicuous on the younger stems. *Leaves* opposite or subopposite, pinnately-veined, entire; mostly petiolate, the stipules interpetiolar. *Inflorescences* cymes, axillary, pedunculate. *Flowers* bisexual; floral tube half-spherical to almost conical; sepals (4–)5; petals (4–)5; stamens (4–)5; nectariferous disc apparently absent; ovary more or less superior, incompletely 2-locular, the ovules 2, the style 1, 2-lobed. *Fruit* drupaceous or berrylike, oblong, the endocarp 2-locular; seeds (1–)2, oily, the endosperm absent.

A genus of 12 species, mostly in tropical South America, Cuba, and Jamaica; a single species in Panama.

1. **Rhamnidium caloneurum** Standley, Publ. Field Columbian Mus., Bot. Ser. 4: 224. 1929.

Trees, to 25 m high, the trunk to 30 cm in diameter, with the slender branches subterete, dark brown, and obscurely puberulent to glabrate, the internodes 2–3 cm long. *Leaves* opposite, the petioles 8–11 mm long, slender, sparsely puberulent to glabrate; blade eliptic to oblong-elliptic, 6–11 cm long, 3–4.5 cm wide, abruptly acuminate, the acumen ca. 1 cm long, mucronate, obtuse to rounded basally, chartaceous, green and shiny and glabrous above with the transverse veins prominent, pale beneath, sparsely puberulent near the veins, the midrib elevated, slender, the lateral veins about 13 on each side, parallel, arcuate, ascending, attenuating at the revolute margins. *Cymes* umbelliform, axillary, few-flowered, the peduncles 6 mm long, the pedicels thick, 5–7 mm long, sparsely puberulent to glabrate; calyx 5-lobed, glabrous, triangular, acute, spreading, 6 mm wide. *Berry* subglobose, 1 cm long and almost the same width, rounded apically and basally, smooth, glabrous; seed 1, compressed.

Known only from the type collection.

BOCAS DEL TORO: Daytonia Farm, *Cooper 434* (F, holotype; US, isotype).

The above description is a translation of Standley's original Latin diagnosis. The type collection is in a fruiting stage, which accounts for the incomplete floral description.

5. ZIZIPHUS

Ziziphus Mill., Gard. Dict. Abr. ed. 4. 1754.

Shrubs or small trees, rarely lianas, mostly deciduous, frequently with stipular spines. *Leaves* alternate, rarely subopposite, 3-nerved, or rarely more or less pinnately nerved, mostly dentate; petiolate, the stipules mostly spinulose and unequal. *Inflorescences* cymose, axillary, few-flowered, rarely thyrses and terminal. *Flowers* bisexual; floral tube shallow; sepals (4–)5, keeled, deciduous; petals (4–)5, clawed; stamens (4–)5, longer than the petals; nectariferous disc surrounding the ovary; ovary inferior to subinferior at anthesis, becoming superior in fruit, 2(–3)-locular, the style 1, the stigmas 2(–3), small. *Fruit* a drupe, ovoid to more or less obovoid; seed 1, ellipsoid.

A tropical and subtropical genus of 40–100 species, some of which, including *Ziziphus mauritiana* Lam., are cultivated for their edible fruits.

a. Undersurfaces of the leaves and young twigs densely tomentose; leaves oval to suborbicular, the apices obtuse to retuse; petals clawed but not conspicuously hooded .... 1. *Z. mauritiana*

aa. Undersurfaces of the leaves glabrous except for small tufts of trichomes at the bases of the 3 main veins; leaves elliptic, the apices acute-acuminate; petals conspicuously hooded .... 2. *Z. strychnifolia*

1. **Ziziphus mauritiana** Lam., Encycl. Méthod. Bot. 3: 319. 1789.—FIG. 7.

Small tree, armed with spines on the older branches, the stems brown-tomentose. *Leaves* alternate, 3-nerved almost to the apex, oval to suborbicular, obtuse to retuse, finely crenate-serrate, each tooth with a small gland at the tip, obtuse to slightly rounded and weakly oblique basally, to 4.5 cm long and 3 cm wide, dull green and glabrous above, densely tomentose beneath, the pubescence on the veins brown; petioles ca. 5–8 mm long, brown-tomentose, the stipules unequally developed, the longer ca. 2–3 mm long on older branches. *Inflorescences* cymes, axillary and sessile, 10–15-flowered. *Flowers* subsessile to shortly pedicel-

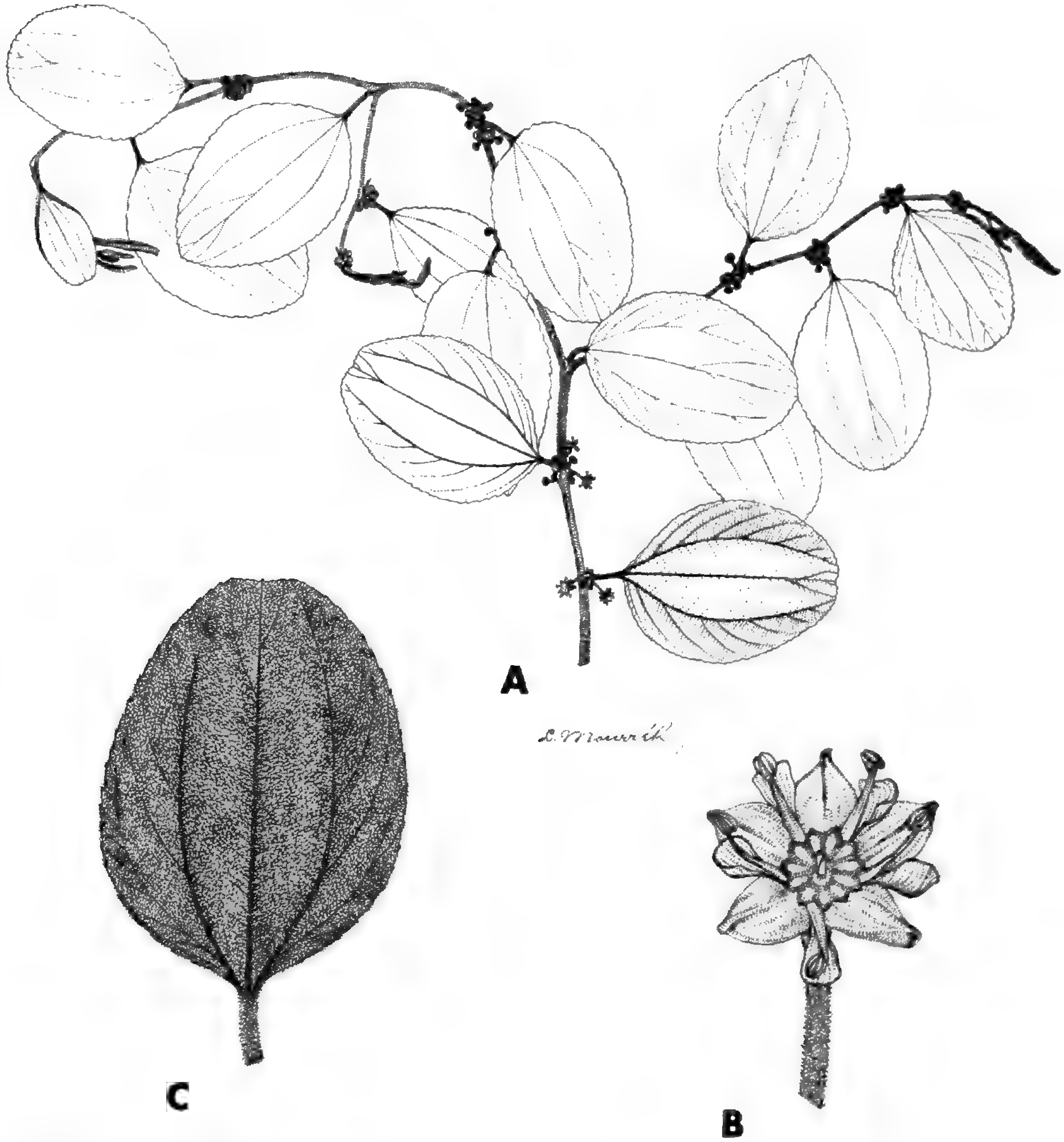

FIGURE 7. *Ziziphus mauritiana* Lam.—A. Habit (× 0.6).—B. Flower (× 7.2).—C. Leaf undersurface (× 1.2). [After *D'Arcy & Croat 4197* (MO).]

late, the pedicels to 4 mm long, tomentose; floral tube shallowly patelliform; sepals (4–)5, deltoid, sometimes slightly unequal, ca. 1.2–1.5 mm long, glabrous and keeled within, tomentose without; petals (4–)5, clawed, white, ca. 1.2 mm long; stamens (4–)5, the filaments subulate, ca. 1 mm long, the anthers ca. 0.4 mm long; nectariferous disc ca. 10-ridged; ovary completely immersed in the disc, the style ca. 0.3–0.4 mm long, the stigmas 2, minute. *Fruit* unknown.

A naturalized species native to southern Asia and Africa.

LOS SANTOS: Salinas de Chitre, *D'Arcy & Croat 4197* (MO).

2. **Ziziphus strychnifolia** Tr. & Planch., Ann. Sci. Nat. Bot., Sér. 5. 16: 380. 1872.

Small tree, to 7 m high, sparsely armed with stipular spines on the older branches, sparsely pubescent on the younger branches, the bark lenticellate. *Leaves* alternate, 3-nerved to the apex, elliptic, acute-acuminate, very finely crenate, each tooth with a small gland at the tip, obtuse basally, to 16 cm long and 6 cm wide, glabrous above, a tuft of trichomes between the bases of the 3 large veins beneath; petioles 5–9 mm long, the stipules rarely developing, if so, the spines paired, equal, 2–3 mm long. *Inflorescences* cymes, axillary, 8–12-flowered, the peduncle 0.5–1 cm long. *Flowers* with the pedicels 2–3 mm long; floral tube obconic; sepals 5, deltoid, ca. 1 mm long, keeled on the inner surface; petals 5, conspicuously hooded, the hood ca. 0.5–0.7 mm long, the claw ca. 0.4–0.5 mm long; stamens 5, the filaments ca. 0.5 mm long, the anthers ca. 0.4 mm long.[3]

Panama and Colombia (?).

DARIÉN: Marraganti and vicinity, *Williams 1012* (NY).

Because of poor material, one collection of *Ziziphus* remains unnamed: Los Santos: 17.8 mi. S of Macaracas, *Lewis et al. 1601* (MO). *Shrub* or woody vine; leaves mostly ovate, acute, shallowly cordate to more or less obtuse basally, to 6 cm long and 4 cm wide, glabrous above and sparsely pubescent on the veins beneath, 3-nerved; petioles 0.5–1 cm long, stipules spinulose, only one developing, to 8 mm long, retrorse. *Inflorescences* axillary, flowers absent.

6. GOUANIA

Gouania Jacq., Select. Stirp. Amer. Hist. 263. 1763.

Lianas, or scandent to arching shrubs, climbing by tendrils. *Leaves* alternate, pinnately-nerved or sometimes 3-nerved from the base, mostly dentate, the teeth frequently glandular; petiolate, the stipules narrow and deciduous or sometimes broad and persistent. *Inflorescences* spicate thyrses composed of glomerules, axillary or terminal. *Flowers* bisexual or polygamous; floral tube obconic to subcampanulate; sepals 5, persistent; petals 5, white to green white, short-clawed; stamens 5, hidden by the petals; nectariferous disc 5-lobed or pentagonal, the lobes opposite the sepals; ovary inferior, immersed in the disc, 3-locular, the style 3-branched more or less basally, the stigmas minute. *Fruit* a schizocarp, 3-locular, generally 3-winged, splitting longitudinally along the margin of each wing into 3, 2-winged mericarps; seeds 3, the seed coat shiny.

A genus of 30–50 species, pantropical but mostly New World.

Gouania is a large and perplexing genus in which the specific boundaries are difficult to assess. The entire genus is sorely in need of critical study, and the absence of any modern revision makes a regional treatment precarious at best. Nevertheless, I make the following changes and comments: After examination of a large number of Panamanian collections, I find that Suessenguth's (Nat. Pfl. ed. 2. 20d: 169. 153) separation of *G. lupuloides* (L.) Urban and

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[3] It is impossible to describe the remainder of the floral parts due to the immaturity of the flowers and their distortion from pressing and drying.

G. polygama (Jacq.) Urban on the basis of the pubescence of the leaf undersurface [only on the veins in *G. lupuloides* versus thickly pubescent (generally?) in *G. polygama*] cannot be maintained due to the great number of transitional forms. I have therefore reduced *G. polygama* to *G. lupuloides*.

Several collections from Barro Colorado Island have very pubescent fruits [*Croat 7984* (MO); *Woodworth & Vestal 326* (A, F)], but except for a more dense pubescence generally the specimens fall within the limits of morphological variation of *Gouania lupuloides*. I have included them with that species.

a. Leaves densely white-tomentose beneath .... 1. *G. hypoglauca*
aa. Leaves glabrous to densely pubescent, but not white-tomentose .... 2. *G. lupuloides*

1. **Gouania hypoglauca** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 89. 1940.

Lianas, climbing by tendrils located near the bases of the inflorescences, the younger stems pubescent, the trichomes brown or white with brown tips. *Leaves* ovate to elliptic, acute, remotely crenate, the teeth glandular-tipped, obtuse to slightly rounded basally, to 6 cm long and 3 cm wide, sparsely pubescent above, densely white-tomentose beneath, tending to be 3-nerved at the base; petioles ca. 0.5–1 cm long, brown-pubescent, the stipules small, caducous. *Inflorescences* thyrses, with the flowers in sessile or subsessile glomerules, the individual spike-like branches to 23 cm long. *Flowers* bisexual, subsessile; bract single, subtending a glomerule, narrowly deltoid, to 1.5 mm long, caducous, densely brown-pubescent; floral tube subcampanulate, pubescent; calyx-lobes deltoid, ca. 0.8–1 mm long, pubescent; petals ovate, ca. 0.6 mm long, the stalk ca. 0.2 mm long; anthers ca. 0.2 mm long; nectariferous disc pubescent, distinctly bilobed between the stamens; style 3-furcate. *Fruit* unknown.

Costa Rica and Panama.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 34* (A), *235* (F, US). PROVINCE UNKNOWN: Western Panama, *Stork 34* (US).

2. **Gouania lupuloides** (L.) Urban, Symb. Antill. 4: 378. 1910.—Fig. 8.

Banisteria lupuloides L., Sp. Pl. 427. 1753.
Rhamnus polygamus Jacq., Enum. Pl. Carib. 17. 1760.
Gouania polygama (Jacq.) Urban, Symb. Antill. 4: 378. 1910.

Lianas, or scandent to arching shrubs, the tendrils at the bases of the inflorescences, the younger stems pubescent, the trichomes grey to brown. *Leaves* inconspicuously 3-nerved at the base, ovate or sometimes elliptic, acute, serrate, the teeth mostly glandular and remote, rounded to shallowly cordate basally, to 11(–13) cm long and 7(–9) cm wide, glabrous to sparsely pubescent above, more or less glabrous, appressed-pubescent on the veins to densely pubescent beneath; petioles 0.5–1.5(–2) cm long, pubescent, the stipules minute, deciduous. *Inflorescences* glomerules, sessile or subsessile, 5–8-flowered, arranged in "spikes" 8–18 cm long, each glomerule subtended by a bract, deltoid, 2–3 mm long, pubescent, the rachis pubescent. *Flowers* mostly bisexual, sometimes functionally carpellate or staminate by reduction; subsessile or with pedicels 1–2 mm long; floral tube more or less obconic, pubescent; sepals deltoid, ca.

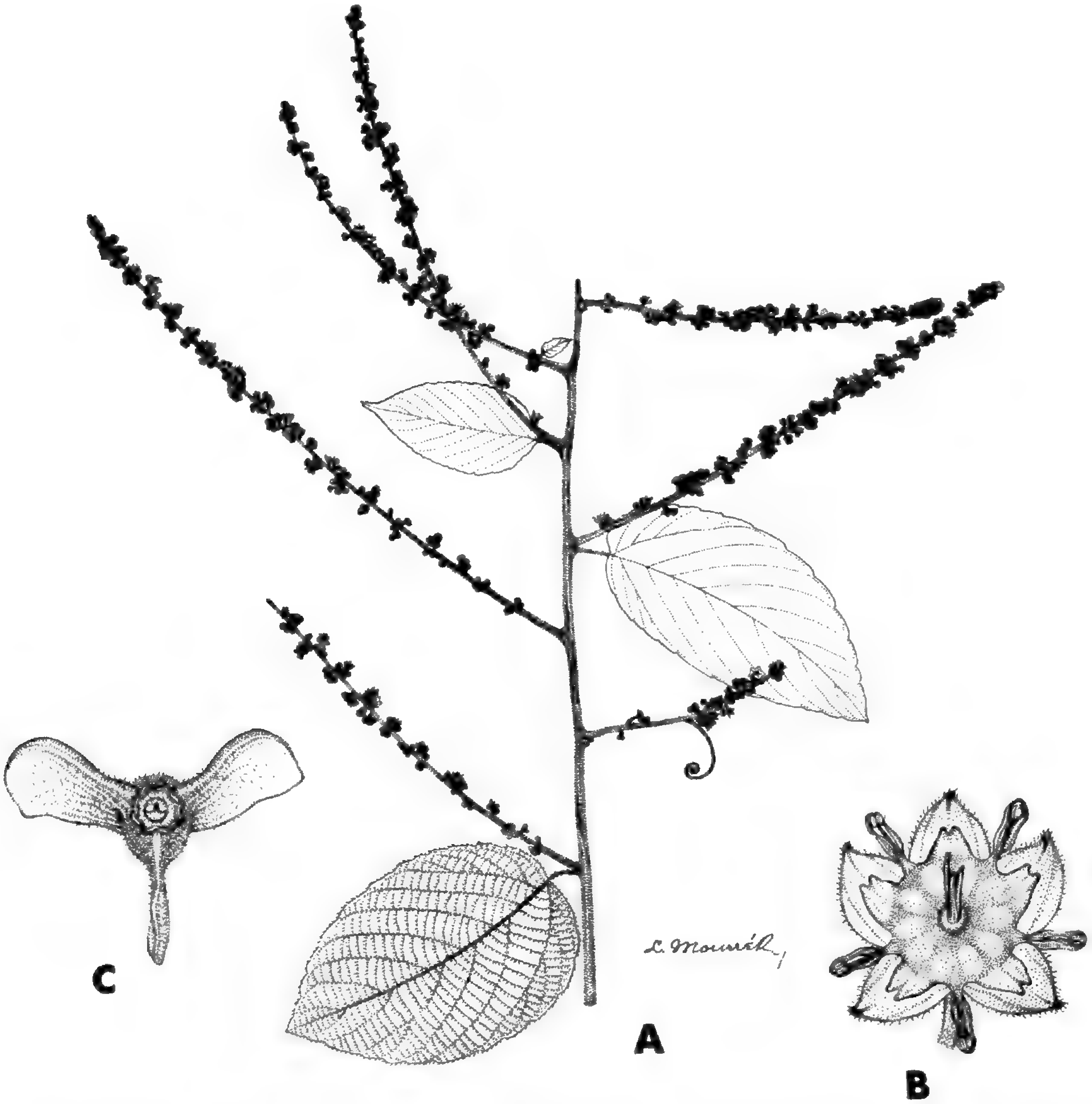

FIGURE 8. *Gouania lupuloides* (L.) Urban.—A. Habit (× 0.6).—B. Flower (× 7.2).—C. Fruit (× 3.0). [A–B, after *Hunter & Allen 99* (MO); C, after *Stern et al. 1715* (MO).]

0.6–1 mm long, keeled on the inner surface, densely pubescent on the outer surface; petals white, ca. 0.8–0.9 mm long; stamens functional or reduced, the filaments ca. 0.5–0.8 mm long, the anthers ca. 0.15–0.2 mm long; nectariferous disc 1- or 2-lobed between the stamens, generally 10-ridged, sparsely pubescent near the emergence of the styles; ovary functional or sometimes reduced, the styles 3, ca. 0.6–0.9 mm long. *Schizocarps* sparsely pubescent on the body, rarely densely so, the body brown to green-black, ca. 3–4 mm high, the wings paler, dolabriform, ca. 5–6 mm high and 4–5 mm wide; seeds 3, brown, ca. 2 mm long.

A variable and wide-ranging species found in Mexico, Central America, the West Indies, and northern South America.

BOCAS DEL TORO: Vicinity of Chiriquí Lagoon, *von Wedel 1834, 1850, 1898* (all MO), *2045* (GH, US). Farm 8, *Cooper 162* (F, GH, US). CANAL ZONE: Balboa, *Standley 25531, 32137* (both US). Barro Colorado Island, *Croat 4709, 7984* (both MO), *Shattuck 444* (MO), 523 (F), *Wetmore & Abbe 48, 67* (both A, GH), *Woodworth & Vestal 326* (A, F), *351* (A). Chagres, *Fendler 108* (GH, US). Along dirt road to Chiva-Chiva, *Correa A. 498* (MO). 5 mi. N of Coclí, *Tyson 3873* (MO). Darien Station, *Standley 31604* (US). Cocolí Road, *Burch et al. 1395* (MO). Between France Field and Catival, *Standley 30249, 30372* (both US). Las Cruces Trail, *Hunter & Allen 702* (MO), *Standley 29202* (US). Vicinity of Miraflores, *White & White 53* (A, F). Along Pan American Highway, *Nowicke et al. 3580* (MO). COCLÉ: Aguadulce, *Pittier 4903* (US). 4 mi. W of Antón on Río Chico, *Tyson & Blum 2590* (MO). El Valle de Antón, *Allen 2863* (F, MO), *Harvey 5165* (F). DARIÉN: Trail between Cana and Boca de Cupe, *Stern et al. 625* (GH, MO, US). Vicinity of Pinogana, *Allen 4290* (F, MO). Along Río Pinas, *Duke 9274, 10550* (both MO). Along Río Sambú, *Pittier 5561* (US). Tucuti, *Terry & Terry 1378, 1384* (both A, F, MO). HERRERA: 4 mi. S of Los Pozos, *Tyson 2674* (MO). 0.5 mi. N of Macaracas of Río La Villa, *Tyson et al. 3138* (MO). Vicinity of Ocú, *Stern et al. 1715* (MO, US). LOS SANTOS: Punta Mala near mouth of Río Caldera, *Tyson 2733* (MO). PANAMÁ: Vicinity of Bella Vista, *Piper 5346* (GH, US), *Standley 25398* (MO, US). Chepillo Island, *Duke 10316* (MO). Sabanas near Chepo, *Hunter & Allen 99* (MO). Between Matías Hernández and Juan Díaz, *Standley 28962* (A, US) *31999* (US). Sabanas N of Panama City, *Bro. Paul 597* (US). Punta Paitilla, *Piper 5397* (US). San José Island, *Erlanson 18* (GH, US), *Johnston 514* (GH, MO), *619* (GH), *906, 1173* (both GH, MO, US), *Tyson & Loftin 5083* (MO). Taboga Island, *Standley 27051* (MO, US), *27906* (US). Taboguilla Island, *Miller 1989* (MO, US). Swamp E of Río Tocumen, *Standley 26557* (US). VERAGUAS: Vicinity of Santiago, *Allen 1078* (F, GH, MO, US). PROVINCE UNKNOWN: Camino de Corozal, *Bro. Heriberto 250* (GH, US).

One collection has distinctively large fruits, a characteristic also found in a Mexican species, *G. conzattii* Greenman. However, comparison with the type of *G. conzattii* (*Conzatti 1567*, F) indicates two different taxa. The material is insufficient for precise identification: Darién: Vicinity of Cana, *Williams 723* (NY, US). *Leaves* ovate, acute, remotely crenate, the teeth glandular-tipped, shallowly cordate basally, 10–11 cm long and 6–7 cm wide, more or less glabrous on both surfaces, slightly coriaceous; petioles ca. 1.5 cm long, more or less glabrous, the stipules apparently deciduous. *Inflorescences* arranged in "spikes" to 18 cm long, the rachis pubescent. *Flowers* unknown. *Schizocarp* pubescent, the body and wings pale brown, the body 7–8 mm high, the wings reniform, 10–11 mm high and 6–7 mm wide; seeds 3, wedge-shaped, ca. 5 mm long.

Index of Latin Names

Numbers in **bold face** type refer to descriptions; numbers in roman type refer to synonyms; numbers with dagger (†) refer to names incidentally mentioned.

FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY

AND COLLABORATORS

Part VIII

FAMILY 150. MYRSINACEAE

CYRUS LONGWORTH LUNDELL[1]

Trees or shrubs, glabrous or pubescent, sometimes dioecious. *Leaves* alternate or subverticillate, often clustered at the ends of the branches, entire, crenulate or serrate, glandular-punctate; stipules none. *Flowers* bisexual, or unisexual, usually 4- or 5-parted, regular, small, white, pink, or green, in terminal and axillary mostly pedunculate inflorescences, or glomerate on short bract-covered axillary shoots; calyx inferior, the segments free or more or less connate, mostly ciliate and glandular-punctate, valvate, imbricate, or sinistrorsely contorted, persistent; corolla regular, usually gamopetalous, rotate to tubular; petals valvate or dextrorsely or rarely sinistrorsely imbricate or contorted, often quincuncial; stamens as many as the petals and opposite them; filaments usually short (absent in *Rapanea*), sometimes equaling or longer than the petals, connate with the corolla tube or almost wholly free; anthers mostly dorsifixed, sagittate, cordate, ovate, elliptic or linear, dehiscent by introrse slits or by apical pores, often punctate dorsally; ovary globose, ovoid or clavate, free, sessile, 1-loculed, the placenta central, usually globose, the ovules numerous or few, uniseriate or pluriseriate, the style long, or short, or rarely absent (*Rapanea*), the stigma punctiform, capitate, discoid, conic, lobed or morchelliform. *Fruit* drupaceous, 1-seeded; seeds with a thin testa, the endosperm copious, smooth or rarely ruminate, the embryo cylindric or curved, the cotyledons small, the radicle elongate.

Genera about 40, widely dispersed in tropical regions of both hemispheres.

Useful references:

Mez, C. Myrsinaceae. Pflanzenreich IV. 236. 1902.

Lundell, C. L. Flora of Guatemala: Myrsinaceae. Fieldiana: Bot. 24(8): 135–200. *Fig. 38–56.* 1966.

———. The Genus *Parathesis* of the Myrsinaceae. Contr. Texas Res. Found., Bot. Stud. 5: xiv + 206. *35 pl. 71 fig.* 1966.

a. Inflorescences reduced, axillary, often with flowers borne on short bract-covered shoots, the shoots usually shorter than the petioles; anthers sessile; style none, but the stigmas of pistillate flowers large, usually lobed .... 1. *Rapanea*

aa. Inflorescences large, axillary and terminal, paniculate or racemose, pedunculate; anthers never sessile; style well developed.

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[1]Texas Research Foundation, Renner, Texas 75079.

ANN. MISSOURI BOT. GARD. 58: 285–353. 1971.

b. Inflorescences strictly racemose; leaves essentially linear, sessile .... 2. *Grammadenia*
bb. Inflorescences paniculate, the flowers in umbels, corymbs, or racemes; leaves not linear.
c. Sepals and petals valvate; petals densely pubescent .... 3. *Parathesis*
cc. Sepals and petals imbricate, often convolute in bud; petals glabrous (except in *Weigeltia*).
d. Anthers minute, wider than long; style short, thick; the Panamanian species with simple stems and large terminal subverticillate leaves .... 4. *Weigeltia*
dd. Anthers elongate, mostly lanceolate, rarely ovate or cordate, always longer than wide; style slender; leaves strictly alternate.
e. Flowers unisexual or bisexual; style of staminate flowers short, subequaling the abortive ovary, the style of carpellate flowers elongate, much exceeding the ovary; ovules few, uniseriate; sepals and petals contorted in bud .... 5. *Stylogyne*
ee. Flowers bisexual; style long and slender; ovules usually numerous, pluriseriate; sepals and petals imbricate or contorted in bud.
f. Anthers small, cordate; stamens exserted; filaments long and slender; corolla greenish or white; flowers corymbose .... 6. *Gentlea*
ff. Anthers usually large, elongate; stamens included; filaments usually short, if elongate the flowers either racemose or spicate; corolla pink or white .... 7. *Ardisia*

1. RAPANEA

Rapanea Aubl., Hist. Pl. Gui. Fr. 1: 121. *t. 46.* 1775.

Shrubs or trees, glabrous or pubescent. *Leaves* petiolate, sometimes lepidote or pubescent, entire or nearly so. *Flowers* small, unisexual or bisexual, 4- or 5-merous, axillary, often borne on short bracteate shoots, fasciculate, appearing glomerate by reduction of the inflorescence; sepals small, usually connate basally, imbricate or valvate, ovate or triangular, often ciliolate, usually punctate or puncticulate; petals connate below, spreading or recurved, usually lineate, often papillose on the margins; stamens borne in the throat of the corolla or above on corolla lobes, the filaments obsolete, the anthers sessile, dehiscent by introrse slits, abortive in carpellate flowers; ovary globose or ellipsoid, the stigma sessile in carpellate flowers, large, subcapitate, morchelliform, or lobed; ovules few, uniseriate. *Fruit* 1-seeded, dry or fleshy, the endocarp crustaceous to ligneous; seeds globose, smooth, intruded basally, the endosperm corneous, sometimes slightly ruminate, the embryo elongate, transverse, usually curved.

A genus of perhaps 200 species in the tropics and subtropics of both hemispheres. Five species are included from Panama, but additional species are represented by material inadequate for positive identification.

a. Young branchlets and petioles pubescent.
b. Leaves narrow, lanceolate or oblong-lanceolate, to 2.5 cm wide, the apex usually acute or acuminate; stems and petioles short villous to villous-tomentose .... 1. *R. myricoides*
bb. Leaves wider, elliptic or oblanceolate, to 3.7 cm wide, the apex obtuse; apices of stems sparsely pubescent with short trichomes, the upper surface of petioles puberulent .... 2. *R. panamensis*
aa. Young branchlets and petioles glabrous.
c. Pedicels 2–3 mm long; sepals to 1.4 mm long, acuminate; montane .... 3. *R. allenii*

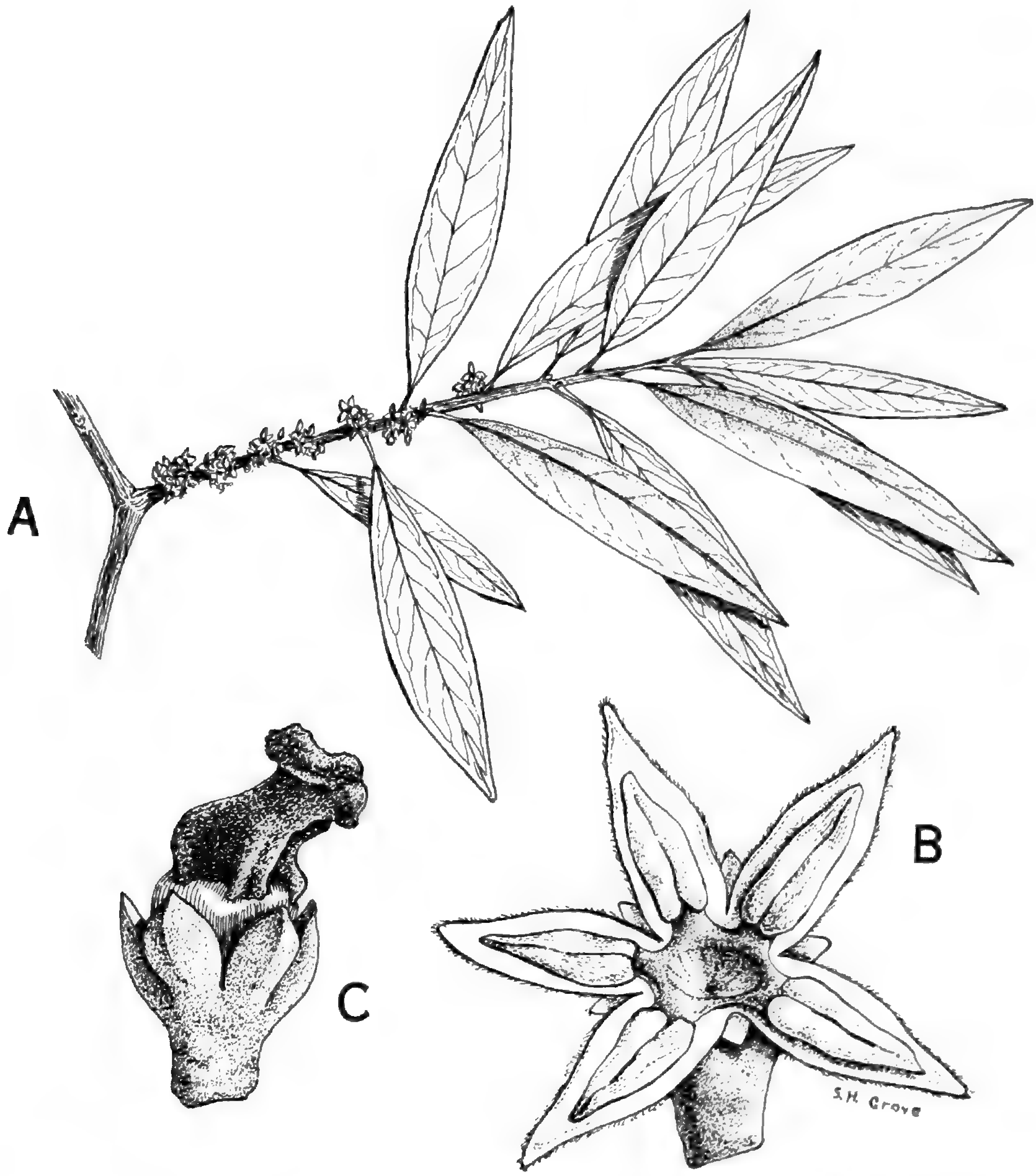


FIGURE 1. *Rapanea myricoides* (Schlecht.) Lundell.—A. Habit (× ¾).—B. Carpellate flower, spread out to show abortive anthers (× 15).—C. Incrassate sepals, and ovary of carpellate flower, showing large, sessile, morchelliform stigma (× 15). [After *Skutch 1880* (F).]

cc. Pedicels 1–1.5 mm long or shorter; sepals not over 1 mm long, acute or rounded; middle altitudes or sea level.
d. Leaves rounded apically, mostly obovate; sea level .... 4. *R. punctata*
dd. Leaves narrowed and acutish to obtuse apically, mostly oblong-elliptic; middle altitudes above 1000 m .... 5. *R. pellucido-punctata*

1. **Rapanea myricoides** (Schlecht.) Lundell, Wrightia 3: 109. 1964.—FIG. 1.

Myrsine myricoides Schlecht., Linnaea 8: 525. 1833.
M. guatemalensis Gandoger, Bull. Soc. Bot. France 65: 57. 1918.

Shrubs of 2–3 m, or sometimes small trees to 10 m high, branchlets puberulent or sparsely short-villous to densely villous-tomentose with reddish trichomes, glabrate, often densely leafy. *Leaves* usually short-petiolate, the petioles sometimes to 12 mm long, rarely longer; leaf blades lanceolate or oblong-lanceolate, mostly 6–13 cm long and 1–2.5 cm wide, acute, acuminate, or obtuse, attenuate to the base, chartaceous or subcoriaceous, dark green and often shiny above, paler and usually silver-green beneath, sometimes villous at first, especially along the midvein on both surfaces, glabrescent, entire. *Inflorescences* 3–9-flowered, glomerate, arising in the leaf axils or from defoliate nodes; flowers sessile or with pedicels to 1.5 mm long. *Flowers* unisexual, 1.8–3.5 mm long, the staminate larger, papillose-puberulent, or glabrous or nearly so; calyx lobes triangular-ovate, 0.4–1 mm long, acute or subacute, epunctate to more or less black-punctate; petals connate scarsely ¼ basally, subacute to rounded apically, lineate; anthers sessile, those of carpellate flowers abortive, less than 1 mm long, those in staminate flowers shorter than the petals, 1.5–1.8 mm long, attached at the apex of the corolla tube; ovary abortive in staminate flowers, subglobose in carpellate flowers, with a large sessile stigma, the ovules 3, uniseriate, imbedded in a fleshy placenta. *Fruit* blackish at maturity, glabrous, 2.5–3.5 mm in diameter, punctate with large glands.

Mexico, south to Panama, and probably elsewhere in tropical America.

CHIRIQUÍ: Boquete, 3800 ft, *Davidson 614* (F). Pastures around El Boquete, 1000–1300 m, *Pittier 2857* (US). Vicinity of El Boquete, *Maxon 5108* (US); hills E of the Río Caldera, 4500–6500 ft, *Allen 4658* (MO, US); llanos area S of town, 3500 ft, *Stern et al. 33739* (MICH, MO); from Boquete to 3 mi. N, 3300–4200 ft, *Oliver 591* (F). Rio Chiriquí Viejo valley, near El Volcán, *White 193* (MO). COCLÉ: Foothills of Cerro Pilón, near El Valle, ca. 900 m, *Duke & Correa 14715* (LL). El Valle, *Correa 309* (MO). Between Las Margaritas and El Valle, *Woodson et al. 1294* (MO). PANAMÁ: Along dirt road to Cerro Campana, ca. 2300 ft, *Correa & Dressler 855* (MO). Cerro Campana, *Allen 2083* (MO, US), 2900 ft, *McDaniel 6877* (MO); elfin forest beyond Motel Su-Lin, 2700–3000 ft, *Duke 8658* (MO).

Stearn (Bull. Brit. Mus. (Nat. Hist.), Bot. 4: 175, *fig. 25, E–H.* 1969) recognizes *Myrsine coriacea* (Sw.) R. Br. [≡*Rapanea coriacea* (Sw.) Mez] as the older name for the slender leaved pubescent species of the mainland and Jamaica. There appear to be minor differences in the degree of fusion of the petals, nature of the stigma, and in punctation which appear to distinguish *R. myricoides* from *R. coriacea.*

2. **Rapanea panamensis** Lundell, Wrightia 4: 169. 1971.

Shrubs or small trees to 9 m high, the branchlets rather thick, rather sparsely pubescent at first with short reddish trichomes. *Leaves* with petioles pubescent at first above, the petioles marginate, 4–10 mm long; leaf blades thin, membranaceous to subchartaceous, narrowly elliptic or oblanceolate, 4–12 cm long and 1.8–3.7 cm wide, narrowed to the obtuse apex, basally revolute, concolorous, entire, the costa nearly plane above, elevated beneath, the primary veins slender, discernible but rather obscure, pellucid-punctate. *Inflorescences* axillary, the flowers densely glomerate on short shoots, the shoots tightly enveloped by fimbriate bracts. *Staminate flowers* 4- or 5-merous, the pedicels to 1 mm long, rather stout; calyx ca. 1 mm long, the sepals connate ⅓–½, ovate, acute, ciliolate, thin, punctate with few very small blackish glands; petals oblong-lanceolate, 2–2.4 mm long, connate basally ca. 0.5 mm, cucullate, acutish, papillose-puberulent, black-punctate mostly above the middle with black rounded and short linear glands, these comparatively few; anthers thick, elliptic or ovate-elliptic, ca. 1.3 mm long, slightly shorter than the petals, attached dorsally to the corolla lobes above the corolla tube, rounded and minutely apiculate, epunctate; gynoecium abortive. *Fruit* subglobose, punctate with elevated pellucid glands, the pedicels of the fruit to 1.5 mm long.

Native to the lowlands of Panama.

PANAMÁ: Cerro Campana, *Porter et al. 4317* (LL). Bald savanna like areas along road toward top if Cerro Campana, *Duke 5998* (LL). Hills NE of Hacienda La Joya, 50–300 m, *Dodge et al. 16898* (MO). Sabana de Dormisolo, near Chepo, 60–80 m, *Pittier 4657* (US). San José Island, along road between Bodega Bay and Río Mata Puerco, *Duke 12545* (LL); W of Mata Puerco, *Johnston 441* (LL, holotype; MO, US, isotypes). VERAGUAS: La Mesa, *Tyson 6072* (MO).

3. **Rapanea allenii** Lundell, Wrightia 4: 168. 1971.—Fig. 2.

Trees, ca. 12 m high, the branchlets rather thick, glabrous. *Leaves* glabrous, petiolate, the petioles 5–10 mm long, slender, narrowly marginate; leaf buds ciliate, otherwise glabrous; leaf blades chartaceous, drying dull gray, opaque, the venation obscure and scarcely evident, the blades oblanceolate or oblong-oblanceolate, 6–10 cm long and 2–2.8 cm wide, apically bluntly obtuse, basally narrowed, acute, revolute, decurrent on the petiole, the midvein plane above, elevated beneath, entire, the glands obscure. *Inflorescences* with the flowers borne on short bract-covered axillary shoots mostly on defoliated old wood, the shoots probably perennial; bracts blackish, ciliate, tightly enveloping the shoots. *Staminate flowers* 5-merous, fasciculate at the ends of the shoots, the pedicels erect, 2–3 mm long; sepals free almost to the base, lanceolate, 1–1.4 mm long, acuminate, punctate with orange glands, ciliolate, revolute when dry; petals lanceolate, 3 mm long, connate ca. 1 mm basally, apically obtuse, minutely papillose-puberulent, punctate with orange glands; anthers thick, borne at the apex of the corolla tube, oblong-elliptic, ca. 1.3 mm long, apically rounded and apiculate; ovary ovoid, glabrous. *Carpellate flowers* unknown.

Native to Panama.

CHIRIQUÍ: N forested slope of Cerro Copete, an eastern spur of Chiriquí Volcano, 8000–8500 ft, *Allen 4869* (US, holotype; MO, isotype; LL, fragment).

4. **Rapanea punctata** (Lam.) Lundell, Wrightia 4: 121. 1969.

Sideroxylum punctatum Lam., Tab. Encycl. Meth. Bot. 2: 42. 1794.
Myrsine punctata (Lam.) Stearn, Bull. Brit. Mus. (Nat. Hist.), Bot. 4. 177. 1969, non *M. punctata* (Lev.) Wilbur, Pacific Sci. 19: 522. 1965.
M. floridana A. DC., Trans. Linn. Soc. London 17: 107. 1834.

Shrubs or small trees, 9 m high or less, the trunk 15 cm or less in diameter, branchlets glabrous. *Leaves* with short thick petioles to 7 mm long; leaf blades oblong-obovate, oblong-elliptic, or oblanceolate, 4–10 cm long and 2.5–4 cm wide, apically rounded or obtuse-rounded, cuneately nar-

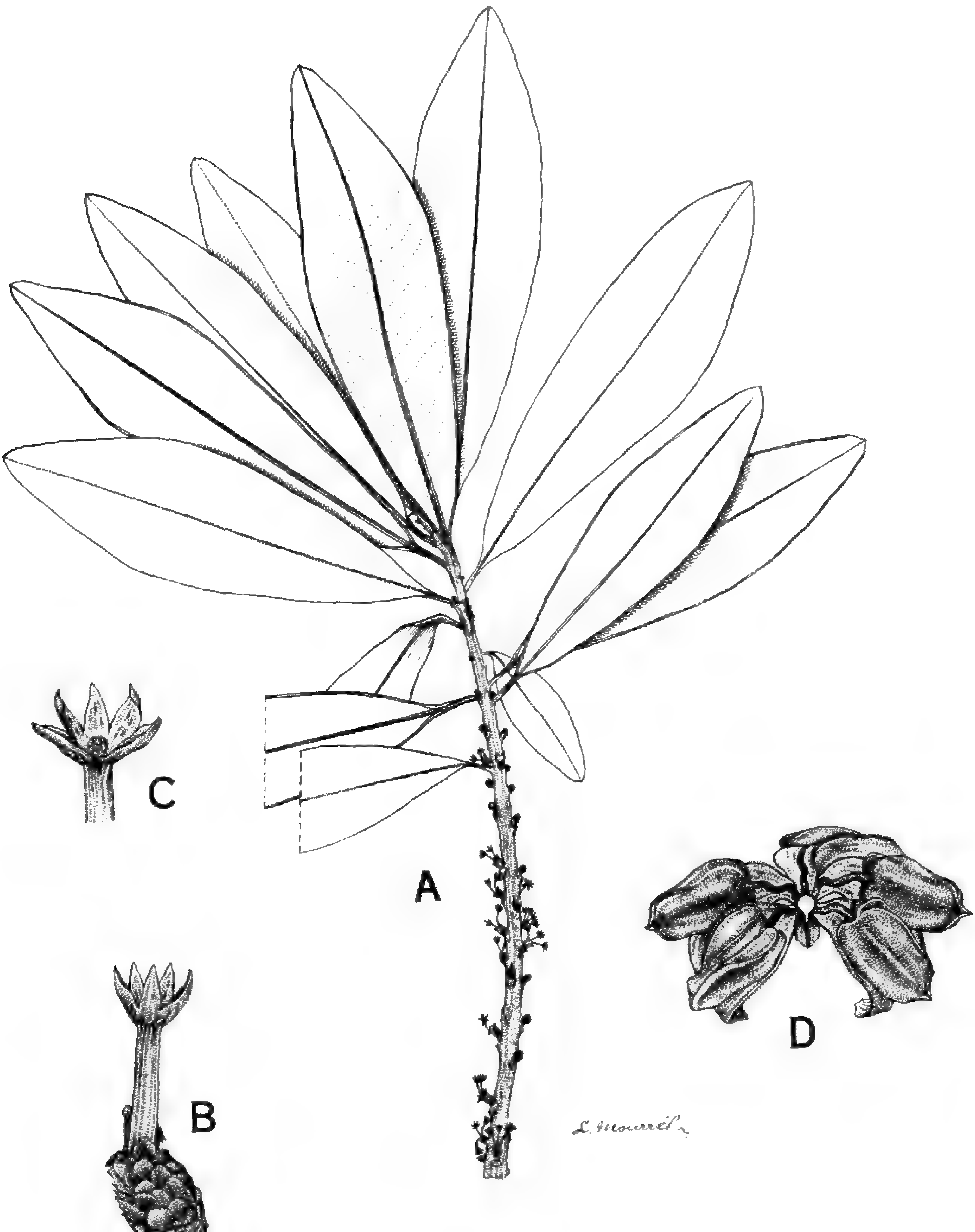


FIGURE 2. *Rapanea allenii* Lundell.—A. Habit (× ⅔).—B. Floral shoot, pedicel, and calyx (× 5⅓).—C. Calyx, spread out (× 6⅔).—D. Petals and stamens (× 10⅔). [After *Allen* 4869 (MO, isotype).]

rowed to the revolute base, lustrous above, somewhat paler beneath, entire, chartaceous to subcoriaceous. *Inflorescences* shorter than the petioles, 3–7-flowered, the flowers glomerate mostly on short axillary spur-like shoots. *Flowers* unisexual, 2–2.5 mm long, greenish, punctate, the pedicels 1.5 mm long or less; sepals connate basally, ovate or ovate-lanceolate, less than 1 mm long, puncticulate; petals short-connate, elliptic, to 2.5 mm long, puncticulate, the margin papillose-puberulent; anthers included, sessile, attached at the apex of the corolla tube, to 1.5 mm long in staminate flowers, apiculate, epunctate, abortive in carpellate flowers; ovary subglobose, the ovules 2 or 3; the stigma in carpellate thick, subcapitate, irregularly short-lobed. *Fruit* pellucid-punctate, black and globose at maturity, ca. 4 mm in diameter smooth.

Florida, Bahama Islands, Mexico, Central America, and probably elsewhere in the West Indies and South America. Vernacular name: "crabwood."

BOCAS DEL TORO: Bar Mouth, Changuinola Valley, *Dunlap 529* (F, US). Bocas Island, *Cooper 463A* (K).

This species has been confused with *Rapanea guianensis* Aubl. of South America, as pointed out by Stearn (Bull. Brit. Mus. (Nat. Hist.), Bot. 4: 177. 1969).

5. **Rapanea pellucido-punctata** (Oerst.) Mez, Pflanzenreich IV. 236: 393. 1902.

Myrsine pellucido-punctata Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1861: 133. 1861.

Trees, sometimes to 13 m high, the branchlets rather thick, glabrous. *Leaves* glabrous, when young bordered with a reddish fringe which disappears early, the petioles marginate, 5–10 mm long; leaf blades rather thin, subchartaceous to chartaceous, slightly paler beneath, oblanceolate-oblong or oblong-elliptic, 5–11 cm long and 1.6–4.3 mm wide, apically narrowed and acutish to obtuse, basally acute, revolute, decurrent, entire, punctate and with conspicuous pellucid glands, the glands rounded to linear, the veins slender and inconspicuous. *Inflorescences* with flowers borne at the apices of short bract-covered axillary shoots, the fringed bracts tightly enveloping the shoots. *Flowers* 5-merous, fasciculate at the ends of the shoots, the pedicels short, rather thick, to 1 mm long; calyx thin, ca. 1 mm high, the lobes connate ¼–½, ovate-triangular, ciliolate, the glands scattered and minute or absent; corolla of carpellate flowers ca. 1.7 mm long, the petals connate ca. 0.7 mm, papillate-puberulent apically, occasionally punctate with minute blackish glands, lanceolate-oblong, acutish; aborted anthers shorter than the petals, attached at the apex of the corolla tube, acutish, eglandular; ovary ellipsoid, glabrous, the ovules 3, imbedded in a globose fleshy placenta; the stigma large, fleshy, lobed, 1–1.4 mm long. *Fruit* globose, with conspicuous elongated surface glands.

Costa Rica and Panama.

CHIRIQUÍ: Boquete, 3800 ft, *Davidson 614* (MO, US), *633* (F). Along streams, rocky plains ca. 5 mi. S of Boquete, 3000 ft, *Allen 4709* (MO). Vicinity of Boquete, Llanos Francia, 3300 ft, *Stern et al. 1194* (MO, US); llanos area S of town, 3500 ft, *Stern et al. 1943* (LL, MICH, MO). Lava fields near town of Volcán, ca. 4600 ft, *Duke 9199* (MO).

Davidson 614 is a mixed collection of *Rapanea pellucido-punctata* and *R. myricoides*.

The description of the carpellate flowers is based on *Stern et al. 1943.* I have examined the Costa Rican collections cited by Oersted in the original description, and the Panama tree of middle altitudes seems to be referable to this species.

2. GRAMMADENIA

Grammadenia Benth., Pl. Hartweg. 2: 218. 1846.

Shrubs, often epiphytic, glabrous. *Leaves* sessile, entire, punctate or lineate. *Inflorescences* axillary, racemose. *Flowers* 5-merous, usually bisexual, pedicellate, with conspicuous bracts; sepals short-connate or nearly free basally, imbricate or quincuncial or dextrorse, rounded or acute apically, margin nude or ciliolate, usually punctate or lineate; petals connate basally, spreading at anthesis, ovate; stamens opposite the petals attached at the apex of the corolla tube, alternating with rounded fleshy lobes; the filaments short and thick, anthers usually wider than long, apex rounded and sometimes emarginate, punctate dorsally or concolorous, subsessile, ovary glabrous, globose or ovoid, the ovules 2–4, the style short with a truncate stigma. *Fruit* globose or ovoid, 1-seeded, the endocarp crustaceous, the embryo cylindrical, transverse.

A small genus of 10 or 12 species of the West Indies, Costa Rica, Panama, and the Andes of South America.

1. **Grammadenia linearifolia** Lundell, Wrightia 4: 70. 1968.—Fig. 3.

Shrubs, branchlets thick, glabrous. *Leaves* sessile, glabrous, chartaceous, linear or narrowly oblanceolate-linear, 5.5–9 cm long and 7–12 mm wide, rounded basally, acutish and apiculate apically, sparsely orange-punctate. *Inflorescences* axillary, slender, racemose, to 6.5 cm long, sparsely glandular-puberulent, the bracts membranaceous, ovate or oblong-elliptic, 1–2 mm long, orange-punctate; pedicels 2.5–4 mm long. *Flowers* glabrous; sepals ovate-triangular, ca. 0.7 mm long, orange-punctate; petals imbricate, broadly ovate, 1.2–1.4 mm long, orange-punctate; anthers subsessile, small, orange-punctate dorsally; ovary punctate, the ovules 2.

Native to Panama.

BOCAS DEL TORO: Robaldo Trail, N slopes of Cerro Horqueta, 6000–7000 ft, *Allen 4803* (MO, holotype).

An epiphytic shrub growing in the tops of giant trees, *Grammadenia linearifolia* is known only from a single twig. Its noteworthy features include the long, essentially linear leaves, almost as wide at the base as medially, the long slender racemes of pale greenish-yellow flowers on elongated pedicels, and the orange glands on all parts. The margin of the leaves is hyaline, and the submarginal vein is well developed.

3. PARATHESIS

Parathesis (A. DC.) Hook. f. *in* Benth. & Hook. f., Gen. Pl. 2: 645. 1876.

Ardisia sect. *Parathesis* A. DC., Prod. 8: 120. 1844.

FIGURE 3. *Grammadenia linearifolia* Lundell, habit (ca. × 1). [After *Allen 4803* (MO, holotype).]

Trees or shrubs, the young branchlets commonly ferruginous-tomentose with stellate or dendroid trichomes, often glabrescent. *Leaves* petiolate, usually pubescent on the lower surface, the trichomes stellate or dendroid, often appressed and bizonal, the margins entire, crenulate, or dentate. *Inflorescences* paniculate, axillary or terminal. *Flowers* bisexual, usually (4–)5(–6)-merous, mostly pink or white, umbellate, corymbose, or subcorymbose-racemose; sepals small, open in the bud, connate basally, commonly tomentulose and papillose; corolla rotate, usually tomentulose outside, papillose-tomentose inside at least apically and along the edges, the petals connate basally, valvate, narrow, acutish; stamens (4–)5(–6), inserted near the base of the corolla tube, the filaments well developed, slender to stout, the anthers sagittate, lanceolate to ovate, acute or mucronate or obtuse apically, dorsally punctate or epunctate, dehiscent by introrse slits or apical pores, usually dorsifixed above the base, erect or versatile; ovary ovoid or subglobose, the ovules few to numerous, usually 1-seriate, sometimes partially 2-seriate, or rarely pluriseriate on the placenta, enclosed or exposed apically, the style long and slender, the stigma punctiform. *Fruit* 1-seeded, the endocarp crustaceous, the embryo cylindric, transverse.

A genus of about 75 species in tropical America, chiefly in the mountainous regions of southern Mexico and Central America. Eight species are recorded for Panama.

Useful reference:

Lundell, C. L. The Genus *Parathesis* of the Myrsinaceae. Contr. Texas Res. Found., Bot. Stud. 5: xiv + 206. 35 pl. 71 fig. 1966.

a. Inflorescences terminal.
  b. Anthers versatile at anthesis.
    c. Leaves sub-bullate, to 22.5 cm long and 10 cm wide; branchlets conspicuously red-tomentose, the trichomes dendroid, persistent .... 1. *P. amplifolia*
    cc. Leaves not sub-bullate, to 11.5 cm long and 4.2 cm wide; branchlets minutely puberulent and papillose at first, glabrescent .... 2. *P. panamensis*
  bb. Anthers erect at anthesis.
    d. Sepals ovate, 1 mm long or less; inflorescences to 7 cm long; leaves to 11 cm long .... 3. *P. microcalyx*
    dd. Sepals narrowly triangular, to 1.8 mm long; inflorescences usually over 15 cm long; leaves to 17 cm long.
      e. Branchlets persistently rufous-pubescent; leaves elliptic or obovate-elliptic, crenulate, with appressed stellate bizonal pubescence beneath; ovary glabrous .... 4. *P. fusca*
      ee. Branchlets essentially glabrous (in fruit); leaves lanceolate, entire, glabrous; ovary with scattered short trichomes apically and at the base of the style (in fruit) .... 5. *P. tenuifolia*
aa. Inflorescences axillary.
  f. Anthers slender, linear-lanceolate, concolorous or with 1–3 minute black glands dorsally; leaves mostly lanceolate, tapering to the acuminate apex .... 6. *P. seibertii*
  ff. Anthers thick, ovate-lanceolate or lanceolate-elliptic, usually black-punctate dorsally; leaves mostly oblanceolate or obovate, abruptly or subabruptly acuminate.
    g. Stamens 2.2–2.5 mm long, filaments equaling the anthers; leaves reticulate-veined, with a distinct submarginal vein .... 7. *P. montana*
    gg. Stamens 3–4 mm long, filaments shorter than the anthers; leaves not reticulate-veined, without a distinct submarginal vein .... 8. *P. glabra*

1. **Parathesis amplifolia** Lundell, Wrightia 4: 151. 1970.

Trees, ca. 6 m high, the branchlets thick, compactly tomentose with dense dark red dendroid trichomes. *Leaves* with red-tomentose elongated stout petioles 3.5–5.5 cm long, the petioles canaliculate; leaf blades subcoriaceous, elliptic or oblong-elliptic, 13–22.5 cm long and 6.5–10 cm wide, short-acuminate apically, acutish basally, glabrous early above, persistently fine-tomentose beneath with appressed indument, bizonal, the costal zone with red dendroid trichomes intermixed, costa and primary lateral nerves impressed above, conspicuous beneath, the primary lateral veins ca. 20 pairs. *Inflorescences* terminal, openly pyramidal, tripinnately paniculate, to 22 cm wide, leafy at base, conspicuously red-tomentose, the trichomes dendroid. *Flowers* corymbose, finely red-tomentose, the buds at anthesis ovoid-ellipsoid, 5–6 mm long; pedicels to 5 mm long; calyx black-punctate, the sepals ovate-triangular, 1.5–2 mm long, acute; petals linear-lanceolate, tapering from the base to the apex, 6 mm long, black-punctate in lines, villous within except basally; stamens ca. 3.5 mm long, the anthers versatile, slender, linear-lanceolate, ca. 2 mm long, conspicuously black-punctate the entire length, including the basal lobes, the filaments flattened, ca. 2.4 mm long, glabrous; ovary red-tomentose over the entire surface, the ovules 9, uniseriate, the placenta depressed-globose; the style glabrous, 5 mm long, punctate with lines.

Native to Panama.

PANAMÁ: Cerro Jefe, *Duke 9466* (MO). Beyond Goofy Lake along road to Cerro Jefe, *Correa & Dressler 472* (MO, holotype).

2. **Parathesis panamensis** Lundell, Wrightia 3: 69. 1963.—Fig. 4.

Trees, the branchlets stout, red-puberulent and papillose at first, glabrescent. *Leaves* slender-petiolate, the petioles to 1.5 cm long; leaf blades oblanceolate or oblanceolate-oblong, 6.5–11.5 cm long and 2–4.2 cm wide, subabruptly short-acuminate apically, the acumen obtuse, acuminate basally, decurrent, entire, black-punctate, thin, at first minutely pubescent on the lower surface with sessile stellate red subappressed trichomes, glabrescent, the costa elevated beneath, nearly plane above, the veins fine and reticulate. *Inflorescences* terminal, paniculate, 4–7 cm long and to 4 cm wide at the base, densely and minutely pubescent with reddish trichomes. *Flowers* papillose and puberulent with minute trichomes, corymbose, the buds at anthesis slender, pyriform, ca. 5 mm long; pedicels 4–6 mm long; calyx small, densely black-punctate, the sepals subulate, 1.7–2 mm long; petals lanceolate-linear 5 mm long, black-punctate in lines; stamens 4 mm long, the anthers versatile, dorsifixed medially, lanceolate-oblong, 1.5 mm long, black-punctate dorsally with glands extending into the basal lobes, the filaments slender, 3–3.5 mm long, black-punctate in lines; ovary puberulent apically with minute reddish trichomes, the ovules 5 or 6, erect, enclosed, uniseriate, the placenta depressed-globose, minutely apiculate.

Native to Panama.

BOCAS DEL TORO: Talamanca Valley, *Cooper & Slater 153* (US, holotype; LL, Y, isotypes).

3. **Parathesis microcalyx** Donn. Sm., Bot. Gaz. (Crawfordsville) 48: 295. 1909.—Fig. 5.

Shrubs or small trees, the twigs slender, covered with minute reddish and closely appressed tomentum. *Leaves* small, slender-petiolate, the petioles to 2 cm long, canaliculate, with fine appressed stellate tomentum beneath, glabrous above; leaf blades oblanceolate or oblanceolate-oblong, 7.5–11 cm long and 2.6–4 cm wide, acuminate basally, subabruptly acuminate apically, thin, paler beneath, essentially entire, pellucid-punctate with short horizontal linear glands, glabrous above, with fine stellate reddish tomentum on the lower surface in a narrow costal zone, the lateral veins fine on both surfaces. *Inflorescences* terminal, shorter than the leaves, pyramidal, slender-branched, to 7 cm long, covered with minute reddish closely-appressed tomentum. *Flowers* few, subcorymbose, borne on slender finely reddish-tomentose pedicels 1.5–4 mm long; buds ovoid, ca. 3 mm long, the tomentum fine, reddish; calyx finely reddish-tomentose, black-punctate, the sepals ca. 1 mm long, connate basally; petals linear-punctate, narrowly triangular, ca. 3 mm long, connate basally, papillose-tomentose within along the edges and apically; stamens ca. 1.75 mm long,

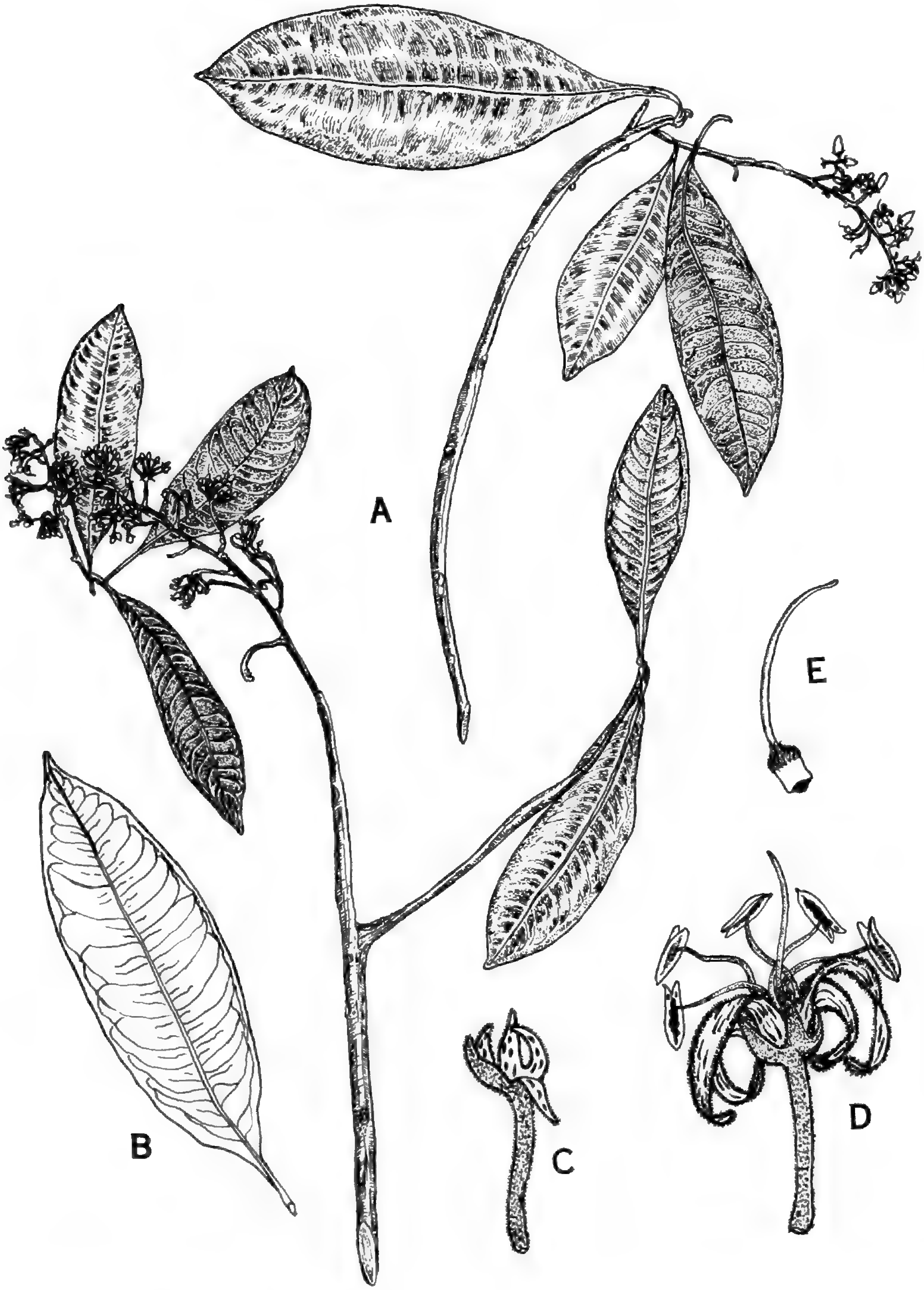


FIGURE 4. *Parathesis panamensis* Lundell.—A. Habit (× ½).—B. Leaf, showing lower surface (× ½).—C. Pedicel and calyx (× 5).—D. Flower, showing long slender filaments and versatile anthers (× 5).—E. Gynoecium (× 5). [After *Cooper & Slater 153* (US, holotype).]

FIGURE 5. *Parathesis microcalyx* Donn. Sm.—A. Habit (× ⅜).—B. Calyx, spread out (× 6).—C. Flower (× 6).—D. Gynoecium (× 6). [After *Pittier 7591* (US, holotype).]

FIGURE 6. *Parathesis fusca* (Oerst.) Mez.—A. Habit (× ½).—B. Calyx, spread out (× 5).—C. Petals and stamen (× 5).—D. Gynoecium (× 5). [After *Oersted* 37 (C, holotype).]

the filaments glabrous, subequaling the anthers, the anthers erect, ovate, densely black-punctate dorsally, dorsifixed ca. ⅓ above base; ovary ovoid, black-punctate, covered with minute reddish tomentum, the ovules 5–7, uniseriate, the style slender, 2.5–3 mm long, sparsely hairy. *Fruit* blackish-purple at maturity, in dense clusters, subglobose, drying 4–6 mm in diameter.

Nicaragua, Costa Rica, and Panama.

DARIÉN: Cana, *Williams 719* (LL, NY, US). Vicinity of El Real, Río Tuira, trail between Río Escucha Ruido and Río Tuira, *Stern et al. 571* (LL, MO). CANAL ZONE: Gatún, *Hayes 207* (NY), *706* (BM).

4. **Parathesis fusca** (Oerst.) Mez, Pflanzenreich IV. 236: 175. 1902.—Fig. 6.

Ardisia fusca Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1861: 127. *t. 2.* 1861.
Tinus fusca (Oerst.) O. Kuntze, Rev. Gen. Pl. 2: 974. 1891.

Shrubs, the branchlets stout, densely appressed ferruginous-tomentose. *Leaves* with slender petioles, the petioles 5–15 mm long, canaliculate, tomentose on the undersurface; leaf blades elliptic, oblong-elliptic, or rarely obovate-elliptic, 6–17 cm long and 2.5–6 cm wide, acuminate and decurrent on petiole basally, subabruptly acuminate apically, thinly chartaceous, obscurely bizonal, pubescent on the undersurface with appressed or subappressed sessile stellate trichomes, the marginal zone glabrescent, sparingly papillose above at first along the costa, rarely sparingly pubescent, the margin finely crenulate, the costa elevated and stellate-pubescent beneath, plane above, the lateral veins slender but conspicuous and reticulate on the undersurface, sparsely punctate. *Inflorescences* terminal, paniculate, to 15 (–22) cm long, ferruginous-pubescent or tomentose with short sessile stellate trichomes, papillose. *Flowers* corymbose or subracemose-corymbose, the calyx and corolla ferruginous-tomentose with short sessile stellate fine bristly trichomes, papillose; pedicels slender, 2.5–6 mm long; bud before anthesis ovoid, 4–5 mm long or sometimes slightly longer; sepals narrowly triangular, 1–1.6 mm long, attenuate-acuminate, the apex usually cuspidate and often recurved after anthesis, usually orange-punctate, but sometimes black-punctate; petals linear-lanceolate, 4–5 mm long or sometimes slightly longer, acuminate, connate basally, papillose-tomentose within along margins and above the middle; stamens 2.5–3.5 mm long, the filaments stout, glabrous, ca. 1.4 mm long, the anthers erect, lanceolate, 1.8–2 mm long, dorsifixed one-third above the base, with a conspicuous oblong-triangular punctate area above the attachment and with glands extending down into the lobes, obtuse or rounded and minutely apiculate apically; ovary and style glabrous, the ovules 6–8, erect, uniseriate, enclosed, the placenta broadly obovoid, the style slender, 3.5–4.5 mm long. *Fruit* black-purple, globose, 7–9 mm in diameter (dry).

From Honduras south into Colombia and Venezuela. Vernacular name: "fruta pava," *fide* Duke.

PANAMÁ: Vicinity of El Llano, *Duke 5854* (LL). Near Jenine along Pan-American Highway, by stream, Río Canita, *Duke 3880* (LL, MO). Río Tocumen, moist forest, *Standley 29349, 29365* (both US). LOCALITY UNKNOWN: *Seemann 1611* (BM).

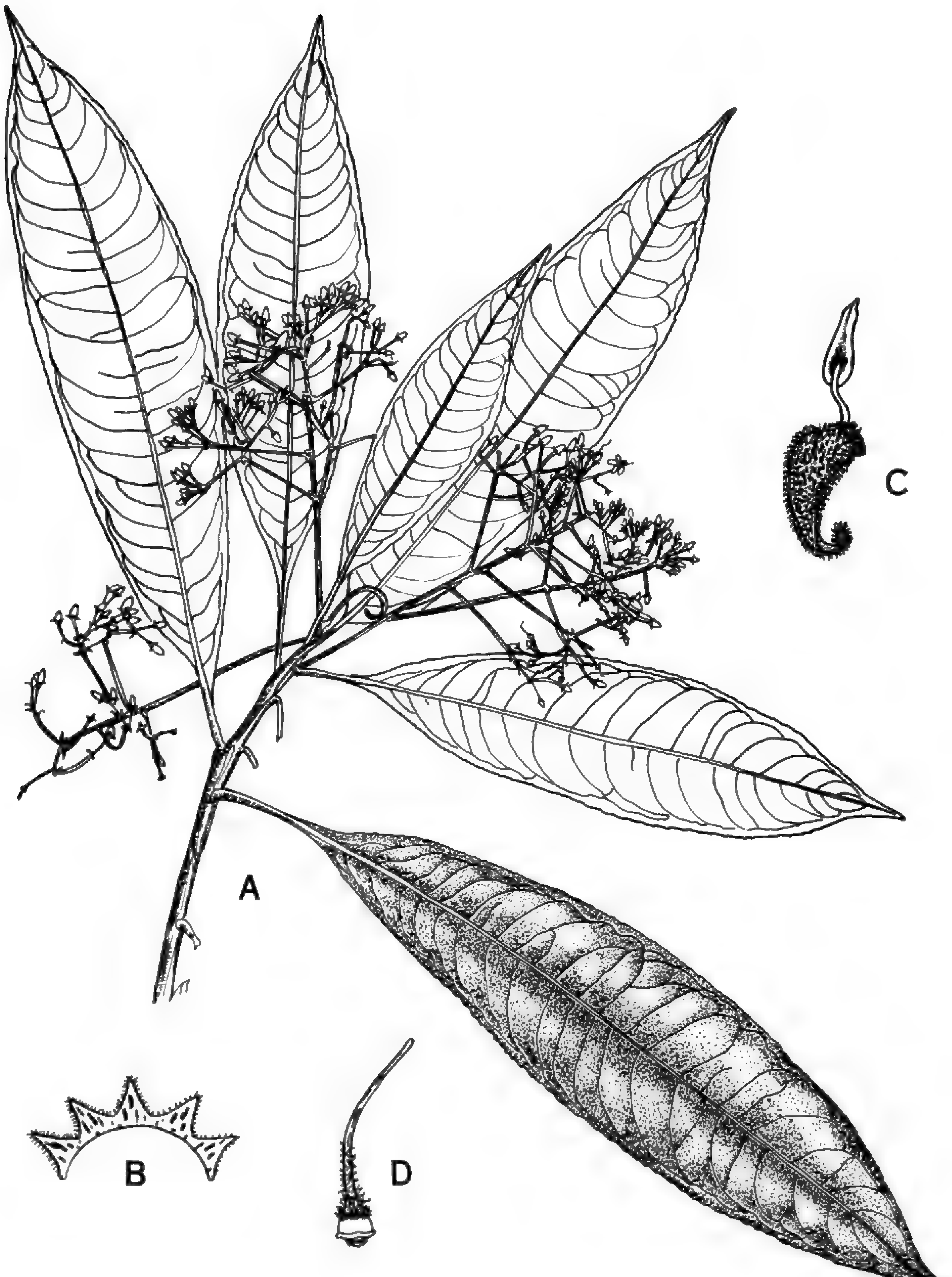


FIGURE 7. *Parathesis seibertii* Lundell.—A. Habit (× ½).—B. Calyx, spread out (× 5).—C. Petal and stamen (× 5).—D. Gynoecium (× 5). [After *Peggy & Gene White 27* (MICH, holotype).]

5. **Parathesis tenuifolia** Lundell, Wrightia 4: 167. 1971.

Trees, ca. 10 m high, 10 cm in diameter, the branchlets slender, minutely and sparsely lepidote, glabrate. *Leaves* with long slender petioles 1.5–2.3 cm long, the petioles canaliculate, sparsely and minutely lepidote beneath at first; leaf blades membranaceous, glabrous, conspicuously black-punctate, oblanceolate or oblong-oblanceolate, 7–15 cm long and 2.5–4.6 cm wide, subabruptly acuminate apically, attenuate basally, decurrent on the petiole, the margin entire or subentire, the midvein nearly plane at the base above, elevated beneath, the primary lateral veins slender, 15–17 pairs, ascending at a wide angle, finely reticulate beneath, the veins less evident above. *Inflorescences* terminal, exceeding the leaves, narrowly tripinnately paniculate, to 15 cm long, minutely and densely papillate-puberulent; pedicels slender, 3–5 mm long; flowers unknown; calyx subtending the fruit minutely papillate-puberulent, the sepals narrowly triangular, 1.3–1.6 mm long, acute, black-punctate. *Fruit* globose, 5–6 mm in diameter at maturity, the persistent bases of the styles and the fruit apex at the base of the style with scattered short reddish trichomes.

Native to Panama. Vernacular name: "crabwood."

BOCAS DEL TORO: Bocas Island, *Cooper 463* (F, holotype; LL, fragment).

6. **Parathesis seibertii** Lundell, Ann. Missouri Bot. Gard. 26: 293. 1939.—Fig. 7.

P. woodsonii Lundell, Ann. Missouri Bot. Gard. 28: 458. 1941.

Trees to 15 m high, the branchlets slender to stout, apically ferruginous-lepidote with minute closely appressed stellate trichomes, these scarcely discernible. *Leaves* with slender petioles 1–1.5 (–2.5) cm long; leaf blades lanceolate, oblong-elliptic, or oblanceolate, 5–20 cm long and 1.5–5 cm wide, acuminate apically and basally, chartaceous or membranaceous, obscurely crenulate to entire, at first minutely and sparsely lepidote beneath with appressed stellate trichomes, conspicuously black-punctate, striolate, the costa elevated beneath, the primary lateral veins slender. *Inflorescences* axillary, paniculate, to 15 cm long, long-pedunculate, the peduncles and branches slender, 1- or 2-branched, sparsely and minutely puberulent; pedicels slender, (4–)6.5–11 mm long, minutely puberulent. *Flowers* subcorymbose, minutely papillose-puberulent, to 6 mm long at anthesis; sepals triangular, to 1.2 mm long, red-black punctate; petals narrowly lanceolate, to 6 mm long, papillose-tomentose over almost the entire inner surface, densely red-black punctate in lines; stamens 3–3.5 mm long, the filaments slender, glabrous, 1.5–2 mm long, not punctate, the anthers erect, dorsifixed ⅓ above the base, lanceolate, 1.75–2.4 mm long, attenuate apically and apiculate, epunctate or with 1 to several minute black glands dorsally; ovary puberulent or tomentulose to the middle and at the base of the style or only apically, the ovules 7–9, uniseriate, enclosed, the placenta depressed-globose, apiculate, the style slender, ca. 5 mm long, punctate in lines. *Fruit* purple, depressed-globose, drying ca. 7 mm in diameter.

Native to Panama.

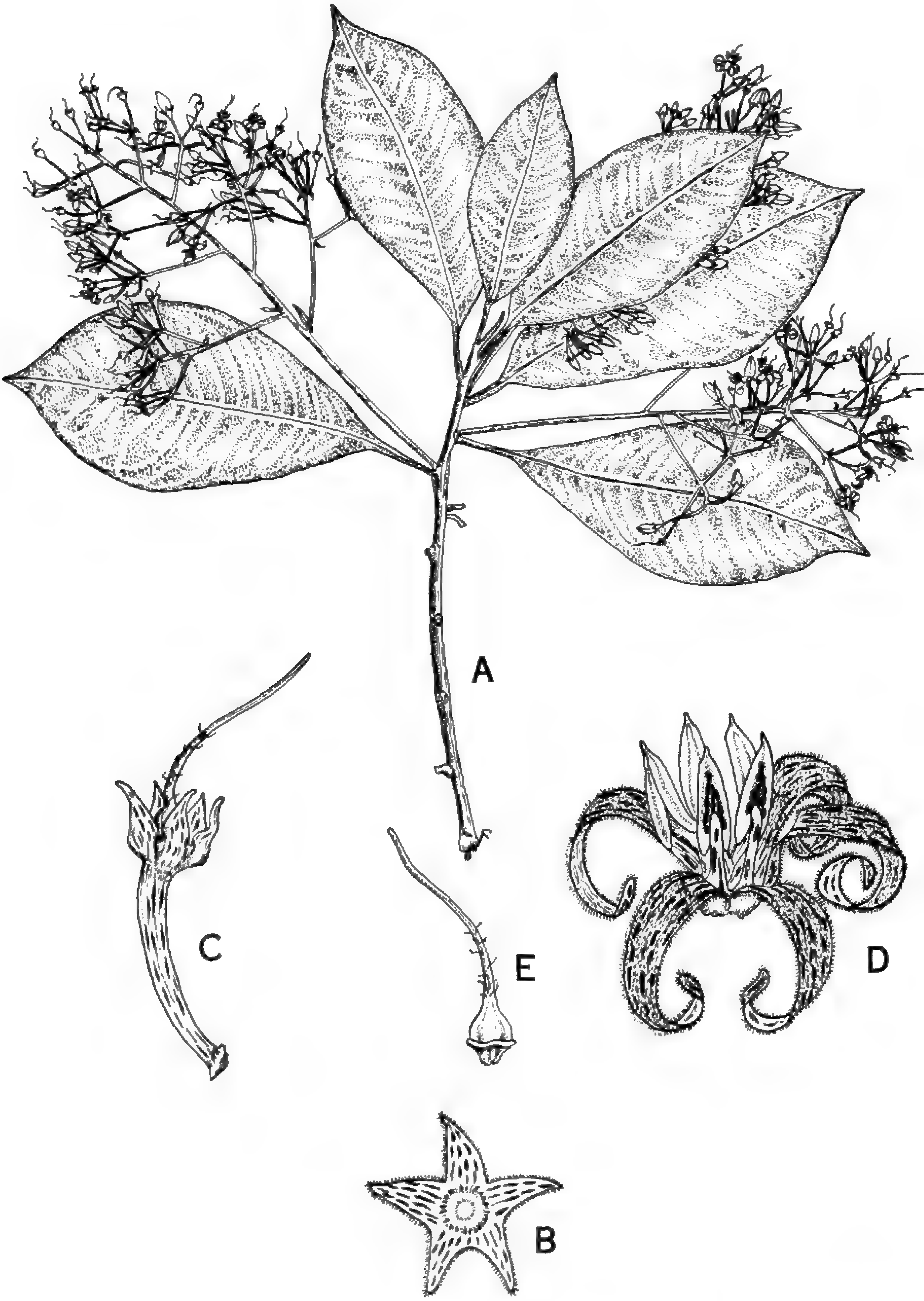


FIGURE 8. *Parathesis glabra* Donn. Sm.—A. Habit (× ⅗).—B. Calyx, spread out (× 6).—C. Pedicel, calyx, and gynoecium (× 6).—D. Petals and stamens (× 6).—E. Gynoecium (× 6). [After *Rodriguez C.* 489 (UC).]

CHIRIQUÍ: Mountains above Bambito, 1 mi. S of Cerro Punta, 6000 ft, *Tyson 5785* (MO). Boquete, Finca Collins, ca. 5000 ft, *Dwyer & Hayden 7658* (LL); 6000 ft, *Kirkbride 113* (MO). Cerro Horqueta, cloud forest, 5000–7000 ft, *Kirkbride 134* (MO). Cerro Punta, 2000 m, *Allen 3485* (F, G, MO, NY, P, S, UC, US). Finca Lérida to Peña Blanca, 1750–2000 m, *Woodson & Schery 331* (MICH, holotype of *P. woodsonii*; GH, K, isotypes). Trail from Paso Ancho to Monte Lirio, 1500–2000 m, *Allen 1598* (GH, LL, MO, US). Río Chiriquí Viejo valley, between El Volcán and Cerro Punta, *Gene White 19* (F, MO). Valley of the upper Río Chiriquí Viejo, 1300–1900 m, *White & White 27* (MICH, holotype; A, LL, MO, NY, isotypes).

Kirkbride 113 and *Dwyer & Hayden 7658* have atypically small flowers about 3 mm long, but the anthers, although scarcely 1 mm long, are typical of the species.

7. **Parathesis montana** Lundell, Wrightia 4: 166. 1971.

Shrubs, the branchlets stout, minutely ferruginous-puberulent at first, the apical buds with closely appressed rufous indument. *Leaves* with slender petioles 1.5–2.5 cm long; leaf blades oblanceolate or oblanceolate-elliptic, 12.5–18.5 cm long and 4.5–5.5 cm wide, subabruptly acuminate apically, acute or subacuminate basally, membranaceous, entire, at first sparingly puberulent on the lower surface, the appressed stellate trichomes minute, glabrescent, punctate, the glands rounded and lineate, the costa elevated beneath, nearly plane above, the primary lateral veins slender, 9 or 10 pairs, arcuately ascending, anastomosing into the submarginal vein, openly reticulate. *Inflorescences* axillary, lax, long-pedunculate, bipinnately-paniculate, the panicles to 12 cm long, minutely papillose-puberulent, glabrate; pedicels slender, 5–7 mm long, minutely papillose-puberulent. *Flowers* subcorymbose, ca. 5 mm long at anthesis; sepals triangular, 1–1.3 mm long, acute, orange-red–punctate, minutely papillose-puberulent; petals lanceolate, ca. 5 mm long, papillose-puberulent dorsally, short villous-tomentose on the inner surface except for a small glabrous basal area, reddish-punctate in lines; stamens 2.2–2.5 mm long, the filaments ca. 1.4 mm long, glabrous, not punctate, the anthers ovate-lanceolate, ca. 1.4 mm long, acute apically, with a few small red-black glands dorsally, dorsifixed ca. ⅛ above the base; ovary ovoid, smooth, tapering into the style, hirtellous apically and at the base of the style, a few short trichomes extending up the style, the ovules 5 or 6, uniseriate, enclosed, the placenta obovoid, with minute red glands basally, the style ca. 4 mm long, punctate. *Fruit* depressed-globose.

Known only from Panama.

DARIÉN: Cloud forest, mossy forest, Cana Trail between Cerro Campamiento and Las Escalera to "Paramo" E of Tres Bocas, *Kirkbride & Duke 1340* (MO, holotype; LL, fragment). Cerro Pirre, 2500–4500 ft, *Duke & Elias E13693* (LL).

8. **Parathesis glabra** Donn. Sm., Bot. Gaz. (Crawfordsville) 31: 115. 1901. —FIG. 8.

P. storkii Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 8: 31. 1930.

Shrubs or slender trees to 15 m high, the branchlets stout, apically tomentose with minute closely appressed stellate trichomes. *Leaves* with petioles to 1.8 cm long; leaf blades elliptic, oblong-elliptic, or oblanceolate-elliptic, 8–15 cm long and 3.5–7 cm wide, subabruptly acuminate apically, acute or acuminate and decurrent basally, subchartaceous, entire or obscurely crenulate, black-punctate, striolate, minutely appressed stellate-lepidote beneath at first and along the petiole, glabrescent early, the costa nearly plane above, elevated beneath, the primary lateral veins slender. *Inflorescences* axillary, rarely terminal (*White 156*, MO), paniculate, 5–18 cm long, usually shorter than the leaves, slender-pedunculate usually to the middle or above, 1- or 2-branched, sparsely and minutely puberulent at first, glabrescent early; pedicels slender, to 1 cm long. *Flowers* sub-umbellate to corymbose, to 7 mm long at anthesis, the corolla minutely papillose-puberulent; sepals minutely puberulent, densest apically, lanceolate-triangular, 1.2–2 mm long, acuminate, densely red-black punctate; petals linear-lanceolate, ca. 7 mm long, papillose-tomentose on the inner surface except basally, densely black-punctate in lines; stamens 3–4 mm long, the filaments thick, black-punctate, to 2 mm long, the anthers ovate-lanceolate, to 2.75 mm long, dorsifixed ca. ¼ above the base, tapering to the acute apex, conspicuously black-punctate dorsally, the glands extending down into the lobes; ovary ovoid, glabrous or sparsely short villous apically and at the base of the style; the ovules 7–9, uniseriate, enclosed, the placenta obovoid, apiculate, the style 4.5–6 mm long, black-punctate in lines. *Fruit* depressed-globose, drying ca. 8 mm in diameter.

Native to Costa Rica and Panama.

CHIRIQUÍ: Bajo Chorro, rain forest, 6000 ft, *Davidson* 379 (A, F, MO, US). Boquete, Volcán de Chiriquí, 7000 ft, *Davidson* 907 (A, F, MO, US). 6 mi. NE of El Volcán, 7000–7500 ft, *Tyson 811, 819, 820* (all MO). Vicinity of "New Switzerland," central valley of the Río Chiriquí Viejo, 1800–2000 m, *Allen* 1352 (GH, LL, MO, NY, US). Río Chiriquí Viejo valley, *G. White 58* (GH, LL, MO); near river on island, *P. White 156* (LL, MO). Volcán de Chiriquí, vicinity of Casita Alta, ca. 1500–2000 m, *Woodson et al. 798* (A, K, MO, MICH); Potrero Muleto to summit, 3500–4000 m, *Woodson & Schery 384* (GH, LL, MO).

The Panama population of *Parathesis glabra* from Chiriquí is atypical in that the anthers are smaller, the filaments longer, and the petals are papillose basally within. Also, the leaves are smaller and narrower, and the inflorescences shorter than in *P. glabra* in Costa Rica.

4. WEIGELTIA

Weigeltia A. DC., Trans. Linn. Soc. London 17: 102. 1834.

Weigeltia Reichb., Consp. Regni Veg. 155. 1828 (nomen, Leguminosae), fide Index Kewensis.
Comomyrsine Hook. f., Gen. Pl. 2: 643. 1876.

Shrubs or small trees, dioecious, glabrous or slightly and minutely lepidote (apparently rarely puberulent). *Leaves* petiolate, often large, usually remote, sometimes exceptionally crowded at the apex of the thick branches and pseudoverticillate, either entire or serrate. *Flowers* pedicellate in axillary ordinarily more or less pendent panicles, (3–)4(–5)-merous and unisexual; sepals and petals both usually imbricate, rarely dextrally convolute and connate basally or sometimes to the middle; filaments always well-developed, the anthers never longer than broad, ovate or suborbicular, rarely acutish, longitudinally dehiscent; ovary ovoid, usually glabrous, the ovules few, uniseriate, the stigma of the obvious style often lobed. *Fruit* globose, crustaceous, 1-seeded.

A genus with some 40 dioecious species in tropical America, ranging from Costa Rica and the West Indies through tropical South America. Only the two following have been recorded from Central America.

a. Staminate inflorescences paniculate, many-flowered, congested, equaling or subequaling the petioles, subsessile; flowers 4(–5)-merous; petals of the staminate flowers puberulent on both surfaces, punctate with occasional glands .... 1. *W. panamensis*

aa. Staminate inflorescences open, few-flowered, narrowly paniculate, to 25 cm long, long-pedunculate; flowers 3-merous; petals of the staminate flowers glabrous on the inner surface, densely black-punctate .... 2. *W. spectabilis*

1. **Weigeltia panamensis** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 164. 1940.

Shrubs, to 1 m high, the stems simple, subterete, 1.5 cm in diameter. *Leaves* subapical, appearing to be verticillate, long-petiolate, the petioles stout, to 12 cm long, with sordid indument at first, glabrate; leaf blades chartaceous, elliptic-obovate or oblong-obovate, to 45 cm long and 21 cm wide, rounded and retuse or apiculate apically, acute basally, glabrous above, sordid-puberulent beneath, especially along the midvein and lateral veins, the thick costa and primary nerves conspicuous, elevated beneath, the primary lateral nerves ca. 18 pairs, the veins openly reticulate on the lower surface, the margin entire. *Inflorescences* of staminate flowers paniculate, dense, shorter than or equaling the petioles, to 13 cm long, with short peduncles, vinaceous, papillose-puberulent, the minute trichomes appearing to be glandular; pedicels absent or abbreviated. *Staminate flowers* 4(–5)-merous, ca. 3 mm wide; sepals linear-lanceolate, to 0.7 mm long, acuminate, punctate; petals spreading, nearly free, papillose-puberulent on both surfaces, lanceolate, 1.5–2 mm long, acutish, with occasional medial glands; stamens shorter than the petals, to 1.5 mm long, the filaments connate basally, well-developed, the anthers minute, depressed-globose, emarginate, ca. 0.2 mm long, ca. twice as wide; gynoecium abortive, without vestige.

Known only from Panama.

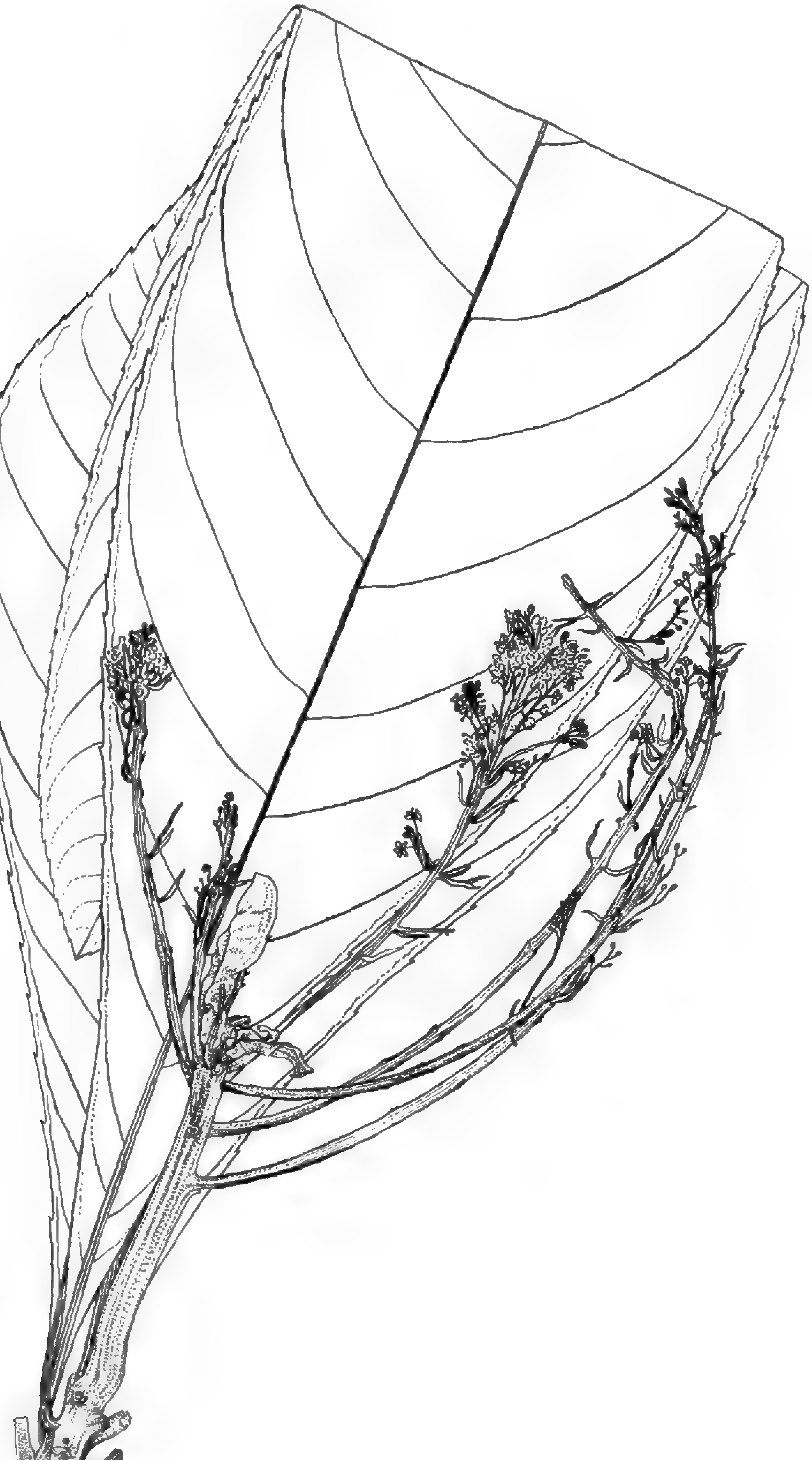
DARIÉN: Chepigana District, Caná-Cuasi Trail, rain forest, 3000 ft, *Terry & Terry 1490* (MO, isotype).

This taxon seems to be very close to *Weigeltia simplex* (Hook. f.) Mez, of which I have seen only a photograph of the type. The type is carpellate.

2. **Weigeltia spectabilis** (Standley) Lundell, Wrightia 4: 169. 1971.—Fig. 9–10.

Ardisia spectabilis Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 893. 1938.
Weigeltia triandra Asplund, Bot. Not. 1939: 802. *fig. 5a–d, 6.* 1939.

Shrubs, to 2 m high, the stems thick, at first with minute appressed red-glandular indument, glabrate. *Leaves* large, appearing verticillate, crowded at the apex of the stems, petiolate, the petioles thick, to 2 cm long, marginate to the base; leaf blades thin, subchartaceous, oblong-oblanceolate or oblanceolate, to 55 cm long and 15 cm wide, broadly acute or acuminate apically, attenuate and decurrent on the petiole basally, margin remotely serrulate or



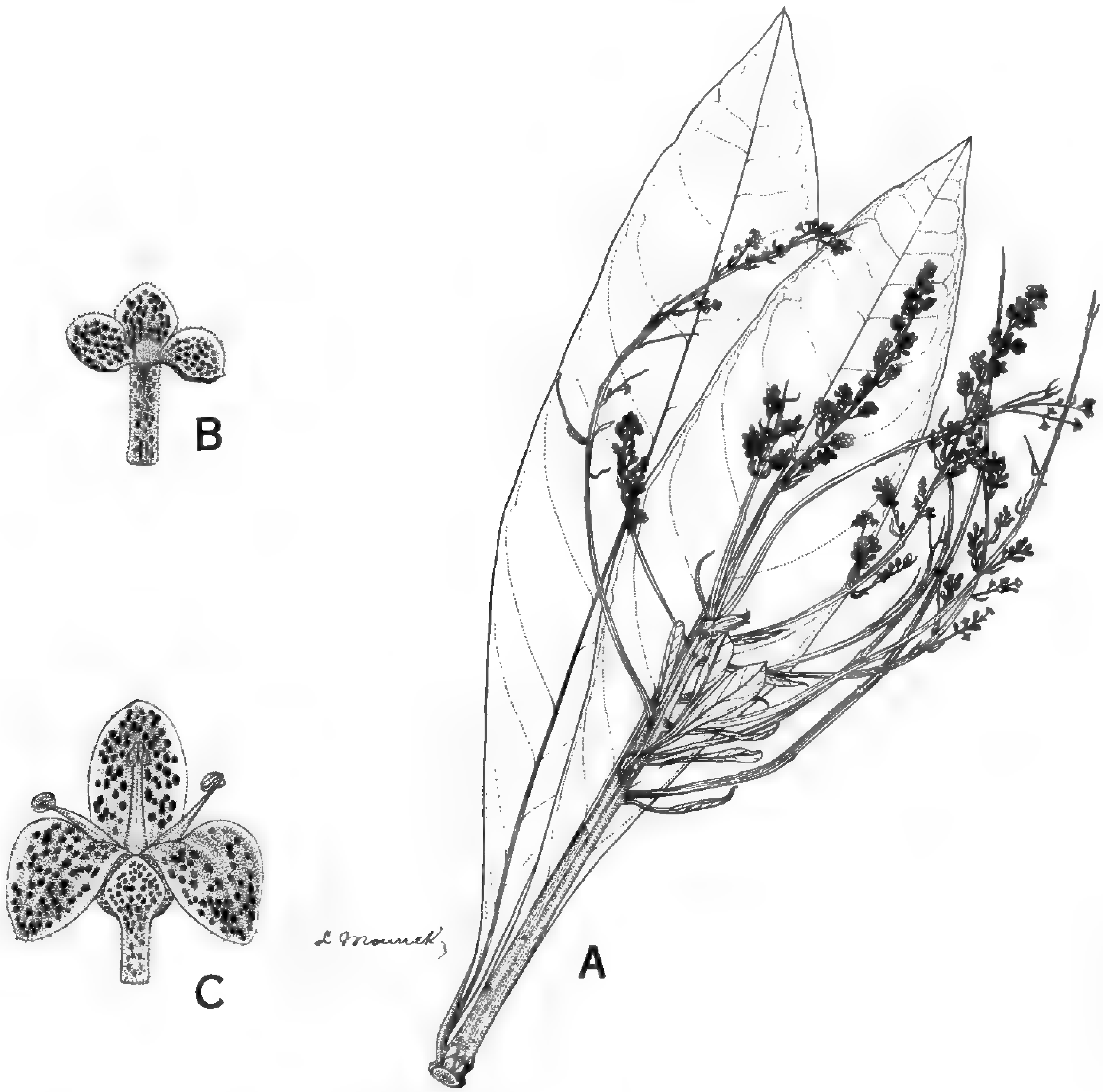


FIGURE 10. *Weigeltia spectabilis* (Standl.) Lundell.—A. Habit (× 3⁄10).—B. Calyx, spread out (× 6).—C. Flower (× 6). [After *Allen 3965* (MO).]

entire, the primary lateral veins 9–12 pairs, the midvein narrow and elevated above, prominent beneath, the lateral nerves slender and widely ascending, the veins reticulate, the entire surface striolate. *Inflorescences* paniculate, in the axils of foliaceous bracts at the apex of elongated stems, the bracts to 6 cm long; the axillary panicles to 25 cm long, including a peduncle to 15 cm long, strongly ascending, with short lateral branches, the lower to 2.5 cm long, the indument red minute and apparently glandular. *Staminate flowers* 3-merous, racemose, crowded, the pedicels 1–2 mm long; sepals ovate, 1–1.2 mm long, ciliolate, densely black-punctate medially and basally, with a wide hyaline

←

FIGURE 9. *Weigeltia spectabilis* (Standl.) Lundell, habit (× ½). [After *Brenes 20530* (F, holotype).]

margin; petals glabrous, oblong-elliptic, 3–3.5 mm long, conspicuously maculate with conspicuous black glands, rounded apically, nearly glabrous; stamens attached ca. 0.8 mm above the base of the corolla, to 2.6 mm long, the filaments free, well-developed, 1.6–2.2 mm long, the anthers eglandular, cordate, ca. 0.5 mm long, rounded; gynoecium rudimentary.

Costa Rica, Panama, and probably Colombia.

PANAMÁ: Cerro Campana, 800 m, *Allen 3965* (LL, MO).

This species is close to *Weigeltia schlimii* (Hook. f.) Mez, but appears to be sufficiently different to be recognized. The eglandular anthers, smaller flowers, and sepals and petals densely punctate with red-black glands are distinguishing features. From description and illustrations, *W. triandra* Asplund, described from Colombia, belongs here.

5. STYLOGYNE

Stylogyne A. DC., Ann. Sci. Nat. Bot., Sér. 2. 16: 78. 1841.

Shrubs or trees, glabrous or nearly so. *Leaves* alternate, petiolate. *Inflorescences* paniculate, terminal or axillary. *Flowers* unisexual or bisexual, small, umbellate or subcorymbose, pedicellate, usually white, (4–)5-merous; sepals dextrorsely contorted in bud, free or short-connate basally, punctate or lineate; petals short-connate basally, dextrorsely contorted in bud, commonly lineate; stamens usually shorter than the petals, the filaments slender, the anthers elongate, subsagittate basally, dorsifixed or basifixed, usually dehiscent by introrse slits; ovary ovoid in carpellate flowers, with the slender style subequaling or exceeding the stamens, abortive in staminate flowers, with the short style less than 1 mm long; placenta with 3–5 uniseriate ovules. *Fruit* drupaceous, 1-seeded, the endocarp crustaceous or osseous; seed globose or depressed, the endosperm corneous, excavate, not ruminate, the embryo transverse, elongate.

A difficult genus of perhaps 60 dioecious species in tropical America, ranging from Mexico and the West Indies into South America, where it is most abundantly represented.

a. Leaves membranaceous, strongly-veined, sub-bullate above, the primary lateral nerves 11–15 pairs, prominent and sharply reticulate beneath; branchlets minutely puberulent .... 1. *S. hayesii*
aa. Leaves chartaceous to subcoriaceous, the veins slender and inconspicuous; branchlets glabrous.
  b. Inflorescences terminal; leaves elliptic or obovate-elliptic; stamens included, shorter than the petals .... 2. *S. turbacensis*
  bb. Inflorescences axillary; leaves lanceolate, lanceolate-oblong, or rarely oblanceolate; stamens exserted, to 6 mm long, longer than the petals .... 3. *S. standleyi*

1. **Stylogyne hayesii** Mez, Pflanzenreich IV. 236: 272. 1902.—Fig. 11.

Shrubs, the branchlets usually slender, minutely puberulent at first, glabrate, subterete. *Leaves* petiolate, the petioles 1–1.5 cm long, slender, canaliculate, puberulent beneath at first in young leaves; leaf blades glabrous, membranaceous, elliptic or oblanceolate-elliptic, 9–20 cm long and 3–7 cm wide, acuminate or subabruptly acuminate apically, acute basally, the margin cren-

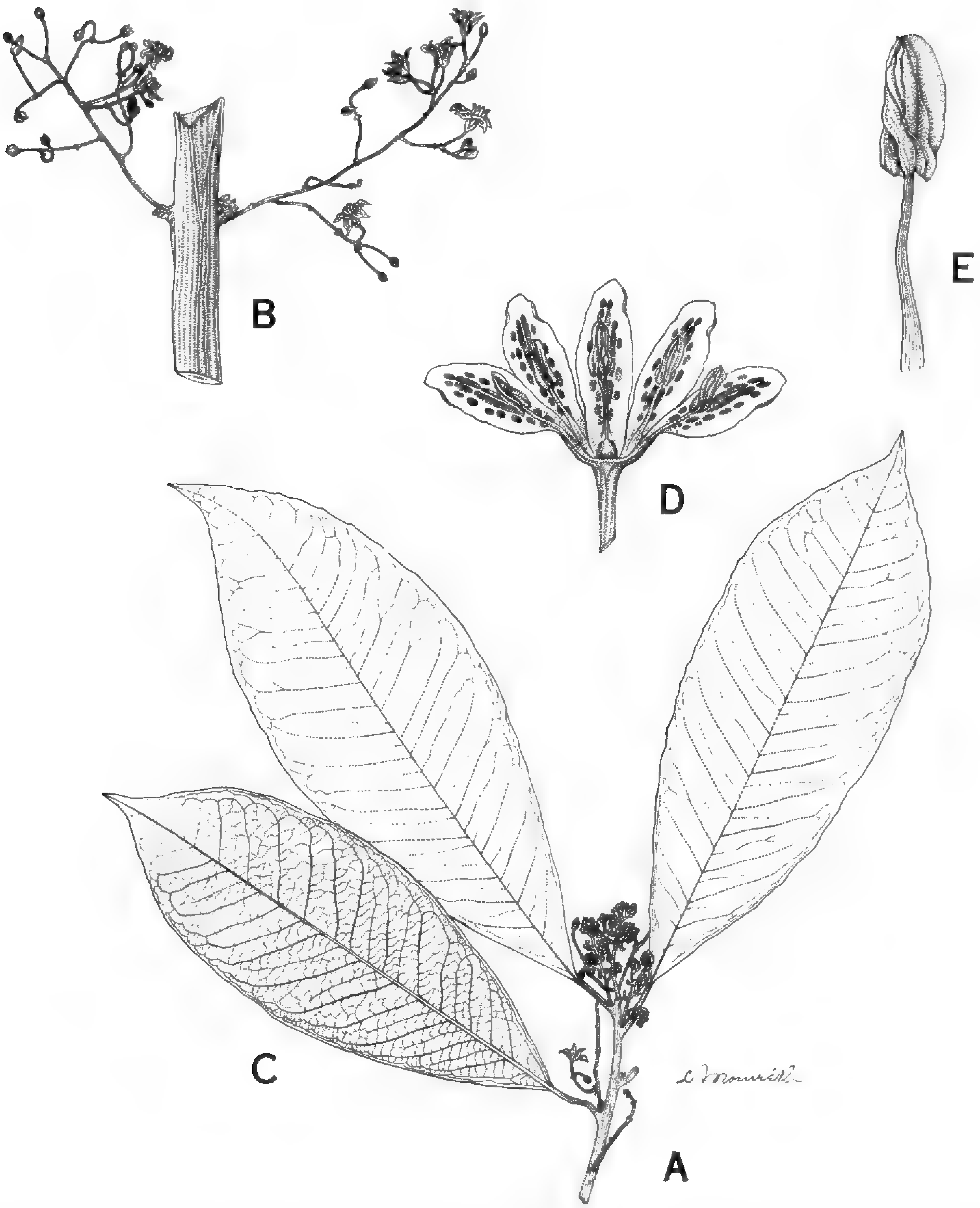


FIGURE 11. *Stylogyne hayesii* Mez.—A. Habit (ca. × ½).—B. Inflorescences at defoliated nodes (× 1⅓).—C. Leaf, showing venation (ca. × ½).—D. Flower, spread out to show petals, stamens, and abortive gynoecium (× 7⅓).—E. Stamen (× 18). [After *Hayes 662* (K, isotype).]

ulate, the costa impressed above, prominent beneath, the primary lateral veins 11–15 pairs, prominent and sharply reticulate, impressed above, elevated beneath, punctate with small rounded glands. *Inflorescences* axillary and terminal, slender, minutely puberulent, laxly bipinnately-paniculate, few-flowered, 2.5–7 cm long, the pedicels slender, to 3.5 mm long. *Staminate flowers* usually umbellate, sometimes appearing subracemose, 5-merous bracts; thin, slender, falling early; buds oblongish, ca. 3 mm long; sepals thin, nearly free, ovate-elliptic, 1–1.3 mm long, punctate with conspicuous reddish glands, the hyaline margin wide, minutely erose, rounded apically; petals thin, connate ⅓ at the base, 3–3.7 mm long, lanceolate-elliptic, asymmetric, conspicuously punctate with large reddish oblongish glands; stamens attached medially in the corolla tube, 2–2.5 mm long, the filaments filiform, ca. 1 mm long, the anthers linear-lanceolate, 1.2–1.4 mm long, concolorous, obtusish; ovary abortive, glabrous, ovoid, the short style slender, 0.4–0.75 mm long, the stigma minute.

Native to Panama.

DARIÉN: Río Areti, *Duke & Nickerson 14905* (MO). PANAMÁ: In thick woods, Mamner Station, Panama Rail Road, *Hayes 662* (K, isotype).

The ovary in each collection is abortive, with the style very slender and short. *Stylogyne hayesii* has strongly veined leaves with the upper surface sub-bullate, giving this species a distinctive appearance.

2. **Stylogyne turbacensis** (Kunth) Mez, Pflanzenreich IV. 236: 270. 1902.

Ardisia turbacensis Kunth, Nov. Gen. Sp. Pl. 3: 244. 1818.
Stylogyne guatemalensis Blake, Contr. U. S. Natl. Herb. 24: 16. 1922.

Shrubs or small trees, glabrous; branchlets slender to stout, terete. *Leaves* with canaliculate petioles mostly 1–1.5 cm long; leaf blades elliptic or obovate-elliptic, 6–15 cm long and 3–8 cm wide, rounded and abruptly short-acuminate or acutish apically, cuneate or acute and decurrent on the petiole basally, entire, chartaceous to subcoriaceous, finely- and closely-veined, the costa plane or nearly so above, elevated beneath. *Inflorescences* terminal, pinnately-paniculate, sessile or nearly so, to 6 (–10) cm high and 6 (–12) cm wide. *Flowers* unisexual or apparently bisexual, 5-merous, subcorymbose; pedicels mostly 3–6 (–11) mm long, rigid in fruit. *Staminate flowers*: sepals thin, ovate-elliptic, 1.3–1.75 mm long, orange-punctate, the margins wide and thin, minutely erose; petals oblong-elliptic, thin, 4.5–5.5 mm long, asymmetrical, connate basally, orange-lineate; stamens 2.5–3.5 mm long, the filaments 0.5–2 mm long, the anthers linear-oblong, 1.8–2 mm long, dorsifixed above the base, concolorous, twisted, rounded apically; gynoecium abortive, the style 0.5–0.75 mm long. *Carpellate flowers*: 4.5–5 mm long at anthesis, conspicuously punctate; sepals ovate-oblong to lanceolate-oblong, 1.4–2 mm long, rounded, dorsally punctate with elevated glands, the margin thin and paler; petals oblong-elliptic, 4–4.8 mm long, connate for ca. 1.5 mm basally, obtuse, rounded or obliquely emarginate, orange-lineate; stamens 2–2.22 mm long, the filaments 0.8–1 mm long, the anthers 1.2–1.7 mm long, basifixed, concolorous, epunctate; ovary ovoid, 1.2 mm long, the ovules 3–5, uniseriate, erect, the style slender, 2.5–2.8 mm long. *Fruit* black at maturity, subglobose, drying 6 mm in diameter.

Guatemala, south into Panama and Colombia. Vernacular name: "uvito."

CANAL ZONE: Along the Río Trinidad, near sea level, *Pittier 4001* (F, US). CHIRIQUÍ: Boca Chica, *Pittier 5120* (LL, P, US). COCLÉ: Mountains beyond La Pintada, 400–600 m, *Hunter & Allen 517* (LL, MO). Vicinity of Olá, 100–350 m, *Pittier 5035* (US). HERRERA: Ocú, *Ebinger 1060* (LL). LOS SANTOS: Guayabo, several mi. W of Tonosí, *Stern et al. 33700*

(MICH, MO). Los Toretos, *Dwyer 2441* (MO). 16 mi. S of Macaracas at Quebrada Bejuco, *Tyson et al. 3097* (MO). VERAGUAS: Cañazas, *Tyson 3605, 3735* (both MO). Río de Jesús, *Dwyer 1314-A* (staminate flowers, MO). San Francisco, *Dwyer 1288, 1290* (both MO).

The type at Paris, *Humboldt & Bonpland 1446*, a specimen in fruit, closely matches the Central American collections. Since the species is dioecious, and the flowers are quite variable as to length of filaments and anthers in both staminate and pistillate flowers, the taxon is a difficult one to interpret. Most collections are in fruit. Evidently the anthers are functional in the carpellate flowers, so we appear to have staminate flowers, as well as flowers which may be perfect.

3. **Stylogyne standleyi** Lundell, Wrightia 3: 110. 1964.

Shrubs or small trees, glabrous, the branchlets thick. *Leaves* petiolate, the petioles 1–2 cm long; leaf blades lanceolate or lanceolate-oblong, rarely oblanceolate, 15–25 cm long and 5–9 cm wide, acuminate apically, acute basally, chartaceous or subcoriaceous, pellucid-punctate, the margin entire, venation slender, reticulate, with a double marginal vein. *Inflorescences* axillary, sessile or nearly so, many-flowered, paniculate, to 7.5 cm long, white; pedicels 2–5 mm long; bracts thin, the lower ovate-lanceolate, orange-punctate, caducous. *Staminate flowers*: 5-merous, subcorymbose, ca. 5.5 mm long in bud; sepals orange-punctate, ovate or ovate-elliptic, to 1.4 mm long, with a wide hyaline margin; petals orange-lineate, oblong, ca. 5.5 mm long, connate for ca. 1.2 mm basally, asymmetrical, obliquely emarginate, revolute; stamens exserted, to 6 mm long, sometimes exceeding the petals, the filaments to 5 mm long, the anthers lanceolate, to 1.3 mm long, concolorous, becoming twisted after anthesis; ovary small, abortive, the ovules 3–5, minute, uniseriate, the style ca. 0.8 mm long. *Carpellate flowers*: sepals densely orange-punctate, ovate or ovate-elliptic, 1–1.4 mm long, rounded apically, the margin hyaline; petals oblong, ca. 4.5 mm long, connate for ca. 1.2 mm basally, asymmetrical, conspicuously punctate with mostly oblongish orange glands, revolute; stamens not exserted, much shorter than the petals, ca. 3 mm long, the filaments slender, ca. 1.4 mm long, the anthers linear-oblong, ca. 1.3 mm long, concolorous, becoming twisted; ovary ovoid, glabrous, the ovules 2–4, uniseriate, the placenta obovoid, the slender style ca. 3 mm long, the stigma small, capitate. *Fruit* globose, the fruiting pedicels rigid, 2–7 mm long.

Panama, and probably Costa Rica, Colombia, and Venezuela.

CANAL ZONE: Albrook, *Dwyer 6566* (MO), *Dwyer & Robyns 48, 66* (both MO). Ancón Hill, *Standley 26396* (US). Barro Colorado Island, *Brown 41* (F), *Carpenter 53* (F), *Standley 31430* (US), *Shattuck 75, 532, 718* (all F), *Woodworth & Vestal 306, 435* (both F); junction of Wheeler and Pearson trails, *Wetmore & Abbe 118* (F). Vicinity of Fort Sherman, *Standley 31002* (US). Gamboa, *Standley 28385* (US). Around Gamboa, *Pittier 2607* (US). Forests of Juan Díaz, near Panama City, 20–50 m, *Pittier 2556* (US). Las Cruces Trail, *Hunter & Allen 458* (MO). W of Limon Bay, N base of Mindi Hills, along Quebrada Morito, *Johnston 1741* (MO). Near Piña, *Duke 9251* (MO). Quebrada Bonita, *Steyermark & Allen 17072* (K, MICH, MO). DARIÉN: Trail between Pinogana and Yaviza, ca. 15 m, *Allen 248* (F, MO). Tumaganti, *Duke 14148* (LL). PANAMÁ: Pacora, *Bro. Paul 247* (US). Near Punta Paitilla, *Standley 26229* (US). Near Río Pacora, *Miller 1779* (US). Río Tapía, *Standley 28253* (US), *28290* (MO, US). Near big swamp E of Río Tocumen, *Standley 26561, 29357* (both US). LOCALITY UNKNOWN: *Seemann s.n., 560* (both K).

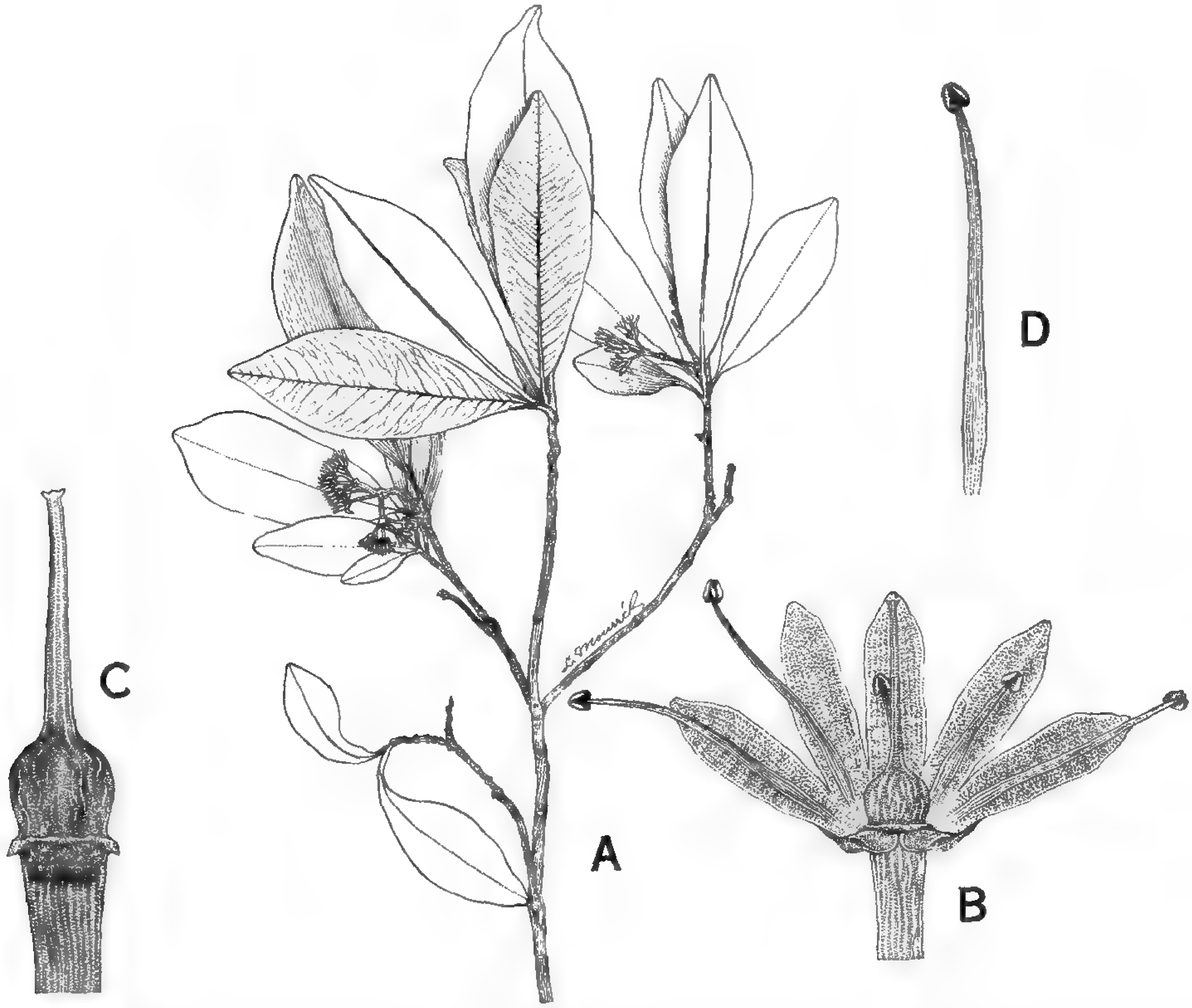


FIGURE 12. *Gentlea austin-smithii* (Lundell) Lundell.—A. Habit (× 3/5).—B. Flower (abnormal), showing petals, stamens, and gynoecium (× 7⅖).—C. Gynoecium (× 10⅘).—D. Stamen (× 9⅗). [After *Smith A673.*]

It is possible that *Stylogyne laevis* (Oerst.) Mez is represented in Panama by a fruiting collection, but all the specimens cited appear to be referable to *S. standleyi*, which is notable primarily for the long exserted stamens of the staminate flowers and the large, mostly lanceolate leaves. The two are related. Regarding S. *laevis* and S. *ramiflora* (Oerst.) Mez, its synoym, I refer you to Lundell, Fieldiana:Bot. 24(8): 194. 1966.

6. GENTLEA

Gentlea Lundell, Wrightia 3: 100. 1964.

Ardisia Swartz subgen. *Walleniopsis* Mez, Pflanzenreich IV. 236: 77. 1902.

Shrubs or small trees. *Leaves* alternate, petiolate. *Inflorescences* terminal, paniculate, broader than long, short-pedunculate or subsessile; bracts and bractlets thin, caducous. *Flowers* corymbose, pedicellate, bisexual, (4–)5(–6)-merous, greenish or white; sepals inconspicuously imbricate, connate basally or nearly free; petals connate ¼–½ into tube, the lobes imbricate in bud, spreading and sometimes appearing valvate at anthesis; stamens exserted, exceeding the petals, the filaments long and slender, the anthers minute, cordate, dorsifixed, epunctate or inconspicuously glandular-punctate dorsally; ovary ovoid or subglobose, the ovules in 2 or more series, the placenta few to multi-ovulate, the style slender, sometimes subequaling the corolla, the stigma punctiform, minute. *Fruit* subglobose.

A small distinctive genus of eight species ranging from Mexico (Jalisco, Chiapas) south through Central America into Venezuela and Peru. All except *Gentlea venosissima* (Ruiz & Pavon) Lundell, the type species, are of local distribution. Only the following is known from Panama.

1. **Gentlea austin-smithii** (Lundell) Lundell, Wrightia 4: 68. 1968.—Fig. 12.

Ardisia minor Standley, Jour. Washington Acad. Sci. 17: 522. 1927, non King & Gamble, Jour. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 74: 146. 1906.
Ardisia austin-smithii Lundell, Contr. Univ. Michigan Herb. 7: 36. 1942.
Gentlea minor (Standley) Lundell, Wrightia 3: 104. 1964.

Shrubs or small trees, to 10 m high, the bark brownish, the branchlets slender, the internodes short. *Leaves* glabrous, petiolate, marginate, the petioles 3–7 mm long; leaf blades chartaceous, narrowly elliptic, oblong-elliptic, or oblanceolate, 2.5–7 cm long and 1–2.5 cm wide, obtuse or subacuminate apically, often rather abruptly so, the acumen obtuse, acute or acutely cuneate and decurrent basally, the costa slightly impressed above, prominent beneath, the primary veins slender, prominulous on both surfaces, the ultimate veins laxly reticulate, the margin entire. *Inflorescences* terminal, small, shorter than the leaves, the rachis and branches stout, crowded, few-flowered, bipinnately-paniculate, glabrous or minutely lepidote; bracts thin, caducous, obovate, to 7 mm long, erose; pedicels 2.5–5.5 mm long. *Flowers* umbellate, (4–)5(–6)-merous; calyx sparsely lepidote, the sepals ovate-orbicular, ovate, or oblong-lanceolate, 1.5–2 mm long, broadly rounded, acute or obtuse, erose, sparsely orange-punctate; corolla lepidote, 3–4.2 mm long, the petals narrowly triangular-lanceolate or oblong-elliptic, rounded or obtuse, asymmetric, connate basally into a tube ca. 1.2 mm long, punctate medially above with small orange-red glands; stamens attached slightly above the base of the corolla tube, exserted, to 5.5 mm long, the filaments slender, the anthers minute, cordate, ca. 0.5 mm long, obtuse-rounded and minutely apiculate apically; ovary glabrous or rarely lepidote, depressed-globose, the ovules 8–10, in several series, the placenta ovate, apiculate, the style exserted, 3.5–4.5 mm long. *Fruit* globose, black, ca. 6 mm diameter at maturity; endocarp finely costate.

A cloud forest species of Costa Rica and western Panama.

CHIRIQUÍ: Bajo Chorro, 6000 ft, *Davidson 388* (F, MO, US). Cerro Horqueta, cloud forest, 6000 ft, *von Hagen & von Hagen 2044* (MO).

The flowers of the Davidson collection are diseased and abnormal.

7. ARDISIA

Ardisia Sw., Nov. Gen. Sp. Pl. 3: 48. 1788, *nom. cons.*

Shrubs or trees. *Leaves* alternate, petiolate or rarely sessile, entire, dentate, or serrate. *Inflorescences* varied in form, the racemes, umbels, corymbs, and glomerules paniculate. *Flowers* pedicellate or subsessile, bisexual, (4–) 5-merous, small, white, pink, or lilac, dextrorsely or rarely sinistrorsely imbricate or contorted, often quincuncial; sepals short-connate or nearly free; petals connate basally or sometimes almost to the middle, recurved or spreading, rarely erect; stamens free, inserted at or slightly above the base of the corolla, the filaments usually elongate, rarely short, the anthers dorsifixed, mostly elongate and subsagittate, concolorous or glandular-punctate, dehiscent by apical or subapical pores and longitudinal slits; ovary ovoid or subglobose, the ovules few to numerous, usually pluriseriate, the style long and slender, often exserted, the stigma minute, punctiform. *Fruit* globose or subglobose, bearing the persistent style base apically, 1-seeded, the endocarp crustaceous or osseous; seed globose.

Species numerous, mostly in tropical America and Asia. In the Western Hemisphere the genus is most abundantly represented in Panama and Costa Rica. Fifty species are reported from Panama. Additional taxa are represented by specimens which are inadequate for either interpretation or description.

a. Inflorescences terminal, or sometimes both axillary and terminal (axillary and long-pedunculate in 24. *A. pleurobotrya*); flowers not clustered in a single corymb at the end of the peduncle; native species.
  b. Flowers aggregated in glomerules (racemose in fruit in 13. *A. darienensis*), the glomerules in paniculate racemes or spikes .... KEY B
  bb. Flowers not aggregated in glomerules.
    c. Inflorescences open paniculate racemes or spikes .... KEY A
    cc. Inflorescences paniculate umbels, corymbs, or corymbiform racemes .... KEY C
aa. Inflorescences axillary; flowers clustered in a single corymb at the end of the peduncle; naturalized and cultivated Asiatic species .... 50. *A. solanacea*

KEY A

Inflorescences terminal, usually glabrous, rarely puberulent or finely lepidote; the lateral and secondary branches elongated with the flowers regularly spaced; flowers in open paniculate racemes or spikes.

a. Bracts small, thin, caducous, not enveloping the mature flower buds.
  b. Branchlets glabrous; racemes bipinnately-paniculate; sepals mostly ovate-oblong, maculate, the black glands dispersed; pedicels 4–6 (–10) mm long .... 1. *A. revoluta*
  bb. Branchlets finely lepidote; racemes tripinnately-paniculate; sepals broadly ovate, densely black-punctate with the glands fused medially; pedicels 10–13 mm long .... 2. *A. nigrita*
aa. Bracts large, cucullate, persistent in bud, completely enveloping the mature flower buds.
  c. Leaves usually widest above the middle, mostly obovate, 17–32 cm long, to 9.5 cm wide; bracts thick.
    d. Inflorescences to 30 cm long; flowers sessile, the sepals 6 mm long. 3. *A. perinsignis*
    dd. Inflorescences to 15 cm long; flowers subracemose, the pedicels 1–4 mm long, the sepals 3–4.5 mm long .... 4. *A. allenii*
  cc. Leaves widest at the middle, oblongish, 9–16 cm long, to 5 cm wide; bracts thin .... 5. *A. granatensis*

KEY B[2]

Inflorescences terminal, conspicuously furfuraceous or lepidote; the lateral and secondary branches of the inflorescences thick, either elongated or spur-like; the flowers aggregated in glomerules (racemose in fruit in *A. darienensis*); the glomerules in paniculate racemes or spikes.

[2]See Lundell (Wrightia 4: 181–182. 1971) for descriptions of two additional species of this group from Panama: *A. horquetensis* Lundell and *A. rufa* Lundell.

a. Bracts large, cucullate, persistent in bud, completely enveloping the mature buds; leaves strongly veined, subamplexicaul basally .... 6. *A. nervosissima*
aa. Bracts small, thin, ovate, not enveloping the buds; leaves decurrent basally, not amplexicaul.
b. Inflorescences 4- or 5-pinnately paniculate, pyramidal, large, with many small flowers, to 60 cm wide at the base and equally long, the branches zigzag .... 7. *A. palmana*
bb. Inflorescences 2- or 3-pinnately paniculate.
c. Sepals symmetrical; leaves large, to 130 cm long .... 8. *A. megistophylla*
cc. Sepals asymmetrical, oblique; leaves not over 40 cm long, usually much shorter.
d. Leaves to 13 cm long and 4 cm wide.
e. Leaves elliptic or ovate-elliptic; pedicels ca. 1 mm long; inflorescences tripinnately paniculate .... 9. *A. tysonii*
ee. Leaves narrowly elliptic-oblong; pedicels 3–5 mm long; inflorescences bipinnately paniculate .... 10. *A. dwyeri*
dd. Leaves 15–40 cm long and 5.5–13.5 cm wide.
f. Leaves rigidly coriaceous, the veins slender and obscure; secondary branches of the inflorescences spur-like, thicker than long .... 11. *A. crassipes*
ff. Leaves chartaceous, the veins slender but conspicuous on the lower surface; secondary branches of the inflorescences elongated.
g. Indument of scales and coarse dendroid trichomes .... 12. *A. glomerata*
gg. Indument of scales only.
h. Secondary branches of the inflorescences flexuous, elongated, to 15 cm long; flowers glomerate in interrupted racemes; racemose in fruit, the pedicels thick, 3–6 mm long .... 13. *A. darienensis*
hh. Secondary branches of the inflorescences spur-like; flowers glomerate, subsessile .... 14. *A. hagenii*

KEY C

Inflorescences terminal, or sometimes both axillary and terminal (axillary and long pedunculate in *A. pleurobotrya*), glabrous, glandular-puberulent, or lepidote; flowers in paniculate umbels, corymbs or corymbiform racemes.

a. Leaf buds glabrous or minutely puberulent; panicles glabrous or puberulent, sometimes glandular-puberulent and villous.
b. Leaves pectinate-dentate with close, spreading, subulate teeth; panicles glandular-puberulent and villous .... 15. *A. pellucida*
bb. Leaves entire, crenulate, or obscurely crenulate, the teeth never subulate; panicles glabrous, rarely with a few glands on the pedicels.
c. Flowers in slender elongated corymbiform racemes .... 16. *A. lewisii*
cc. Flowers in umbels or corymbs.
d. Sepals 4–8 mm long.
e. Sepals 4–5 mm long.
f. Leaves subcoriaceous, lucid, entire; pedicels to 2 cm long .... 17. *A. subcoriacea*
ff. Leaves membranaceous, conspicuously crenulate (in the type); pedicels 6–10 mm long .... 18. *A. wagneri*
ee. Sepals 5–8 mm long.
g. Leaves to 8 cm long and 2–4 mm wide .... 19. *A. picturata*
gg. Leaves 12–25 cm long and 3.5–7.5 cm wide .... 20. *A. opegrapha*
dd. Sepals 1.8–2.25 mm long.
h. Flowers 4–5-merous; petals 5 mm long, glabrous within basally .... 21. *A. romeroi*
hh. Flowers 5-merous; petals 7–8 mm long, glandular-papillose within basally.
i. Leaf blades lanceolate or oblong-lanceolate, 1.8–4.3 cm wide .... 22. *A. bartlettii*
ii. Leaf blades elliptic, 3.5–7 cm wide .... 23. *A. lilacina*
aa. Leaf buds lepidote or furfuraceous; panicles lepidote or furfuraceous, often glabrate.
b. Inflorescences axillary, long pedunculate .... 24. *A. pleurobotrya*
bb. Inflorescences terminal, or sometimes terminal and with axillary inflorescences below.

c. Anthers 5–7 mm long, nearly sessile.
  d. Anthers connivent basally, to 7 mm long; sepals ovate, rounded and obliquely emarginate apically .... 25. *A. pittieri*
  dd. Anthers free, 5 mm long (in bud); sepals narrowly lanceolate, sharply acuminate .... 26. *A. stenophylla*
cc. Anthers 1–4 mm long, usually with distinct slender filaments.
  e. Flowers 4(–5)-merous in the same inflorescence; inflorescences usually with axillary panicles below the terminal; anthers slender, linear.
    f. Ovules (5–)8–12(–14); sepals 1.2–1.4 mm long .... 27. *A. guianensis*
    ff. Ovules 20–23; sepals 1–1.3 mm long .... 28. *A. alstonii*
  ee. Flowers all 5-merous.
    g. Inflorescences filiform, with small petiolate bracts subtending the lower lateral branches; anthers ovate-cordate, 1 mm long; leaves thin, lanceolate, to 10 cm long, caudate .... 29. *A. tenuis*
    gg. Inflorescences not filiform anthers more than 1 mm long; leaves not caudate.
      h. Inflorescences with a sharply zigzag rachis, and lateral and secondary branches (also see 7. *A. palmana* and 34. *A. nigropunctata*).
        i. Punctate with large black conspicuous glands; bracts subtending the lateral branches of the inflorescences petiolate, small; leaves to 7 cm long; anthers lanceolate, 1.5 mm long, caudate .... 30. *A. panamensis*
        ii. Punctate with inconspicuous glands; bracts subtending the lateral branches of the inflorescences petiolate, large, sometimes subequaling the leaves; leaves to 15 cm long; anthers oblongish, 2.5–3 mm long, acute. .... 31. *A. glanduloso-marginata*
      hh. Inflorescences not sharply zigzag.
        j. Anthers conspicuously black-punctate dorsally .... 32. *A. pulverulenta*
        jj. Anthers concolorous, the dorsal glands, if present, inconspicuous.
          k. Leaves mostly 20–40 cm long.
            l. Leaves rounded basally, sessile or nearly so; inflorescences narrowly paniculate, the lateral branches short and spurlike; the peduncle of the inflorescence to 13 cm long .... 33. *A. wedelii*
            ll. Leaves acute basally, petiolate.
              m. Leaves thin; sepals broadly ovate, 1.6–2 mm long; pedicels 3–5 mm long .... 34. *A. nigropunctata*
              mm. Leaves firmer; sepals ovate, 1–1.3 mm long; pedicels 1.5–2 mm long .... 35. *A. dukei*
          kk. Leaves usually less than 15 cm long, mostly much smaller (rarely to 20 cm long in 41. *A. antonensis*, 49. *A. copeyana*, and 48. *A. fendleri*).
            n. Sepals minute, ca. 0.75 mm long and 0.6 mm wide; pedicels 2–3 mm long (see also 40. *A. furfuracella*).
              o. Inflorescences to 20 cm long and wide; petals ca. 4 mm long; anthers to 2 mm long; style 3.5 mm long .... 36. *A. scheryi*
              oo. Inflorescences less than 10 cm long; petals ca. 5.5 mm long; anthers 2.3–2.8 mm long; style 5 mm long .... 37. *A. microcalyx*
            nn. Sepals at least 1 mm long and wide, usually much larger; pedicels usually much longer.
              p. Flowers 7–8 mm long; leaves coriaceous; pedicels rigid, to 10 mm long.
                q. Leaves obtuse or rounded, 4–6(–10) cm long and 1.5–3.5 cm wide, the petioles 2–6 mm long .... 38. *A. maxonii*
                qq. Leaves acuminate, 7.5–13 cm long and 3.5–5 cm wide, subsessile .... 39. *A. subsessilifolia*
              pp. Flowers 4–6 mm long.

r. Anthers ovate, ca. 1.5 mm long; pedicels 1.5–3 mm long .... 40. *A. furfuracella*

rr. Anthers not ovate, not less than 2 mm long, usually much larger; pedicels 3–10 mm long.

s. Sepals 1–1.3 mm long.

t. Leaves long-acuminate, 13–22 cm long and 4.5–6.8 cm wide, with thick petioles, coriaceous .... 41. *A. antonensis*

tt. Leaves often subacuminate and obtusish, less than 12 cm long and 5 cm wide, with slender petioles.

u. Leaves rigidly coriaceous, often rhomboid, 3.5–6.5 cm long and 2–3.2 cm wide, obtuse apically .... 42. *A. rigidifolia*

uu. Leaves not rigidly coriaceous, more than 3.5 cm long and 2 cm wide

v. Pedicels slender, 5–10 mm long; inflorescences less than 5 cm long, the branches slender .... 43. *A. geniculata*

vv. Pedicels 3–5.5 mm long; inflorescences to 10 cm long.

w. Leaves oblong or oblong-lanceolate, 4.5–10 cm long and 1.3–3.5 cm wide .... 44. *A. opaca*

ww. Leaves obovate or obovate-elliptic, 6–13 cm long and 3.5–5 cm wide, with numerous (15–19 pairs) slender primary veins and intermediaries.

x. Corolla not persistent after anthesis; filaments ca. 2 mm long; anthers 2.8–3 mm long; style 5.5 mm long .... 45. *A. whitei*

xx. Corolla persistent, reflexed; filaments to 2.5 m long; anthers 2–2.4 mm long; style 4 mm long .... 46. *A. reflexiflora*

ss. Sepals 1.5–2.5 mm long.

y. Leaves obovate or obovate-elliptic, 3–6 (–9.5) cm long and 2–5 cm wide; petals densely orange-punctate with round glands .... 47. *A. obovalifolia*

yy. Leaves mostly oblong-elliptic, 6.5–20 cm long and 4–9.5 cm wide; petals not densely orange-punctate with round glands.

z. Leaves subchartaceous; pedicels slender, 5–7 mm long; petals lineate-punctate medially, smooth when dry .... 48. *A. fendleri*

zz. Leaves coriaceous; pedicels 3–4 mm long; petals inconspicuously orange-punctate, rugose when dry .... 49. *A. copeyana*

1. **Ardisia revoluta** Kunth, Nov. Gen. Sp. Pl. 3: 246. 1818.

A. scopulina Brandegee, Zoe 5: 215. 1905.

Shrubs or small trees, sometimes 8 m high, the branchlets stout, glabrous; leaf buds ciliate and minutely ferruginous-tomentose. *Leaves* with marginate petioles, usually short, sometimes to 1.2 cm long; leaf blades oblanceolate, obovate-oblong, elliptic, or obovate-elliptic, mostly 9–19 cm long and 3.5–8 cm wide, obtuse or often rounded apically, attenuate to the decurrent base, glabrous, subcoriaceous or chartaceous, entire, drying pallid, the costa prominent beneath, the veins slender and obscure. *Inflorescences* terminal, punctate, glabrous or sparsely puberulent and glabrescent, the racemes in sessile or subsessile bipinnate or rarely tripinnate panicles, the panicles usually less than 15 cm long; pedicels usually 4–6 (–10) mm long, sometimes shorter. *Flowers* 5-merous, white, 6–9 mm long at anthesis; sepals ovate-oblong or elliptic, 1.5–2.8 mm long, rounded apically, ciliate, the margin scarious, maculate medially with lineate or oblong dispersed black glands, papillose within basally, otherwise glabrous; petals dextrorsely imbricate, oblong or oblong-elliptic, to 8 mm long, rounded and laterally notched apically, connate basally into a tube ca. 2 mm long, glandular-papillose within basally, the petals otherwise glabrous, black-punctate with conspicuous lineate glands; stamens 4–6.5 mm long, attached near the base of the tube, the filaments glabrous, slender, sometimes to 4.8 mm long, the anthers dorsifixed 0.5–0.8 mm above the base, narrowly triangular, 2–3.2 mm long, apiculate, epunctate; ovary glabrous, the ovules numerous, pluriseriate, immersed, the style slender, 5–6 mm long. *Fruit* coarsely punctate with large elevated glands, subglobose, 4–5 mm in diameter when dry, turning purple-black at maturity.

Mexico, Central America, and Colombia.

CANAL ZONE: Albrook Forest, vicinity of the end of road C-16, *Blum 2234a* (MO); vicinity of TTC tower site, *Blum & Dwyer 2092* (MO). Vicinity of Río Cocolí, road K-9, edge of stream, *Stern et al. 319* (MO, US). Tortuguillo Point, cliffs overhanging the sea, *Johnston 1790* (MO). CHIRIQUÍ: 12.4 mi. N of David, *Lewis et al. 699* (LL, MO). Francés Arriba School, ca. 14 mi. N of David, *Lewis et al. 670* (LL, MO). COCLÉ: Vicinity of El Valle, *White & White 71* (LL, MO). Río Teta, *Blum & Tyson 1869* (MO). HERRERA: Road from La Avena to Pesé, *Burch et al. 1299* (LL, MO). 4 mi. S of Los Pozos, *Tyson 2692* (MO). Vicinity of Ocú, *Allen 4068* (MO). Ocú, *Ebinger 1095* (LL). 2.5 mi. N of Ocú, *Graham 228* (MICH). PANAMÁ: Along Chiva-Chiva trail to Search Light Station beyond Chiva-Chiva, *Allen 953* (K, MO, P). Along road between Panamá and Chepo, *Dodge et al. 16638* (K, MICH, MO, P). Río Las Lajas, *Allen 1614* (MO). LOS SANTOS: Loma Prieta, 800–900 m, *Duke 11847* (MO). Cerro Grande, 2400–2800 ft, *Lewis et al. 2196* (LL). Along road from Tonosí to Guanico, *Dwyer 3127* (MO). VERAGUAS: Isla de Coiba, *Dwyer 1673* (MO), *2364* (MICH). Headwaters of the Río Cañazas, *Allen 148* (MO). LOCALITY UNKNOWN: *Seemann s.n.* (K); *Duchassaing s.n.* (P).

2. **Ardisia nigrita** Lundell, Wrightia 4: 161. 1971.

Shrubs, the branchlets slender, subterete, minutely lepidote at first, the indument reddish. *Leaves* petiolate, the petioles slender, 7–15 mm long, canaliculate; leaf blades glabrous, chartaceous, elliptic, 6.5–13.5 cm long and 3–7 cm wide, obtuse or subacuminate apically, the acumen obtuse, acute basally, slightly decurrent, conspicuously punctate at first, the margin entire, the midvein nearly plane above, conspicuous beneath, the veins slender and inconspicuous. *Inflorescences* glabrous, terminal, ample, tripinnately paniculate, open, pyramidal, to 11 cm long and 15 cm wide basally, the rachis and branches black-punctate. *Flowers* 5-merous, racemose, the pedicels rather remote, slender, mostly recurved, 10–13 mm long; sepals broadly ovate or suborbicular, ca. 2 mm long, rounded apically, thick with a hyaline margin, ciliolate at first, densely black-punctate with large glands. *Fruit* immature, subglobose, yellow, ca. 6 mm in diameter, black-punctate with large glands.

Native to Panama.

CANAL ZONE: Coco Solo, U. S. Army Tropic Test Center, Mine Emplacement Center, *Dwyer & Duke 7880* (LL). PANAMÁ: Cerro Jefe, ca. 2900 ft. *Dwyer & Hayden 8092* (LL, holotype).

Ardisia nigrita resembles *A. colombiana* Lundell, a species with strictly glabrous leaf buds and branchlets. Several collections from Panama may be referable to *A. colombiana*: *Hayes s.n.* (S), *707* (K, S), *Miller 2056* (US). They have bipinnately paniculate inflorescences and glabrous branchlets.

3. **Ardisia perinsignis** Lundell, Wrightia 4: 163. 1971.

Trees, to 10 m high, the branchlets thick, drying ca. 9 mm in diameter at the bases of the inflorescences, glabrous, terete. *Leaves* glabrous, short petiolate, the petioles thick, marginate, to 1.5 cm long; leaf blades coriaceous, pallid, narrowly oblong or oblong-oblanceolate, to 32 cm long and 6.5–9 cm wide, subacuminate apically, subcuneate basally, decurrent on the petiole, margin entire, revolute, conspicuously punctate at first, the midvein depressed above, thick and elevated beneath, the lateral veins numerous, slender, arcuately ascending. *Inflorescences* terminal, equaling the leaves, bipinnately paniculate, the peduncle and rachis thick, the basal branches to 20 cm long, glabrous. *Flowers* 5-merous, spicate, sessile, each subtended in bud by a black-punctate ovate cucullate bract longer than the calyx; sepals free, imbricate, ovate, 6 mm long, symmetrical, rounded apically, minutely ciliolate, conspicuously black-punctate, glandular within; corolla ca. 1.3 cm long, the petals connate basally ca. 2.5 mm, linear-oblong, ca. 3 mm wide, emarginate and asymmetrical apically, densely punctate with black glands, glabrous dorsally, glandular within basally; stamens ca. 9 mm long, the filaments inserted in the corolla tube, connate basally, 3.5 mm long, glandular-papillose below, black-punctate, the anthers thick, sagittate-lanceolate, ca. 5.5 mm long, acute, concolorous, not punctate, dehiscent at first by small apical pores; ovary ovoid, punctate, the ovules numerous, pluriseriate, the style slender, ca. 1 cm long.

Native to Panama.

DARIÉN: ca. 10 mi. S of El Real, on the Río Pirre, *Duke 5483* (LL, holotype; MO, isotype).

4. **Ardisia allenii** Lundell, Wrightia 4: 53. 1968.—Fig. 13.

A. guttata Lundell, Wrightia 4: 59. 1968.
A. subcuneifolia Lundell, Wrightia 4: 66. 1968.

Shrubs or trees, to 10 m tall, the branchlets thick, terete, glabrous. *Leaves* large, with thick marginate petioles to 10–12 mm long; leaf blades concolorous, subcoriaceous or coriaceous, glabrous, entire, obovate-elliptic, elliptic, or oblanceolate, 17–23 cm long and 5.5–9.5 cm wide, obtusely short acuminate apically, broadly cuneate basally, decurrent on the petiole, the costa nearly

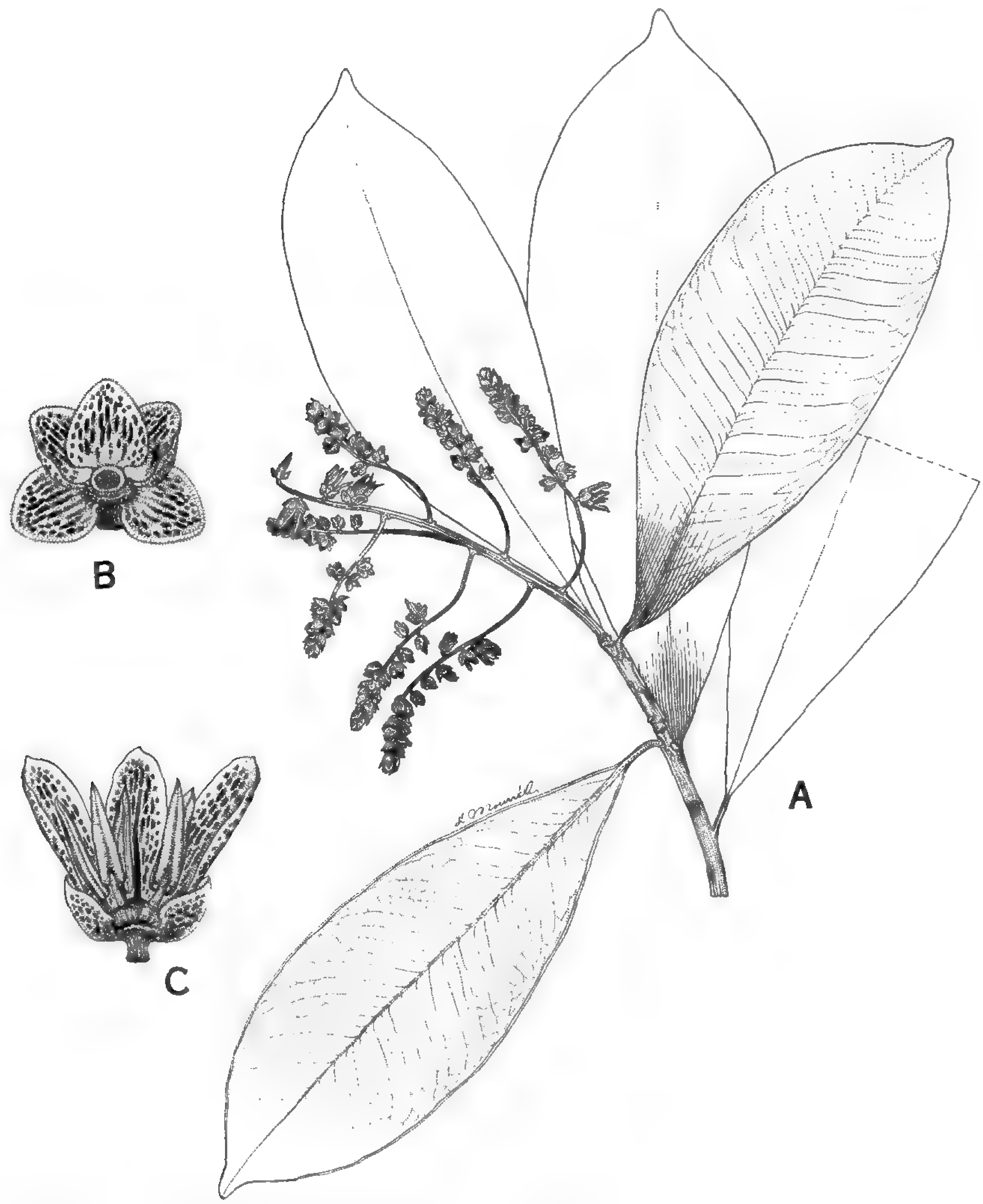


Figure 13. *Ardisia allenii* Lundell.—A. Habit (ca. × ½).—B. Calyx (ca. × 3).—C. Flower (ca. × 3). [After *Allen 4579* (MO, isotype).]

plane above, elevated beneath, the primary lateral veins slender, obscure. *Inflorescences* terminal, bipinnately paniculate, glabrous, pyramidal, to 15 cm long, with a few slender but stiff branches. *Flowers* 5-merous, subspicate or subracemose, large, glabrous, conspicuously black-punctate; pedicels short, thick, 1–2.5 mm long, to 4 mm long in fruit; bracts cucullate, enveloping the buds, black-punctate, short ciliate at first; sepals free, broadly ovate, 3–4.5 mm long, rounded apically, sometimes emarginate laterally, ciliate, conspicuously black-punctate, glandular within basally, petals erect at first, patent at anthesis, narrowly oblong, 10–11 mm long, asymmetrical, connate ca. 2 mm basally, densely glandular within basally; stamens 7–8 mm long, the filaments thick, to 3 mm long, connate basally, the anthers lanceolate, 4.5–5.5 mm long, black-punctate dorsally, tapering to the apex, dehiscent at first by small apical pores; ovary ovoid-ellipsoid, glabrous, the ovules pluriseriate, numerous, the style 7–8 mm long. *Fruit* ovoid, punctate with large black glands.

Native to Panama.

DARIÉN: N of Pucro, *Duke 13008* (MO). Quebrada Nigua below Santa Fé, *Duke 8824* (MO). Between Quebrada Venado and Peje Swamp, headwaters of the Río Tuqueza, *Bristan 1064* (LL). Near Refugio, 15–21 mi. N of Santa Fé, ca. 30 m, *Duke 10270* (LL, holotype of *A. subcuneifolia*). Río Chico, vicinity of Yaviza, 100 ft, *Allen 4579* (US, holotype; LL, MO, P, isotypes). Río Sabana, above Santa Fé, *Duke 14089* (LL).

5. **Ardisia granatensis** Mez, Pflanzenreich IV. 236: 86. 1902.

Shrubs or small trees, to 4 m high, the branchlets thick, at first obscurely and minutely puberulent, essentially glabrous. *Leaves* petiolate or subsessile, the petioles 3–6 mm long, marginate, canaliculate; leaf blades glabrous, chartaceous, oblong or narrowly oblong-elliptic, 9–16 cm long and 2.5–5 cm wide, acuminate, the acumen obtusish, acute basally, decurrent, revolute, margin entire, pale and brownish beneath, opaque, the midvein shallowly impressed above, prominent on the undersurface, the primary lateral veins slender, inconspicuous. *Inflorescences* terminal, bipinnately paniculate, subsessile, congested, to 5 cm long, essentially glabrous, with conspicuous cucullate bracts enveloping the mature buds. *Flowers* 5-merous, glabrous, subspicate, crowded, the pedicels ca. 1 mm long; sepals free, ovate-elliptic, 3 mm long, ciliolate, rounded apically, black-punctate with short oblongish glands; petals connate ca. 1.5 mm basally, narrowly ovate-elliptic or oblong-elliptic, ca. 7 mm long, rounded apically, sparsely black-punctate, glandular basally within; stamens ca. 4.5 mm long, the filaments slender, ca. 2.5 mm long, the anthers lanceolate, ca. 2.4 mm long, widest basally, concolorous, apiculate; ovary ovoid, the ovules numerous, pluriseriate, the style slender, ca. 5.5 mm long. *Fruit* subglobose, 7 mm in diameter.

Panama and Colombia.

DARIÉN: Puerto Santa Dorotea, *Dwyer 2285* (MO). Río Bayano, on water edge, *Peterson 6644* (US).

6. **Ardisia nervosissima** Lundell, Wrightia 4: 62. 1968.

Shrubs, the branchlets thick, furfuraceous at first, glabrate. *Leaves* sessile or subsessile, the petioles broad, to 3 mm long, marginate; leaf blades membranaceous, entire, oblanceolate or oblanceolate-oblong, 10–21 cm long and 2–7 cm wide, acuminate apically, rounded basally, subamplexicaul, lepidote at first with closely appressed scales, glabrate above, punctate, the costa impressed above, the primary nerves 18–30 pairs, shallowly impressed above, elevated and conspicous beneath, the lateral nerves anastomosing into a distinct submarginal vein. *Inflorescences* terminal, bipinnately paniculate, small, furfuraceous, pedunculate, the lower bracts foliaceous, deciduous early, the lateral branches short, thick, to 1 cm long, spur-like. *Flowers* 5-merous, in glomerules, sessile or nearly so, the short pedicels thick; buds enclosed by the bracts; calyx furfuraceous, the sepals thick with a hyaline margin, ovate-orbicular, 2.2–2.5 mm long, ciliate, black-punctate; petals (in bud) connate basally, elliptic, acute, conspicuously punctate; filaments short (in bud), the anthers thick, lanceolate-oblong (in bud), acute; ovary glabrous, the ovules few, the style punctate, equaling the petals. *Fruit* subglobose, 5–6 mm in diameter (dry), punctate with small dispersed black glands.

Native to Panama.

COCLÉ: Cloud forest of Cerro Caracoral, ca. 900 m, *Duke & Dwyer 15132* (LL). Cloud forest, Cerro Pilón, El Valle, 3000 ft, *Duke & Lallathin 14968, 15004* (both LL). Cloud forest, El Valle, *Duke 13150* (LL, holotype; LL, isotype).

The leaves are strongly nerved, as in *Stylogyne hayesii* Mez.

7. **Ardisia palmana** Donn. Sm., Bot. Gaz. (Crawfordsville) 27: 434. 1899.

Trees, to 22 m high, the branchlets thick, angulate, rufous, lepidote, the scales appressed. *Leaves* subsessile to petiolate, the petioles thick, conspicuously marginate, sometimes to 1.5 cm long, lepidote; leaf blades subcoriaceous, oblong-lanceolate, elliptic-lanceolate, or oblanceolate, 12.5–30 cm long and 4–7.5 cm wide, acute or acuminate apically, revolute and decurrent on the petiole basally, acutish, the margin entire, obscurely black-punctate, paler beneath and lepidote with appressed scales, glabrate above, the midvein prominent on the lower surface, impressed on the upper surface, the primary lateral veins approximate, conspicuous beneath, openly reticulate. *Inflorescences* terminal, equaling the leaves, to 30 cm long, pyramidal, pinnately paniculate, rufous, furfuraceous; pedicels short, 1–3 mm long in fruit. *Flowers* 5-merous, subglomerate, numerous, small, ca. 4.5 mm long, glabrous; sepals shortly connate basally, suborbicular, ca. 1.5 mm long, broadly rounded, ciliolate; corolla ca. 4 mm long, the petals asymmetrical, acutish; stamens 4 mm long, attached at the base of the corolla, the anthers lanceolate, subequaling the filaments, acute, not punctate, longitudinally dehiscent; ovary ellipsoid, glabrous, the ovules numerous, pluriseriate, small, the style 3 mm long. *Fruit* depressed-globose.

Costa Rica and Panama.

CHIRIQUÍ: Slopes of Volcán Barú, near town of Cerro Punta, 6300 ft, *Stern & Chambers 96* (MO, US). PANAMÁ: Cerro Jefe, near Río Indio, 2100–2200 ft, *Duke 15229* (MO).

8. **Ardisia megistophylla** Lundell, Wrightia 4: 147. 1970.

Shrubs, 2 m high, furfuraceous, branchlets thick. *Leaves* large, with thick canaliculate petioles conspicuously marginate to the base, the petioles to 4.5 cm long; leaf blades paler beneath, chartaceous, elliptic or oblanceolate-elliptic, to 130 cm long and 18 cm wide, narrowed apically, probably short-acuminate, attenuate and decurrent on the petiole basally, densely covered beneath with closely appressed brownish scales, the midvein impressed above, prominent beneath, the primary lateral veins numerous, slender but conspicuous on the undersurface, less evident above, the nerves almost at right angles to the costa, the intermediaries well developed, the margin entire. *Inflorescences* terminal, paniculate, to 25 cm long, with thick peduncle and rachis, furfuraceous. *Flowers* 5-merous, glomerate, the short thick pedicels ca. 2 mm long; sepals lepidote, ovate-elliptic, to 2 mm long, rounded apically, the margin erose-ciliate but this not always evident, punctate with conspicuous black rounded glands; ovary glabrous, the ovules pluriseriate, numerous. ***Fruit*** depressed-globose, 6–8 mm in diameter.

Panama to Colombia.

VERAGUAS: Mouth of the Río Concepción, beach, cliffs, and adjacent swamp, *Lewis et al. 2808* (LL, MO).

9. **Ardisia tysonii** Lundell, Wrightia 4: 165. 1971.

Shrubs, ca. 3 m high, the branchlets short, thick, furfuraceous-lepidote with large closely appressed brown scales. *Leaves* small, petiolate, the petioles 6–11 mm long, canaliculate, lepidote; leaf blades rigidly coriaceous, elliptic or ovate-elliptic, 5-8.5 cm long and 2–4 cm wide, subabruptly short acuminate apically, rounded and acutish basally, lepidote and paler beneath, glabrous early above, the young leaves conspicuously black-punctate, the margin entire, the midvein elevated beneath, narrowly impressed above, the primary veins slender, evident on both surfaces. *Inflorescences* terminal, tripinnately paniculate, with stout rachis and branches, furfuraceous-lepidote, to 10 cm long. *Flowers* 5-merous, glomerate at the ends of short thick branches, the pedicels short, ca. 1 mm long, thicker than the calyx; sepals broadly ovate-elliptic, 2 mm long and 2.2 mm wide, asymmetrical, rounded apically, the margin uniformly ciliolate, punctate with large black glands medially, with a few orange glands bordering these; ovary ellipsoid, punctate with small black glands, the ovules numerous, pluriseriate.

Native to Panama.

PANAMÁ: Cerro Jefe, 2700–3000 ft, *Tyson et al. 3279* (MO, holotype; LL, isotype).

10. **Ardisia dwyeri** Lundell, Wrightia 4: 145. 1970.—FIG. 14.

Shrubs, ca. 3 m high, branchlets furfuraceous, rigid, slender to thickish. *Leaves* petiolate, the petioles stout, 5–10 mm long, canaliculate, densely furfuraceous on the lower side; leaf blades chartaceous to subcoriaceous, brownish beneath, grayish above, oblong or narrowly elliptic-oblong, 6.5–13 cm long and 2–3 cm wide, acute, apically and basally, the margin entire, persistently brown-lepidote beneath, glabrate above, the midvein narrowly impressed above, prominent beneath, the primary lateral veins slender and inconspicuous. *Inflorescences* small, terminal, bipinnately paniculate, 3.5–6.5 cm long, densely furfuraceous, brown, the bracts small, scale-like. *Flowers* umbellate, 5-merous; pedicels thick, 3–5 mm long, sparsely lepidote; sepals asymmetrical, depressed-orbicular, 1.7–2 mm long, rounded apically, ciliolate, conspicuously punctate with red marginal and black medial glands; corolla glabrous, ca. 6.5 mm long, the petals connate basally, the campanulate tube 1.7–2 mm high, the petals oblong-elliptic, symmetrical, black-punctate; stamens attached medially to the corolla tube, the filaments thick, ca. 1.6 mm long, the anthers thick, lanceolate, widest basally, ca. 2.8 mm long, glandular-punctate dorsally, the

FIGURE 14. *Ardisia dwyeri* Lundell.—A. Habit (× ½).—B. Flower, showing corolla, stamens, and style (× 4). [After *Dwyer & Hayden 8082* (LL, holotype).]

glands inconspicuous, but blackened; ovary glabrous, the ovules pluriseriate, numerous, the style slender, punctate, ca. 4 mm long. *Fruit* subglobose, ca. 8 mm in diameter.

Native to Panama.

PANAMÁ: Cerro Jefe, roadside thicket, ca. 2900 ft, *Dwyer & Hayden 8082* (LL, holotype; MO, US, isotypes). Beyond Goofy Lake along road to Cerro Jefe, *Correa & Dressler 462* (MO).

11. **Ardisia crassipes** Lundell, Wrightia 4: 57. 1968.

Trees, ca. 20 m high, branchlets thick, terete, lepidote at first. *Leaves* alternate, coriaceous, with thick marginate petioles 1–1.5 cm long and ca. 5 mm in diameter; leaf blades drying brownish, persistently appressed-lepidote on the lower surface with small brownish scales, oblong-elliptic, 21–25 cm long and 8–9.5 cm wide, subabruptly acuminate apically, acute and decurrent basally, entire, opaque, the costa shallowly sulcate above, large and elevated beneath, the primary lateral veins slender and inconspicuous on both surfaces, widely ascending. *Inflorescences* (complete) not seen, apparently paniculate, the main branches thick, furfuraceous, bearing the flowers on short thick reduced lateral spurs to 5 mm long; pedicels thick, 1–1.5 mm long, to 4

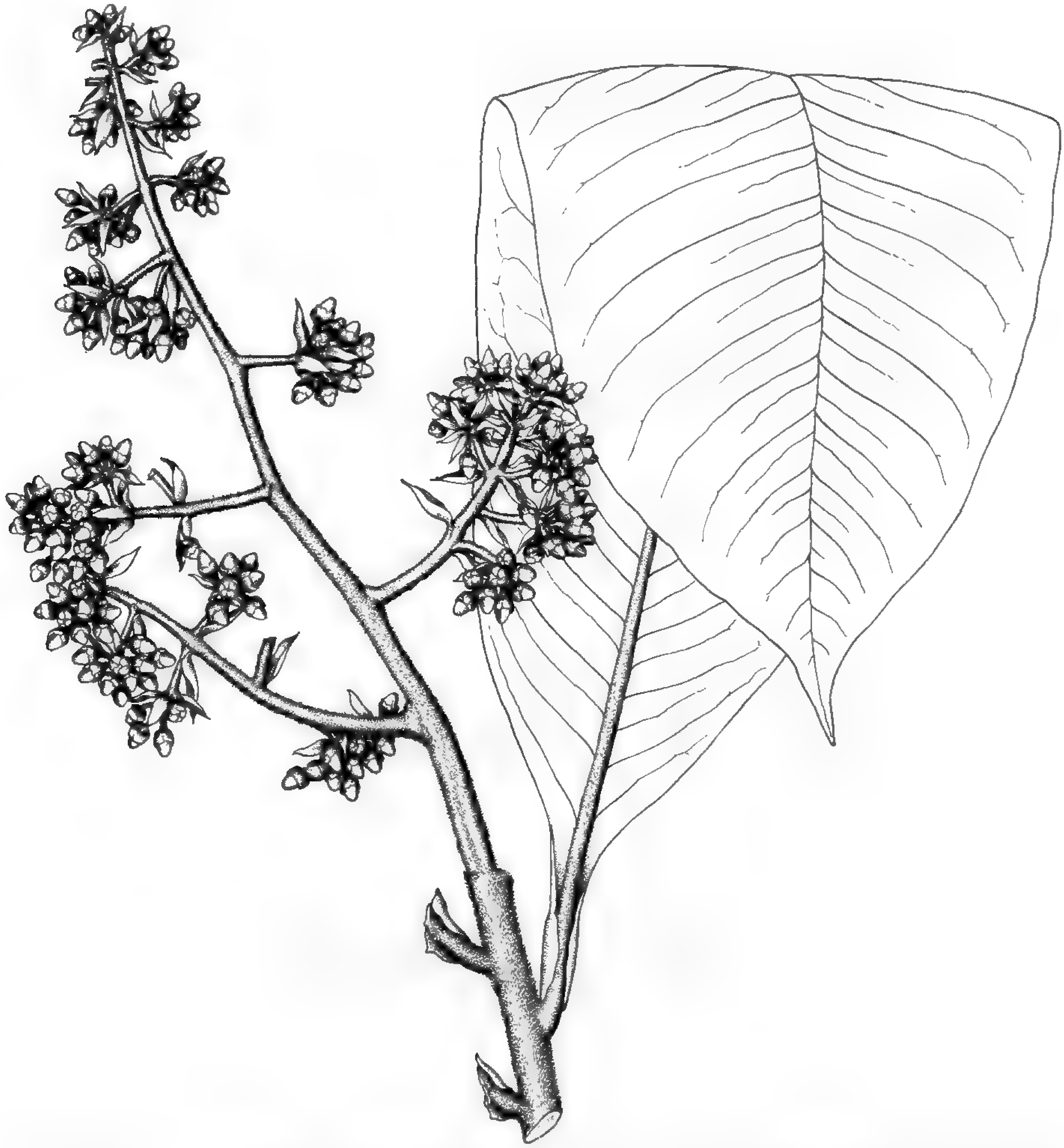


FIGURE 15. *Ardisia glomerata* Lundell, habit (× ½). [After *Allen 2741* (MO, holotype).]

mm in diameter. *Flowers* 5-merous; sepals free, coriaceous, broadly suborbicular, ca. 2.5 mm long, asymmetrical, ciliate, rounded apically, punctate with a few small glands. *Fruit* (immature) obovoid, glabrous.

Native to Panama.

BOCAS DEL TORO: Robaldo Trail, N slopes of Cerro Horqueta, *Allen 4991* (MO, holotype; LL, fragment).

12. **Ardisia glomerata** Lundell, Amer. Midland Naturalist 29: 486. 1943. —FIG. 15.

Trees, to 8 m high, branchlets thick, almost 1 cm in diameter, ferruginous-tomentose with dendroid trichomes, furfuraceous. *Leaves* with petioles broadly marginate to the base, stout, 2–3.5 cm long, essentially glabrous above; leaf blades large, chartaceous, drying brown, paler beneath, oblanceolate-elliptic, to 36.5 cm long and 16 cm wide, subabruptly acuminate apically, subabruptly narrowed basally, decurrent, broadly marginate, entire, glabrous above, lepidote beneath, the costa stout, bearing stalked dendroid trichomes, primary veins ca. 40 on each side, with intermediaries. *Inflorescences* terminal, large, pyramidal, tripinnately paniculate, to 25 cm long; rachis and branches stout, the lateral and secondary branches short, densely ferruginous-tomentose with dendroid trichomes, and furfuraceous; bracts conspicuous, persistent. *Flowers* 5-merous, glomerate, numerous; pedicels stout, 1–5 mm long, furfuraceous; calyx coriaceous, furfuraceous, ca. 4 mm long, the sepals depressed orbicular, ca. 3 mm long and 4–5 mm wide, the margin hyaline, ciliate; corolla 7 mm long (in mature bud), the tube ca. 3 mm long, the petals coriaceous, punctate, oblong, ca. 3.5 mm wide, the margin hyaline; filaments wide, ca. 2 mm long, the anthers thick, 4 mm long, dehiscent by apical pores; ovary glabrous, the ovules numerous, large, in several series, the style 6–7.5 mm long, punctate with small black glands. *Fruit* globose, ca. 9 mm in diameter (dry).

Native to Panama.

COCLÉ: Cerro Pilón, cloud forest, 3000 ft, *Duke & Lallathin 14989* (MO). Foothills of Cerro Pilón, near El Valle, *Duke & Correa 14692* (LL). El Valle de Antón at the foot of Cerro Pilón, ca. 2000 ft, *Dwyer & Correa 7938* (LL). Between Cerro Pilón and El Valle, 700–900 m, *Duke & Dwyer 13964* (LL). Hills N of El Valle de Antón, trail to La Mesa, *Allen 2741* (MO, holotype; LL, fragment; A, isotype).

13. **Ardisia darienensis** Lundell, Wrightia 4: 58. 1968.

Trees, 3–5 m high, branchlets thick, furfuraceous with closely appressed ferruginous scales. *Leaves* subsessile, the short thick broadly marginate petioles to 1 cm long; leaf blades chartaceous, entire, paler and ferruginous below, the lower surface furfuraceous with appressed scales, obovate, obovate-elliptic, or oblanceolate, 11–23 cm long and 5–9.5 cm wide, abruptly short-acuminate apically, the acumen acute, rounded basally, decurrent on the petiole, the costa impressed above, prominent beneath, the primary lateral veins slender and widely arcuate, scarcely discernible above. *Inflorescences* treminal, tripinnately paniculate, to 25 cm long and wide, few-branched, the branches thick and flexuous, open, appressed-furfuraceous. *Flowers* 5-merous, racemose, the apical approximate or subglomerate, the lower remote in the racemes; fruiting pedicels thick, rigid, 3–6 mm long; sepals coriaceous, ovate, ca. 5 mm long, erose-ciliate, rounded apically, free nearly to the base, black-punctate, lepidote. *Fruit* globose, ca. 1 cm in diameter.

Native to Panama.

DARIÉN: Chepigana District, crest of Caná-Cuasi Trail, in rain forest, 5500 ft, *Terry & Terry 1563* (F, holotype; MO, isotype). Cerro Pirre, *Bristan 593* (MO); 2500–4500 ft, *Duke & Elias 13750* (LL); cloud forest, 3700 ft, *Duke 6561* (LL).

14. **Ardisia hagenii** Lundell, Wrightia 4: 59. 1968.—FIG. 16.

Trees, to 11 m high, the branchlets thick, at first furfuraceous with small appressed ferruginous scales. *Leaves* large, with thick marginate petioles to

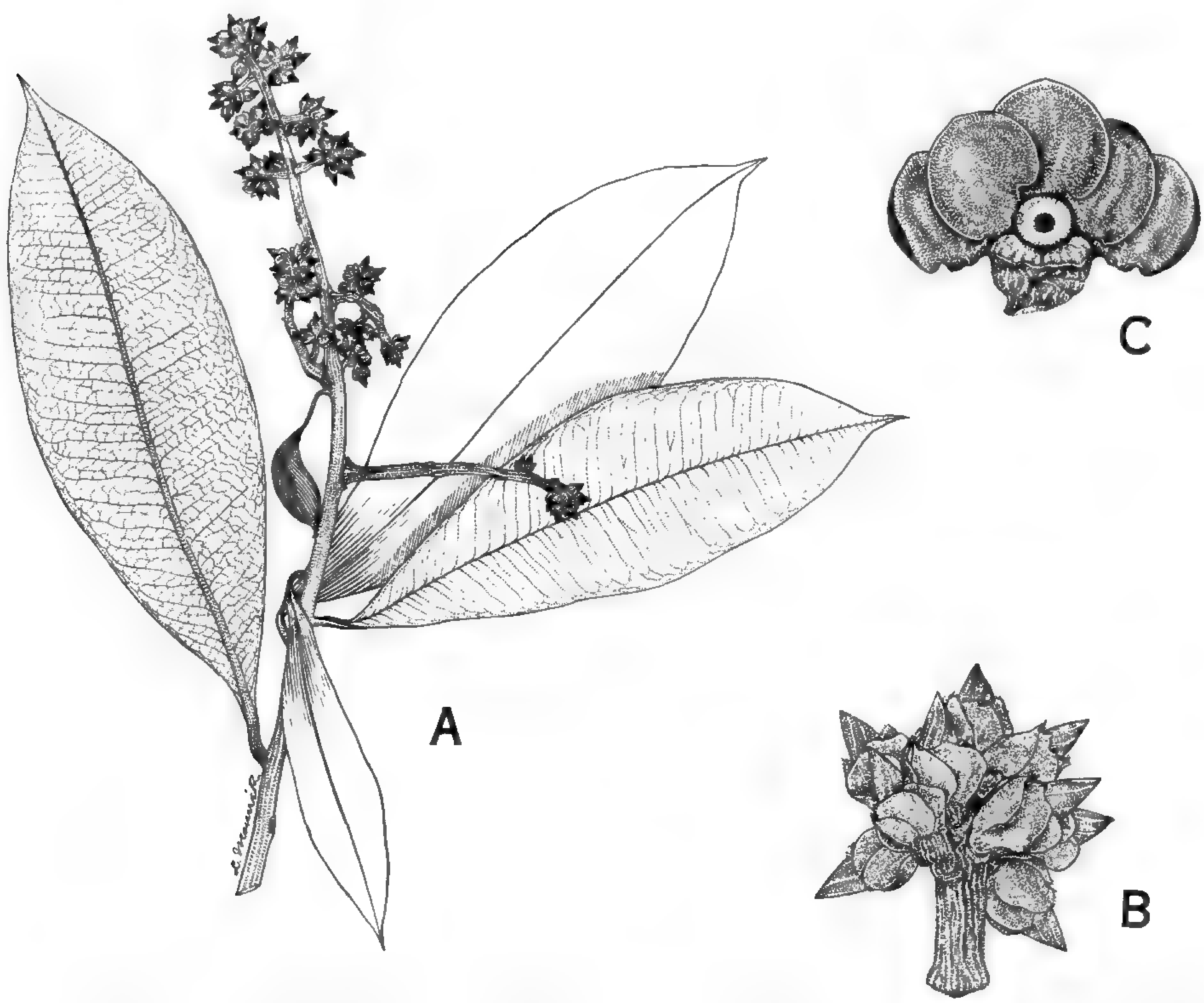


FIGURE 16. *Ardisia hagenii* Lundell.—A. Habit (× 3/10).—B. Glomerule of flowers (ca. × 1⅘).—C. Calyx, spread out (×4⅘). [After *von Hagen & von Hagen 2008* (MO, holotype).]

1.5 cm long; leaf blades chartaceous or subcoriaceous, entire, paler and brown beneath, glabrate above, furfuraceous with appressed scales on the lower surface, lanceolate-oblong or lanceolate-elliptic, 15–23.5 cm long and 6–8 cm wide, abruptly acuminate apically, the acumen acute, narrowed basally, acute and decurrent on the petiole, the costa impressed above, elevated beneath, the primary lateral veins nearly horizontal, prominent beneath, evident but less conspicuous above, reticulate. *Inflorescences* terminal, bipinnately paniculate, narrow, to 15 cm long, few-branched, the secondary branches short, spur-like, congested, furfuraceous, the bracts small, scale-like. *Flowers* 5-merous, glomerate, subsessile; pedicels thick, to 2 mm long; sepals free, indurated, furfuraceous, forming a cupule, fimbriate, depressed ovate-orbicular, 2.5–3.5 mm long, asymmetrical, black-punctate with small glands; corolla (in bud) glabrous, the petals indurated, narrowly elliptic, acute, punctate; stamens (in bud) with short filaments, the anthers (in bud) narrowly lanceolate, acute, longitudinally dehiscent; ovary subcylindrical, widest below, the ovules pluriseriate, numerous, the style 3.4 mm long, conspicuously black-punctate with protruding glands.

Native to Panama.

CHIRIQUÍ: Horqueta, cloud forest, 6500 ft, *von Hagen & von Hagen 2008* (MO, holotype).

15. **Ardisia pellucida** Oerst., Vidensk. Meddel. Dansk Naturhist. Foren Kjøbenhavn. 1861: 130. *t.* 2. 1861.

A. pectinata Donn. Sm., Bot. Gaz. (Crawfordsville) 12: 132. 1887.
A. myriodonta Standley, Jour. Washington Acad. Sci. 17: 13. 1927.
A. pellucida var. *pectinata* (Donn. Sm.) Lundell, Wrightia 3: 99. 1964.

Shrubs, to 2.5 m high, sometimes trees of 7 m, the branchlets thick, apically densely glandular-puberulent and usually villous, the glandular trichomes reddish. *Leaves* large, the petioles 0.5–2.5 cm long; leaf blades obovate, oblanceolate, or oblong-elliptic, mostly 20–40 cm long and 6–12 cm wide, sometimes larger, short-acuminate apically, attenuate and decurrent basally, thin, membranaceous, at first minutely puberulent beneath, especially along the veins, and sparsely lepidote, glabrous otherwise, minutely and densely puncticulate, the margins closely and finely pectinate-dentate with short subulate teeth, the costa large and elevated beneath, the primary lateral veins slender but conspicuous, reticulate. *Inflorescences* terminal, variable in size, 3.5–20 cm long, 2–3-pinnately paniculate, densely and minutely glandular-puberulent, and with interspersed villous trichomes, mostly basally. *Flowers* 5-merous, corymbose, rose-purple, ca. 5 mm long; pedicels 4–11 mm long, papillose; sepals almost free, dextrorsely imbricate, ovate or lanceolate, 2–3 mm long, acute, acuminate, or subulate apically, usually densely punctate with orange-red glands, sometimes obscurely and sparsely punctate, papillose-puberulent, the margins erose and ciliolate; petals dextrorsely contorted, connate ca. 1.5 mm basally, 5–6 mm long, lanceolate, acuminate, minutely puberulent on the outer surface, sparsely punctate or epunctate, minutely glandular-puberulent within basally, the margins obscurely ciliolate; stamens 2–4 mm long, the filaments 0.3–0.75 mm long, attenuate-acuminate or apiculate, dorsifixed 0.1–0.2 mm above the base; ovary ellipsoid, usually black-punctate, the ovules 10 or more, in several series, immersed, the placenta ovoid, the style 2.2–5 mm long. *Fruit* depressed-ovoid, ca. 6 mm in diameter, purple-black at maturity.

Mexico, Central America, and Colombia.

CANAL ZONE: Barro Colorado Island, *Dwyer 1433* (MO), *Standley 40841* (US), *40848* (US, holotype of *A. myriodonta*). 12 mi. S of Colón, vicinity of the Río Providencia, *Blum & Tyson 2316* (MO). DARIÉN: Vicinity of Paya, Río Paya, trail between Paya and Payita, *Stern et al. 395* (MO). 1–4 mi. N of Pucro, *Duke 13024* (MO). Along the Quebrada Maskia off the Río Pucro above Purco, *Duke 13088* (LL). 3 mi. E of Santa Fé, *Tyson et al. 4702* (MO). Tumaganti, ca. 300 m, *Duke 14154* (LL). PANAMÁ: Junction of the Río Pacora and the Río Corso to headwaters of the Río Corso, rain forest, *Oliver 2383* (LL). Forested ridge parallel to the Río Sancanti, ca. 2 mi. upstream from Piria, ca. 120 m, *Duke 14387* (LL).

The flowers are quite variable in size. *Ardisia myriodonta* differs only in its marginally punctate leaves, having the typical leaves, indument, inflorescences, sepals and ovary of *A. pellucida*. The anthers are smallest in the collections from Colombia.

16. **Ardisia lewisii** Lundell, Wrightia 4: 146. 1970.

Shrubs, 1.5 m high, entirely glabrous, the branchlets slender. *Leaves* petiolate, the petioles canaliculate, marginate, 2–5 mm long; leaf blades glabrous, thin, subchartaceous, lanceolate-elliptic or oblong-elliptic, 5.5–10.5 cm long and 2.5–3.8 cm wide, acuminate apically, acutish and decurrent basally, conspicuously punctate, the margin subentire, the midvein nearly plane above, elevated beneath, the lateral veins slender, scarcely discernible. *Inflorescences* terminal, paniculate, subsessile, glabrous, corymbose-racemose; the racemes slender, subcorymbose from the base of the panicle, to 6.5 cm long, the apical ⅔ angled and inconspicuously bracteate, the bract at the base of each pedicel often subulate tipped. *Flowers* 5-merous, pedicels of the flower buds slender, to 6.5 mm long; flower buds ovoid, glabrous; sepals ovate-elliptic, ca. 1.6 mm long (in bud), conspicuously punctate; ovary glabrous, the ovules pluriseriate, numerous, the placenta ovoid.

Native to Panama.

COLÓN: Santa Rita Ridge, ca. 5.5–6 mi. E of the Transisthmian Highway, in rain forest, *Lewis et al. 5377* (LL, holotype).

A fruiting collection from Barro Colorado Island in Gatun Lake, Canal Zone, alt. 120 m, *Standley 41029* (US), appears to be referable here. The branchlets and inflorescences are minutely puberulent, the flowers are corymbose with fruiting pedicels to 9 mm long, and the globose purple-red fruit is 5 mm in diameter (dry).

Ardisia lewisii, known from incomplete material with only flower buds available, is very close to *A. bartlettii* Lundell and probably conspecific.

17. **Ardisia subcoriacea** Lundell, Wrightia 3: 193. 1966.

Shrubs, 1.5 m high, the branchlets slender to thick, terete, glabrous. *Leaves* glabrous, mostly crowded at the apices of the branchlets, the petioles (3–)6–10(–12) mm long, shallowly canaliculate; leaf blades subcoriaceous, lucid, lanceolate or elliptic, 5–13 cm long and 2.5–5 cm wide, subabruptly acuminate apically, acute or subcuneate basally, decurrent on the petiole, perpunctate, the primary lateral veins slender on both surfaces. *Inflorescences* small, terminal, bipinnately paniculate, to 4 cm long, congested, glabrous; pedicels slender, to 2 cm long. *Flowers* 5-merous, corymbose, glabrous; sepals elliptic, 4–5 mm long and 3–3.2 mm wide, black-punctate; corolla 5.5–7 mm long, with the tube ca. 2 mm long, papillate basally within, the lobes broadly ovate, punctate in lines; stamens 3–3.5 mm long, the filaments stout, 1.5–1.75 mm long, papillate below, the anthers lanceolate, ca. 2.5 mm long, dehiscent by apical pores; ovary glabrous, the ovules 14, biseriate, the placenta subglobose, apiculate, the style 4–5 mm long.

Native to Panama.

COCLÉ: El Valle de Antón, vicinity of La Mesa, ca. 1000 m, *Allen 2571* (US, holotype; F, LL, isotypes).

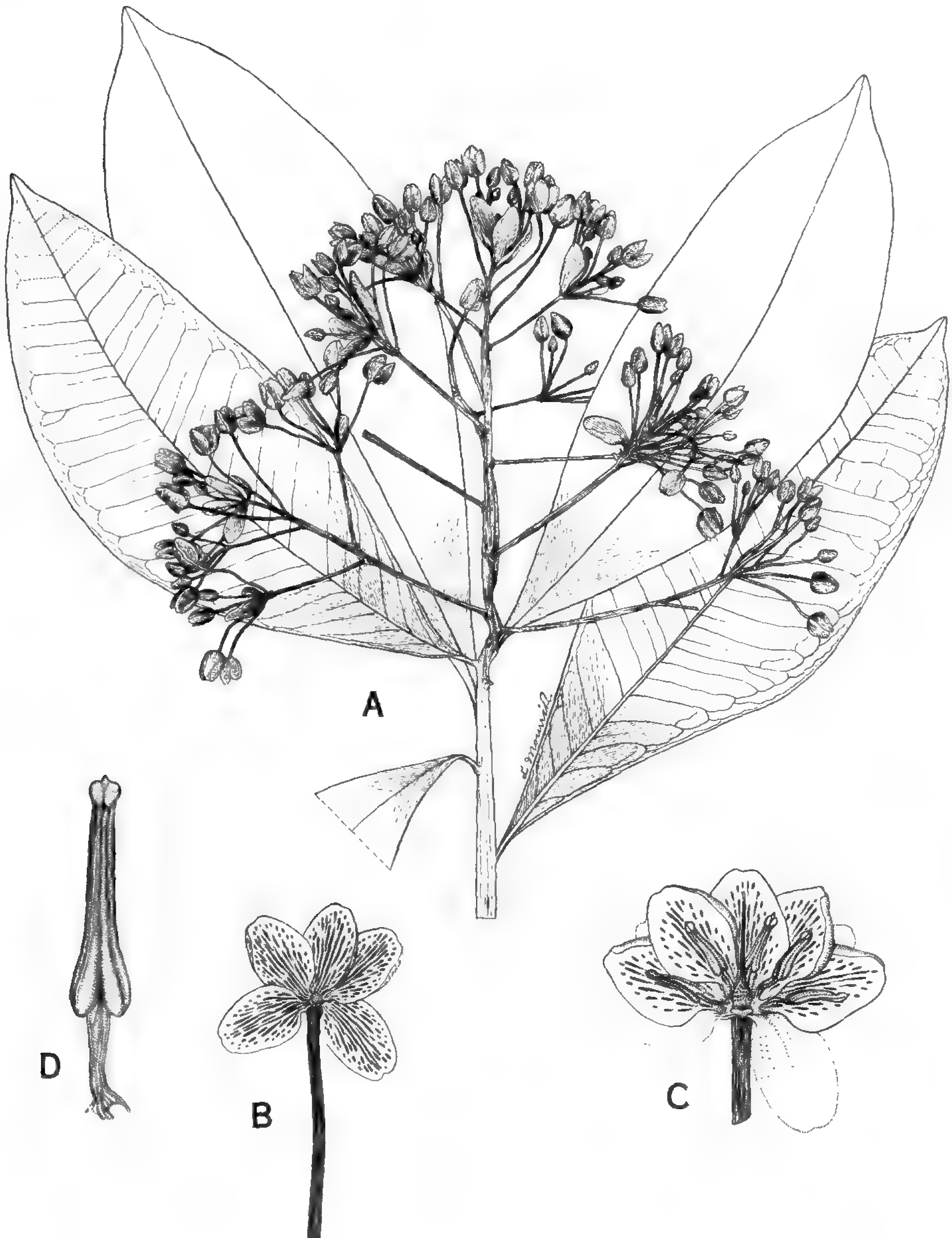


FIGURE 17. *Ardisia opegrapha* Oerst.—A. Habit (× ½).—B. Pedicel and calyx (× 1½).—C. Flower, spread out (× 2).—D. Stamen (× 7). [A, after *Allen 3561* (MO); B–D, after *Allen 2226* (F).]

18. **Ardisia wagneri** Mez, Pflanzenreich IV. 236: 79. 1902.

Shrubs, to 2 m high, the branches slender, terete, glabrous. *Leaves* glabrous, the slender petioles 7–15 mm long, canaliculate, not marginate basally; leaf blades membranaceous, elliptic or obovate-elliptic, 10–18 cm long and 4–6 cm wide, acuminate apically, acute and slightly decurrent on petiole basally, the margin usually conspicuously crenulate, the midvein slender, impressed above, elevated beneath, the primary lateral veins slender, 7–9 pairs, the venation openly reticulate, densely punctate. *Inflorescences* glabrous, terminal, small, densely bipinnately paniculate, pedunculate, to 3.5 cm long, the bracts foliaceous, thin, densely punctate, to 1 cm long, persistent; pedicels slender, 6–10 mm long. *Flowers* 5-merous, glabrous, corymbose; sepals free, membranaceous, obovate-elliptic, to 4.5 mm long, rounded, conspicuously punctate in lines; ovary glabrous, the style elongated, slender. *Fruit* globose, black-punctate.

Native to Panama.

CHIRIQUÍ: Vicinity of San Bartolomé, Península de Burica, 0–50 m, *Woodson & Schery 906* (F, MO).

The type, of which I have seen only the photograph (F, LL, US), is *Wagner 623* collected on Volcán Chiriquí.

19. **Ardisia picturata** Lundell, Wrightia 4: 164. 1971.

Shrubs, ca. 2 m high, glabrous, the branchlets slender. *Leaves* petiolate, the petioles slender, inconspicuously marginate, 5–7 mm long; leaf blades thin, membranaceous, picturate on both surfaces with conspicuous elongated black glands, elliptic or obovate-elliptic, 4.5–8 cm long and (1.6–)2–4 cm wide, subabruptly acuminate apically, acute basally, the margin entire or obscurely crenulate, the midvein shallowly impressed above and with a narrow medial ridge, conspicuous beneath, the primary lateral veins slender, 9–10 pairs, inconspicuous, the reticulation obscure. *Inflorescences* terminal, bipinnately paniculate, branched openly to the base, to 7 cm long in fruit. *Flowers* 5-merous, subcorymbose, appearing umbellate; pedicels of the immature fruit slender, 1.2–1.9 cm long; sepals thin, free almost to the base, elliptic, 6–8 mm long and 3–4.5 mm wide, rounded apically, papillate within below the middle, conspicuously black-punctate in lines, the medial darkest. *Fruit* globose, black-punctate with large elevated glands; style slender and persistent.

Native to Panama.

PANAMÁ: Cerro Campana, above Su Lin Motel, dense woodland bordering roadside, ca. 3000 ft, *Dwyer & Kirkbride 7818* (LL, holotype).

20. **Ardisia opegrapha** Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn. 1861: 126. 1861.—Fig. 17.

A. oliveri Mast., Gard. Chron. 680. 1877.
A. seibertii Standley, Ann. Missouri Bot. Gard. 24: 198. 1937.
A. skutchii Morton, Jour. Washington Acad. Sci. 27: 309. 1937.

Shrubs or small trees, the branches slender, terete, glabrous. *Leaves* petiolate or subsessile, the petioles slender to stout, canaliculate, rarely to 1.5 cm long, usually marginate; leaf blades membranaceous, elliptic-lanceolate, broadly elliptic, or oblanceolate, 12–25 cm long and 3.5–7.5 cm wide, acuminate apically, acute or attenuate basally, decurrent, entire or subentire, glabrous, densely lineolate-punctate beneath, the primary veins slender, evident on both surfaces. *Inflorescences* usually pink throughout, pinnately-paniculate, glabrous, usually shorter than the leaves, rarely reduced. *Flowers* 5-merous, corymbose, to 1 cm long, glabrous, the pedicels 1–2.3 cm long; bracts conspicuous, large, narrow, punctate, finally deciduous; sepals linear, oblong to broadly elliptic, 5–8 mm long, emarginate apically, black-punctate with large linear glands, these often forming ridges, glandular within basally; petals connate basally 2 mm, ovate-elliptic, to 9 mm long, asymmetrical, black-punctate with linear glands, glandular basally within; stamens 5–6 mm long, the filaments slender, to 1.5 mm long, glanduliferous, the anthers concolorous, thick, linear-lanceolate, to 3.2 mm long, dehiscent by flaring apical pores; ovary glabrous, the ovules 12–many, pluriseriate, the style punctate, glabrous, ca. 5 mm long, slender. *Fruit* globose, ca. 5 mm in diameter.

Panama, Costa Rica, and Nicaragua.

Types of all the taxa have been studied. Notable differences occur, particularly in the shape, size, and punctation of the sepals, but intergrading forms are present.

BOCAS DEL TORO: Vicinity of Chiriquí Lagoon, *von Wedel 1109* (MO). Water Valley, *von Wedel 661* (LL, MO), *932* (MO); vicinity of Chiriquí Lagoon, *von Wedel 1536* (LL, MO), *1769* (MO). CHIRIQUÍ: Boquete, 6 mi. N of Concepción, *Ebinger 751* (MO). COCLÉ: El Valle de Antón, 900 m, *Alston 8719* (US), ca. 750 m, *Allen 2577* (F, MO, US), *Allen 3535* (MO), *Blum et al. 2382* (MO). El Valle de Antón and vicinity, 500–700 m, *Seibert 456* (F, holotype of *A. seibertii*; MO, isotype). Vicinity of El Valle, 800–1000 m, *Allen 72* (F, MO), *Allen 786* (LL, MO). N rim of El Valle, *Allen & Alston 1846* (MICH, MO, US). El Valle de Antón, N hills, *Allen 3561* (F, MICH, MO, UC, US). Hills NE of El Valle de Antón, 2000 ft, *Lewis et al. 1803* (LL). Between Las Margaritas and El Valle, *Woodson et al. 1239* (LL, MO), *1746* (MICH, MO). PANAMÁ: Cerro Azul, *Dwyer 2190* (MICH). Cerro Campana, 2800 ft, *McDaniel 6912* (MO); cloud forest, *Lewis et al. 3038* (LL). Summit of Cerro Campana, 800–1000 m, *Allen 2226* (F, MICH). Cerro Campana, trail, Campana to Chica, 600–800 m, *Allen 2661* (LL, MICH). Cerro Trinidad, saddle on SE slope, *Kirkbride & Duke 1642* (MO). VERAGUAS: Isla de Coiba, *Dwyer 1612* (F). Vicinity of Santa Fé, forested slopes of Cerro Tuté, 2500 ft, *Allen 4404* (F, MO).

The plant is a remarkably striking one with beautiful flowers and should become a valuable ornamental in tropical gardens.

21. **Ardisia romeroi** Cuatr., Revista Acad. Colomb. Ci. Exact. 8: 319. 1951.

Shrubs, the branchlets slender, glabrous. *Leaves* with slender canaliculate petioles 3–12 mm long; leaf blades glabrous, obovate-lanceolate, or lanceolate, 5–11 cm long and 1.5–4 cm wide, acuminate apically, the acumen acutish, attenuate and acuminate basally, decurrent on the petiole, the margin crenulate-denticulate, conspicuously punctate with linear and rounded glands, the costa nearly plane above, elavated beneath, the primary veins slender. *Inflorescences* terminal, small, paniculate, shorter than the leaves, glabrous, to 3 cm long; pedicels slender, 5–14 mm long, accrescent. *Flowers* subcorymbose, 4–5-merous, 4.5 mm long; sepals ovate-elliptic, ca. 1.8 mm long, obtusish apically, the margin hyaline and minutely erose-denticulate, the dorsal area densely punctate mostly with oblongish black glands; petals elliptic-oblong, 5 mm long and 1.5 mm wide, connate basally, conspicuously punctate; filaments 1.2 mm long, adnate to the corolla basally, the anthers linear-lanceolate, tapering from the base to the apex, ca. 3 mm long, dehiscent by apical pores, apiculate, concolorous; ovary ovate, the ovules numerous, pluriseriate, the slender style 5 mm long.

Panama and Colombia.

DARIÉN: Río Tuira and Río Paca, *Duke 5025* (LL). Río Tuira 2 mi. upstream from Boca del Cupe, *Duke 5381* (MO).

The Panama collections are in young fruit, but they agree closely with the type from Colombia, *R. Romero C. 1756* (F), which is in flower.

22. **Ardisia bartlettii** Lundell, Contr. Univ. Michigan Herb. 7: 37. 1942.

Shrubs, ca. 2 m high; branchlets slender, terete, glabrous, black-punctate. *Leaves* with slender petioles, the petioles glabrous, slightly marginate, canaliculate, 5–11 mm long; leaf blades glabrous, membranaceous at first, chartaceous with age, lanceolate or oblong-lanceolate, 6–14.5 cm long and 1.8–4.3 cm wide, acuminate apically, the acumen rarely obtusish, acute basally, finely but densely black-punctate, the margin essentially entire, costa conspicuous on both surfaces, primary veins slender and scarcely discernible, ca. 20 on each side, not evident with age. *Inflorescences* terminal, sessile or short pedunculate, usually ca. half as long as the leaves. *Flowers* 5-merous, corymbose, subracemose-corymbose in fruit; bracts leafy, lanceolate, ciliolate; pedicels slender, ca. 1 cm long, slightly enlarged apically, accrescent, becoming 1.5 cm long in fruit; calyx sparsely lepidote outside, densely punctate, the sepals ovate, 2 mm long, obtuse, glandular-papillose within basally, the margin scarious, minutely erose; corolla glandular-papillose within basally, 7–8 mm long, the tube less than 2 mm long, the petals elliptic or ovate-elliptic, densely punctate, the margin scarious, obtuse or rounded apically, obliquely emarginate; filaments stout, ca. 1.2 mm long, the anthers 4 mm long, dehiscent by apical pores, concolorous; ovary ovoid, glabrous, the ovules 13–17, pluriseriate, the style 4 mm long. *Fruit* globose, inconspicuously costate, ca. 5 mm in diameter.

Native to Panama.

CANAL ZONE: Barro Colorado Island, *Shattuck 611* (F), *1098* (F, MO, US); Peña Blanca Trail, *178* (F); Snyder-Molino Trail, 300–600 m, *Ebinger 182* (MO), *Chrysler 4796* (F); along Wheeler Trail, *Bartlett & Lasser 16720* (MICH, holotype; isotypes, LL, MO); Zetek Trail, *Starry 28* (F). Fort Sherman, Atlantic coastal forest, *Hayden 95* (MO). Hills N of Frijoles, *Standley 27570* (US). Mojinga Swamp near the mouth of the Río Chagres, *Allen 865* (MO). Vicinity of Salamanca Hydrographic Station, Río Pequení, ca. 80 m, *Woodson et al. 1569* (F, MO). DARIÉN: Vicinity of Piñas, *Duke 10612* (LL). SAN BLAS: Río Mulatupo, *Kirkbride 216* (MO).

23. **Ardisia lilacina** Lundell, Wrightia 3: 198. 1966.

Shrubs, to 2.5 m high, glabrous, the branchlets slender, terete. *Leaves* with the petioles 4–9 mm long, narrowly marginate; leaf blades subchartaceous, elliptic, 7.5–15 cm long and 3.5–7 cm wide, subacuminate apically, the acumen obtuse or acutish, acute and decurrent on the petiole basally, the margin often undulate, irregularly crenulate, or subentire. *Inflorescences* glabrous, terminal, sessile or nearly so, bipinnately paniculate, to 4 cm high and 7 cm wide. *Flowers* 5-merous, lilac, corymbose; pedicels slender, 1–1.5 cm long; sepals broadly ovate, 2–2.5 mm long, punctate, ciliolate and erose; corolla ca. 8 mm long, the petals connate into a tube basally, black-punctate, glandular-papillose within basally; stamens ca. 4 mm long, the filaments stout, ca. 1.2 mm long, the anthers 3 mm long, dehiscent by apical pores; ovary glabrous, the ovules numerous, pluriseriate, the style ca. 4.5 mm long.

Panama and Venezuela.

COLÓN: Chagres, *Fendler 319* (K). Porto Bello, beach, *Dwyer 4354* (MO, holotype; LL, fragment). Río Indio de Fató, near sea level, *Pittier 4273* (F, K, US). Vicinity of Viento Frio, along beach near sea level, *Pittier 4114* (F, US). SAN BLAS: High hills back of Puerto Obaldía, 50–200 m, *Pittier 4311* (F, US).

24. **Ardisia pleurobotrya** Donn. Sm., Bot. Gaz. (Crawfordsville) 25: 148. 1898.

Trees, to 15 m high, the branchlets rufescent, densely lepidote, the internodes short. *Leaves* petiolate, the petioles 5–15 mm long, lepidote; leaf blades coriaceous, oblanceolate or oblong-elliptic, 4–12 cm long and 1.5–3.7 cm wide, subabruptly acuminate apically, the acumen usually obtusish, acute basally, sometimes attenuate, revolute and decurrent on the petiole, the margin entire, glabrous above, rufescent beneath and densely covered with scales, the lateral nerves somewhat remote, prominent only on the lower surface. *Inflorescences* axillary, lepidote, rufescent, tripinnately paniculate, to 14 cm long, the peduncles to 7 cm long; pedicels slender, 6–10 mm long. *Flowers* 5-merous, 5 mm long, umbellate; sepals lepidote dorsally, free, ovate, 2.5 mm long, coriaceous, emarginate, the margin hyaline and ciliolate; petals connate basally ca. 2 mm, broadly ovate, ca. 4 mm long, oblique and asymmetrical apically, acute; stamens inserted at the middle of the corolla tube, ca. 2.5 mm long, the filaments short, the anthers lanceolate, sharply acute, shorter than the petals, concolorous, not punctate; ovary subglobose, punctate, pluriovulate, the style 3–4 mm long. *Fruit* subglobose, to 1 cm in diameter at maturity.

Costa Rica and Panama.

CHIRIQUÍ: Cerro Pando, valley of the upper Río Chiriquí Viejo, *White 14* (MO).

25. **Ardisia pittieri** Mez, Bull. Herb. Boissier, Sér. 2. 3: 236. 1903.

A. *cutteri* Standley, Jour. Washington Acad. Sci. 17: 521. 1927.
A. *coclensis* Lundell, Ann. Missouri Bot. Gard. 28: 453. 1941.

Trees, to 6 m high; branchlets thick, lepidote at first, glabrate. *Leaves* clustered at the apices of the branchlets, the petioles short, broad, to 1.5

cm long; leaf blades subcoriaceous to rigidly coriaceous, entire, cuneate-oblanceolate, obovate-elliptic, or elliptic-oblong, 15–60 cm long and 5.6–15 cm wide, acute apically, cuneate basally, decurrent, lepidote beneath, the costa slightly impressed above, prominent beneath, the primary lateral veins fine but evident on both surfaces, reticulate. *Inflorescences* furfuraceous, glabrate in fruit, terminal, pyramidal, often subequaling the leaves. *Flowers* 5-merous, corymbose, comparatively few, large, rose-pink; pedicels lepidote, slender, to 1.8 cm long; sepals free almost to the base, broadly ovate, 3–3.5 mm long, rounded and obliquely emarginate apically, lepidote and punctate, ciliate; petals cohering basally only, lanceolate-oblong, 10–11 mm long, acute, inconspicuously punctate, reflexed at anthesis; stamens ca. 9 mm long, the filaments connate into a tube ca. 2 mm long, the anthers erect, lanceolate, acuminate, connivent basally; ovary subglobose, glabrous, the ovules numerous, pluriseriate, the style equaling the stamens. *Fruit* fleshy, globose, to 2 cm in diameter, china-red.

Costa Rica and Panama.

COCLÉ: Foot of Cerro Pilón, above El Valle de Antón, 2000 ft, *Porter et al. 4422* (MO), *4597* (LL); cloud forest in slopes of Cerro Pilón 700–900 m, *Duke 12197* (MO); summit of Cerro Pilón, ca. 2700 ft, *Dwyer et al. 4476* (LL). Vicinity of El Valle de Antón, ca. 600 m, *Allen 2056* (MICH, holotype of *A. coclensis*). Hills N of El Valle de Antón, 1000 m, *Allen 2176* (F), *2271* (F). Loma del Tigre, region N of El Valle de Antón, 1000 m, *Allen 3806* (MO).

On the basis of the unsatisfactory material now available, *Ardisia cutteri* Standl., described from Costa Rica, and *A. coclensis* Lundell are referred to *A. pittieri* Mez. It is probable that the three taxa will be recognized as separate species when adequate collections are made in the respective type localities. The connivent anthers are unique.

26. **Ardisia stenophylla** Donn. Sm., Bot. Gaz. (Crawfordsville) 24: 395. 1897.

A. oblanceolata Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 4: 249. 1929.

Shrubs or small trees, the branchlets slender, minutely lepidote at first, otherwise glabrous. *Leaves* crowded at the ends of the branchlets, the petioles minutely lepidote, 5–7 mm long; leaf blades membranaceous, glabrous, narrowly oblanceolate, 12–20 cm long and 2.5–5 cm wide, acuminate apically, attenuate basally, subcrenulate above the middle, reticulate-veined beneath, the primary lateral veins remote, ca. 10 pairs, arcuate, long-ascending, pellucid-punctate. *Inflorescences* terminal, subsessile, bipinnately paniculate, slender, to 9 cm long, fully as wide basally, minutely lepidote at first, otherwise glabrous. *Flowers* subumbellate, 5-merous; pedicels slender, 9–12 mm long; buds ca. 7 mm long, glabrous, narrowly conical; sepals membranaceous, narrowly lanceolate, 2.5–3 mm long and to 1 mm wide basally, sharply acuminate, ciliolate; petals connate basally, oblong-lanceolate, acute; anthers (in bud) 5 mm long, acute, punctate dorsally, nearly sessile (in bud); ovary and the style equaling the stamens, the ovules numerous, pluriseriate. *Fruit* globose, red, ca. 1 cm long, punctate, the seeds multicostate.

Panama and Costa Rica.

BOCAS DEL TORO: Region of Almirante, *Cooper 370* (F, holotype of *A. oblanceolata*; US, isotype). Vicinity of San San River, Davao Farm, United Fruit Co., Almirante, common in virgin rain forest, *Seibert 1572* (MO, US). Water Valley, *von Wedel 617* (F).

27. **Ardisia guianensis** (Aubl.) Mez, Urb. Symb. Ant. 2: 392. 1901.

Icacorea guianensis Aubl., Hist. Pl. Gui. Fr. 2. Suppl. 1. *t.* 368. 1775.
Ardisia acuminata Willd., Sp. Pl. 1: 1062. 1797, fide Mez, loc. cit. 1901.
A. tetrandra H. B. K., Nov. Gen. Sp. Pl. 3: 243. 1818, fide Mez, loc. cit. 1901.
A. amanuensis Lundell, Amer. Midland Naturalist 29: 485. 1943.

Shrubs or small trees, the branchlets slender, subterete, finely lepidote. *Leaves* subsessile, the petioles thick, marginate, to 5 mm long; leaf blades membranaceous to chartaceous, entire or subentire to crenulate, oblanceolate, obovate, or oblanceolate-elliptic, 6–12 cm long and 2.5–5 cm wide, abruptly short acuminate apically, subcuneate basally, decurrent, lepidote on the undersurface, the costa plane above, prominent beneath, the primary nerves conspicuous, 8–11 pairs, the veins reticulate. *Inflorescences* terminal, tripinnately paniculate, pyramidal with a rounded top, angulate, finely furfuraceous-lepidote, to 9 cm long; pedicels 3–4(–5–7) mm long. *Flowers* 4–5-merous in the same inflorescence, subcorymbose, numerous, crowded; buds slender, fusiform; calyx lepidote, the sepals thin, ovate, 1.3–1.4 mm long, rounded apically with a hyaline margin, obscurely ciliolate or erose at first, punctate with small round outer and inner oblongish orange glands, these usually dispersed; petals 4.5–5 mm long, revolute, connate ca. 1 mm basally, oblong-elliptic, lineate medially with orange glands, with small round orange glands bordering these; stamens 3–4.2 mm long, attached above the base of the corolla tube, the filaments slender, 1–1.5 mm long, the anthers often reddish-black when dry, finely rugose, slender, linear, 2.4–3.3 mm long, apiculate, dehiscent by small flaring apical pores; ovary small, glabrous, ovules small, (5–)8–12(–14) in several series, the style slender, 4.5 mm long. *Fruit* globose, 5–6 mm in diameter.

Central America, the West Indies, and northern South America.

BOCAS DEL TORO: Bar Mouth, Changuinola Valley, *Dunlap 539* (F, US). Flat Rock, region of Almirante, *Cooper 547* (F, US). Old Bank Island, vicinity of Chiriquí Lagoon, *von Wedel 2088* (MICH, holotype of *A. amanuensis*; K, LL, MO, isotypes), *2135* (LL, MO). CANAL ZONE: Cruces, *Seemann 540* (K). Empire Station, *Hayes 26* (BM, K). Obispo, *Standley 31685* (US). Vicinity of Río Cocolí, Road K-9, *Stern et al. 302* (MO, US). Río Pedro Miguel, near East Paraíso, *Standley 29948* (US). PANAMÁ: Río Chagres above Alhajuela *Pittier 3516* (US). Tributary of the Río Chagres, 5 mi. SW of Cerro Brewster, ca. 1000 ft, *Lewis et al. 3493* (LL). Río Charco-Espiritu on Tocumen highway, *Duke 5692* (LL). Along Río Juan Díaz above Juan Díaz, 30 m, *Allen 929* (F, MO, P, S, US). Río Mamoní, above Chepo, 20–25 m, *Pittier 4725* (US). Near Río Pacora, *Miller 1782* (US). Río Tapia, *Standley 28139* (US). Near Río Tapia, Juan Díaz region, *Maxon & Harvey 6713* (US). Tocumen, *Bro. Paul 251* (US). Río Tocumen, *Standley 29335, 29366* (both US), N of Chepo Road, *Hunter & Allen 247* (F, K, MO, US). San José Island, N end of island, *Erlanson 373* (MICH, US); area W of East Loop, *Johnston 389* (MO, US); SE corner of F-area, *Johnston 464* (MO, US); NW slope of Red Hill, *Johnston 93* (MO, P, US); along Río Merino, *Erlanson 545* (US); South beach, *Erlanson 50* (US). SAN BLAS: Isla de Soskatupu, *Duke 8965* (MO). Mulatuppu, *Duke 8532* (MO).

The correct name for this common species appears to be *Ardisia guianensis*. Collections from northern South America have been identified commonly as this taxon, and identical material from Panama referred to *A. compressa* H. B. K. The common denominator of the populations is *A. amanuensis*.

The illustration by Aublet of *A. guianensis* is sufficiently detailed to justify the application of this oldest name, for a majority of the collections have mostly 4-merous flowers, and the leaves range from entire to crenulate. Axillary and terminal inflorescences are found in the populations throughout the range of the taxon.

Ardisia acuminata and *A. tetrandra* are listed as synonyms on the basis of Mez's treatment. I have not seen the types, and ultimate disposition of these taxa will depend upon their study.

The ovule number in the Panama populations of *A. guianensis* is unusually variable for a species in this genus, ranging from 5–14, and the ovules vary also in size. In the type of *A. compressa* at Paris the 13–15 ovules are larger, obovoid, and to 0.2 mm long. *Ardisia compressa,* which has (4–)5-merous flowers in terminal panicles is very close to *A. guianensis*, and collections from Caripe, Venezuela, the type locality, are needed to determine the status of this taxon. *Ardisia compressa* does not occur in Panama according to my revised interpretation of the populations of this complex of species.

28. **Ardisia alstonii** Lundell, Wrightia 4: 159. 1971.—Fig. 18.

Shrubs or small trees, the branchlets slender, finely lepidote with appressed scales. *Leaves* petiolate, the petioles slender, canaliculate, narrowly marginate, 3–7 mm long, lepidote on the lower surface; leaf blades thin, membranaceous or subchartaceous, oblanceolate, obovate, or narrowly elliptic-oblong, 5–12 cm long and 2–5 cm wide, subabruptly acuminate apically, the acumen acutish, acutish basally, decurrent, the margin finely crenulate to essentially entire, lepidote at first on the lower surface, the midvein elevated beneath, the primary lateral veins slender, 12–17 pairs. *Inflorescences* small, axillary and terminal, finely furfuraceous-lepidote, pinnately paniculate, to 8 cm long, the axillary shorter. *Flowers* (4–)5-merous, subcorymbose, the pedicels slender, 4–7(–10) mm long, apparently accrescent; sepals ovate or oblong-ovate, 1–1.3 mm long, usually rounded apically, minutely erose, densely punctate with small mostly rounded orange glands, the margin hyaline; petals oblong, ca. 5 mm long, connate basally ca. 1 mm, asymmetrical and notched apically, punctate with orange glands, these mostly small and scattered; stamens ca. 4 mm long, attached in the corolla tube, the filaments slender, 1.5–2 mm long, the anthers lanceolate-linear, 2.5–3 mm long, dehiscent by apical pores, apiculate, concolorous; ovary ovoid, smooth, the ovules 20–25, pluriseriate, the sender style 5 mm long.

Native to Panama.

CHIRIQUÍ: El Boquete, 1000–1300 m, *Pittier 2976* (F, US); savannas, 4000 ft, *Davidson 842* (F, LL, US). Vicinity of El Boquete, 1000–1300 m, *Maxon 5382* (F, US); 990 m, *Bro. Maurice 748* (US). 6 mi. N of Concepción, *Ebinger 761* (MO). Denuded premontane rain forest between Pinola and Quebrada Seco on the Chiriquicito-Calderas

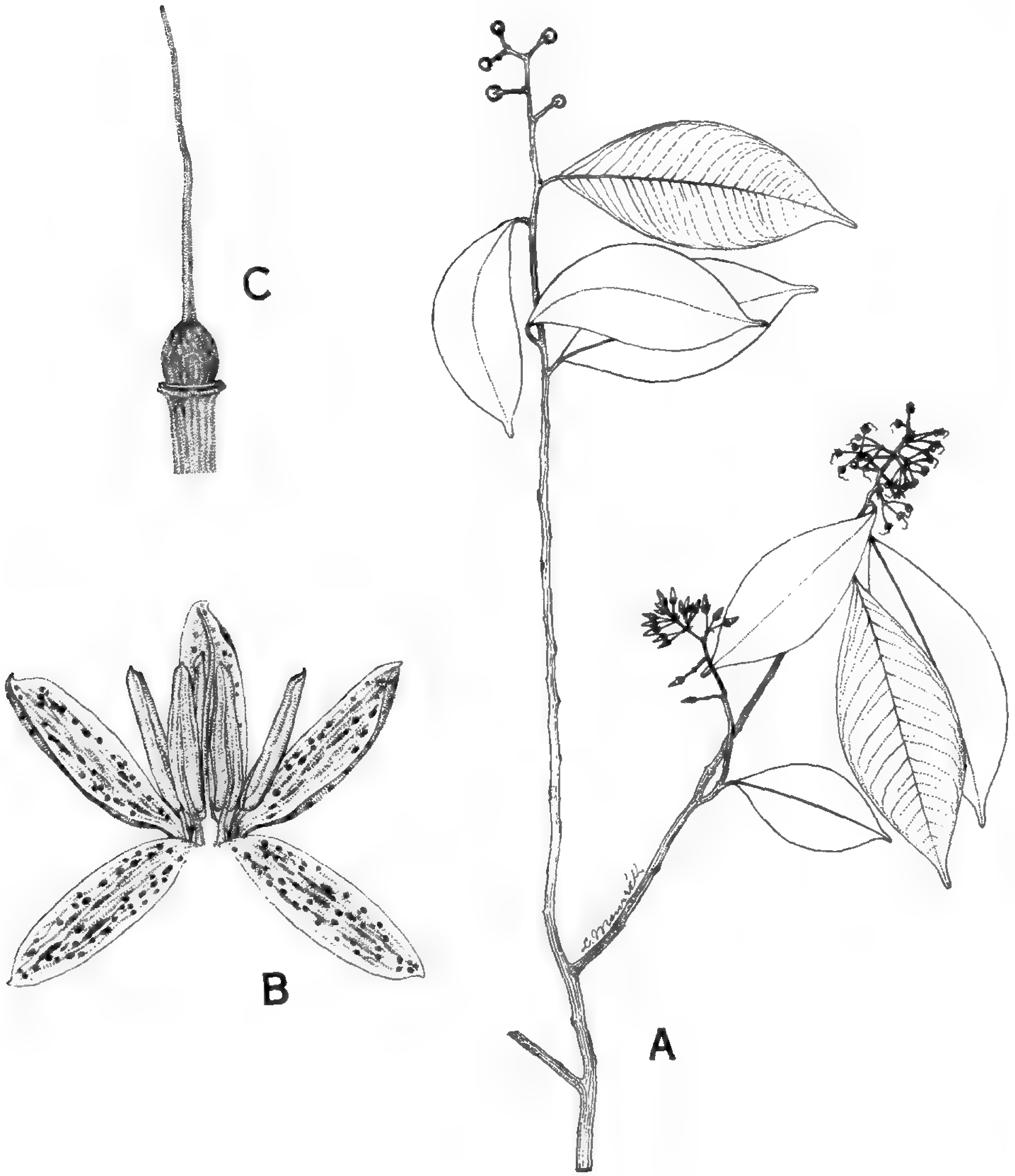


FIGURE 18. *Ardisia alstonii* Lundell.—A. Habit (ca. × ½).—B. Petals, stamens, and gynoecium (× 6).—C. Gynoecium (× 7⅓). [After *Alston & Allen 1852* (MO, isotype).]

trail, *Kirkbride & Duke 1034* (MO). COCLÉ: El Valle de Antón, *Alston 8855* (BM); N rim of El Valle, *Alston & Allen 1852* (LL, holotype; MO, US, isotypes); forest behind Club Campestre ca. 700 m, *Duke 13235* (LL). LOS SANTOS: Loma Prieta, Cerro Grande, 2400–2800 ft, *Lewis et al. 2219A* (LL). Ridge W of Río Pedregal, *Holdridge 6242* (MO).

The more numerous and smaller ovules appear to distinguish this taxon from the common *Ardisia guianensis* (Aubl.) Mez as well as from *A. compressa* H. B. K.

29. **Ardisia tenuis** Lundell, Wrightia 4: 149. 1970.

Shrubs or small trees, the branchlets slender, red-brown, densely furfuraceous. *Leaves* short petiolate, the petioles 2–6 mm long, canaliculate, furfuraceous; leaf blades membranaceous, lanceolate, 5.5–10 cm long and 1.5–3.5 cm wide, caudate-acuminate apically, rounded and acutish basally, subentire, conspicuously black-punctate, thinly lepidote beneath, glabrous above, the midvein impressed above, elevated beneath, the primary lateral veins slender, 9–10 pairs. *Inflorescences* terminal, furfuraceous, slender, leafy basally, tripinnately paniculate, to 8 cm long, the branches few, elongate; pedicels slender, 3.5–7.5 mm long. Flowers 5-merous, umbellate, ca. 3 mm long; sepals ovate, ca. 1–1.4 mm long, acute, black-punctate, sparsely furfuraceous, the margin hyaline, erose; corolla glabrous, 2.5–2.8 mm long, the petals lanceolate-elliptic, connate basally ca. 0.7 mm, black-punctate; stamens ca. 2 mm long, the filaments ca. 0.9 mm long, the anthers thick, ovate-cordate, ca. 1 mm long, apiculate; ovary ovoid, sparsely lepidote, the ovules 6 or 7, biseriate, the style slender, 2.5–3 mm long. *Fruit* globose, ca. 6 mm in diameter.

Native to Panama.

DARIÉN: Cerro Pirre, *Bristan 468* (MO); in elfin forest, 2500–4500 ft, *Duke & Elias 13762* (LL, holotype; GH, MO, US, isotypes). Ascent of Cerro Pirre, from Río Pirre S of El Real, 750–1030 ft, *Duke 5335* (MO). Cloud forest and mossy forest, Cuasi-Caná Trail between Cerro Campamiento and La Escalero to "Paramo," E of Tres Bocas, *Kirkbride & Duke 1265* (MO). Caná Cuasi Trail, Chepigana, crest, in rain forest, 5000 ft, *Terry & Terry 1568* (F).

30. **Ardisia panamensis** Lundell, Wrightia 3: 198. 1966.

A. pallidiflora Standley, Jour. Washington Acad. Sci. 17: 523. 1927, non Ridley, Jour. Asiat. Soc. Straits. 61: 27. 1912.

Shrubs, the branchlets slender, terete, lepidote, the internodes ca. 1 cm long. *Leaves* with stout petioles 5–8 mm long, deeply sulcate on the upper surface, lepidote-furfuraceous with small appressed brown scales; leaf blades narrowly obovate-elliptic, 5.5–7 cm long and 2–3 cm wide, abruptly acute to long-acuminate apically, with an acute tip, obtuse basally, entire, thick and firm, conspicuously punctate with large glands, these most evident on the young leaves, dull, the venation prominulus, paler beneath, sparsely lepidote with minute brown scales, the costa stout and prominent, the lateral nerves prominent, divaricate at a wide angle, connected by the lax reticulation of the ultimate nerves. *Inflorescences* terminal, zigzag, twice branched, lax, many-flowered. *Flowers* 5-merous, umbellate at the ends of the branches, the main rachis strongly zigzag, bearing at the base of each branch a leaflike brown-punctate petioled bract 1–1.5 cm long; bracts at the base of the pedicels 1–2 mm long, persistent, linear, brown-punctate; pedicels slender, 10–13 mm long, pale, sparsely and minutely lepidote, often strongly curved, thickened apically; flower buds 3.5 mm long, acuminate; sepals 1–1.4 mm long, rounded-ovate, obtuse, glabrous, whitish, the margins scarious, bearing on the back a dense group of small reddish glands, the margins minutely denticulate;

petals pale, ovate, 4.6 mm long, acuminate, punctate, a few large black glands, connate basally ca. 1.5 mm; stamens ca. 3.4 mm long, the filaments ca. 1.5 mm long, the anthers lanceolate, 1.5–2 mm long, long-acuminate, concolorous, longitudinally dehiscent; ovary ovoid, minutely punctate, the ovules 17–19, large, in several series, the style slender.

Native to Panama.

CHIRIQUÍ: Humid forest between Alto de las Palmas and top of Cerro de la Horqueta, 2100–2268 m, *Pittier 3255* (US, holotype).

31. **Ardisia glanduloso-marginata** Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn. 1861: 128. 1861.

Trees or shrubs, branchlets slender, furfuraceous. *Leaves* black-punctate, glabrous above, lepidote beneath at first, petiolate, the petioles canaliculate, 1–2 cm long; leaf blades firmly chartaceous, dentate, denticulate, or subentire, elliptic or oblong-elliptic, 7.5–15 cm long and 2.3–6 cm wide, subabruptly acuminate apically, the acumen usually short, sometimes subcaudate, acutish and decurrent on petiole basally, the costa impressed above, elevated beneath, the primary veins slender and widely ascending. *Inflorescences* furfuraceous, 2–3-pinnately paniculate, the rachis and branches sharply zigzag, to 23 cm wide and high. *Flowers* 5-merous, reflexed, the strongly recurved pedicels 3–8 mm long, glabrate; sepals free nearly to the base, ovate or broadly ovate, 2–2.5 mm long, ciliate, obtuse or rounded apically, black-punctate and sometimes with larger red glands apically; corolla 5.5–6 mm long, the petals connate ca. 2 mm, constricted basally into a narrow tube ca. 1 mm long, contorted, ovate-elliptic, asymmetrical, sparsely punctate with black glands; stamens inserted at the apex of the constricted corolla tube, the filaments short, ca. 1 mm long, the anthers thick, lanceolate-oblong, 2.5–3 mm long, acute, dehiscent at first by apical pores, concolorous; ovary glabrous, the ovules pluriseriate, numerous, the style 4–5 mm long, punctate. *Fruit* purple-black with scant pulp, drying 6–9 mm in diameter.

Native to Costa Rica and Panama.

CHIRIQUÍ: Vicinity of Casita Alta, Volcán de Chiriquí, *Woodson et al. 897* (A, MICH, MO). NE of El Volcán, *Tyson 813* (MO). Vicinity of Boquete, Finca Collins, *Stern et al. 2053* (MICH, MO). Boquete Region, La Pleña Blanca, *von Hagen & von Hagen 2005* (MO). Río Chiriquí Viejo valley, *G. White 67* (MICH, MO); near El Volcán, *P. White 172* (LL, MO). Boquete District, Volcán de Chiriquí, *Davidson 987* (F, MO, US). DARIÉN: Cerro Pirre, *Bristan 1236* (LL). PANAMÁ: Cerro Jefe, *Duke 8028* (MO).

The flowers of *Duke 8028* are somewhat larger than those of the type, *Oersted 25* (LL, isotype), and the leaves more conspicuously dentate and subcuspidate.

32. **Ardisia pulverulenta** Mez, Pflanzenreich IV. 236: 88. 1902.

Shrubs or small trees, the branchlets thick, covered at first with large ferruginous scales. *Leaves* subsessile, the stout marginate petioles 3–5 mm long, lepidote below; leaf blades large, membranaceous, elliptic or oblong-elliptic, 17–21 cm long and 6.5–7.5 cm wide, decurrent on the petiole basally, abruptly acuminate apically, crenulate, glabrous above except basally, densely covered beneath with large brown scales, the costa impressed above, prominent beneath, the primary lateral veins slender. *Inflorescences* terminal, paniculate, remotely branched from the base, the branches slender, densely furfuraceous; pedicels 2.5–3 mm long. *Flowers* 5-merous, furfuraceous, small, umbellate or subcorymbose; sepals narrowly ovate, 1.2 mm long, acutish, punctate with large rounded black glands; petals ovate, ca. 2.4 mm long, reflexed, connate ca. 0.5 mm basally, punctate with conspicuous orange and black glands, sparsely lepidote; stamens attached at the apex of the corolla tube, the filaments stout, ca. 0.5 mm long, the anthers ovate, 1.2 mm long, sharply apiculate, longitudinally dehiscent, conspicuously black-punctate dorsally; ovary ovoid, punctate, the ovules pluriseriate, large, 6 in the flower dissected, the placenta ovoid, apiculate, the style slender, ca. 2.5 mm long.

Native to Panama.

VERAGUAS: Locality unknown, *Seemann 1093* (K, holotype).

The description is based on the type collected in February 1848, the only material of the species known from Panama.

33. **Ardisia wedelii** Lundell, Amer. Midland Naturalist 29: 486. 1943.

Trees or shrubs, ca. 3 m high; branchlets thick, almost 1 cm in diameter apically, densely furfuraceous-lepidote, ferruginous. *Leaves* sessile, subchartaceous, drying brown, paler beneath, oblanceolate, 25–40 cm long and 9–12 cm wide, attenuate apically, acuminate, attenuate basally, rounded, sparsely and minutely lepidote above, densely furfuraceous-lepidote beneath with larger scales, the costa impressed above, prominent beneath, the primary veins 30–40 on each side, conspicuous on the undersurface. *Inflorescences* apparently terminal, long pedunculate, narrowly pinnately paniculate, to 20 cm long including a peduncle 13 cm long, less than 2 cm wide, densely furfuraceous-lepidote, the peduncle bearing 1 or 2 bracts below the middle. *Flowers* 5-merous, umbellate, the umbels subsessile; pedicels furfuraceous, to 4.5 mm long; calyx punctate, furfuraceous, the sepals ovate-triangular, ca. 1.2 mm long, acute, ciliate; corolla sparsely lepidote, ca. 4 mm long, the petals connate basally ca. 1.2 mm, oblong-lanceolate, ca. 1 mm wide, punctate; anthers ca. 1.7 mm long, acute, longitudinally dehiscent, the filaments subequaling the anthers, filiform, expanded basally; ovary ovoid, minutely punctate, ovules 12, minute, in several series, the style ca. 4 mm long.

Nicaragua and Panama.

BOCAS DEL TORO: Locality unknown, *von Webel 299* (MO, holotype; LL, fragment). Vicinity of Chiriquí Lagoon, Fish Creek lowlands, *von Wedel 2393* (LL, MO).

The flowers available are in poor condition; the corolla tubes in these are cylindrical and constricted above.

34. **Ardisia nigropunctata** Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1861: 127. *t.* 2. 1861.

A. chontalensis Mez, Pflanzenreich IV. 236: 90. 1902.

Shrubs or small trees, to 8 m high, the branchlets minutely and densely ferruginous-lepidote at first. *Leaves* with short marginate petioles to 1 cm long; leaf blades oblong-elliptic, obovate-elliptic, or oblanceolate, 15–30 cm long and 5–12 cm wide, rarely larger, usually acuminate, acute and decurrent basally, thin, the margin usually entire, sometimes denticulate, minutely and sparsely lepidote, dotted beneath with abundant black glands, the costa and the primary lateral veins elevated beneath, often slightly impressed above. *Inflorescences* terminal, many-flowered, open, large and pyramidal, often longer than the leaves, 2–4-pinnately paniculate, minutely lepidote or furfuraceous-lepidote; pedicels sparsely lepidote, 3–5 mm long. *Flowers* 5-merous, 5 mm long; calyx lepidote basally, otherwise glabrous, conspicuously black-punctate with elevated glands; sepals dextrorsely imbricate, broadly ovate, 1.6–2 mm long, acutish, minutely erose-ciliate; petals dextrorsely imbricate, connate ca. 1 mm at the lepidote base, ovate-lanceolate, slightly asymmetrical, often erose; stamens shorter than the petals, 3.75 mm long, the filaments slender, 1.5–1.75 mm long, the anthers dorsifixed ⅕ above the base, lanceolate-oblong, 2.3–2.6 mm long, with a black line dorsally, apiculate or subulate, longitudinally dehiscent; ovary ovoid, glabrous, the ovules 14–17, pluriseriate, the placenta ovoid, apiculate, the style slender, to 4.5 mm long. *Fruit* globose, 5–6 mm in diameter.

British Honduras, Guatemala, Honduras, Nicaragua, Costa Rica, and Panama.

BOCAS DEL TORO: 1.5 mi. W of Almirante, *Blum 1378* (MO). Between Buena Vista Coffee Finca and Cerro Pilón, on the Chiriquí Trail, *Kirkbride & Duke 683* (MO). Vicinity of Chiriquí Lagoon, *von Wedel 1344* (LL, MO). Laguna de Chiriquí and its neighborhood, *Hart 136* (K, US). Between Quebrada Gutierrez and E slope of La Zorra, headwaters of Río Mali, Chiriquí Trail, *Kirkbride & Duke 728* (MO). 10–15 mi. inland (S) from mouth of the Río Changuinola, *Lewis et al. 986* (LL, MO). Water Valley, *von Wedel 801, 974* (both LL, MO).

35. **Ardisia dukei** Lundell, Wrightia 4: 45. 1968.

Trees, branchlets thick, furfuraceous with small reddish-brown scales. *Leaves* large, subsessile, the marginate petioles to 7 mm long; leaf blades membranaceous, oblanceolate-elliptic, to 30 cm long and 11 cm wide, subabruptly acuminate apically, acute basally, attenuate and decurrent on the petiole, glabrous on the upper surface, appressed furfuraceous beneath. *Inflorescences* terminal, pyramidal, large, tripinnately paniculate, densely furfuraceous, ca. 30 cm high, ca. 30 cm wide basally. *Flowers* subcorymbose, 5-merous; pedicels stout, 1.5–2 mm long; sepals ovate, 1–1.3 mm long, ciliolate, glabrous, black-punctate; ovary subglobose, glabrous, the ovules 22–24, pluriseriate, the style ca. 3 mm long.

Native to Panama.

DARIÉN: Peak ca. 300 ft high between Río Balsa and Río Areti at their confluence, *Duke 8741* (MO, holotype).

36. **Ardisia scheryi** Lundell, Ann. Missouri Bot. Gard. 28: 456. 1941.

Trees, to 20 m high; branchlets reddish, stout, minutely lepidote at first. *Leaves* petiolate, the petioles narrowly winged, to 8 mm long; leaf blades entire, sparsely and minutely lepidote at first, coriaceous, drying reddish-brown, paler beneath, lanceolate or lanceolate-elliptic, 4.5–15 cm long and 1.6–5.4 cm wide, acuminate apically, acutish basally, decurrent, primary veins conspicuous on both surfaces, reticulate. *Inflorescences* terminal, pyramidal, 3–4-pinnately paniculate, to 20 cm long and 25 cm wide, sparsely lepidote, reddish-brown. *Flowers* 5-merous, pale pink, numerous, umbellate; pedicels slender, 2–3 mm long, glabrous; flower buds ovate-elliptic, ca. 3 mm long; sepals ovate, ca. 0.75 mm long and 0.6 mm wide, subentire, scarious, prominently orange-punctate; corolla 4 mm long, the petals short-connate basally ca. 0.75 mm, lanceolate-elliptic, acutish, orange-punctate, glabrous; stamens 3–3.5 mm long, the filaments attached at the base of tube, slender, 1.5 mm long, the anthers thick, oblong-elliptic, or ovate-elliptic, 1.5–2 mm long, rounded and shallowly notched apically; ovary smooth, globose, glabrous, the ovules small, numerous, pluriseriate, the style slender, 3.5 mm long.

Native to Panama.

CHIRIQUÍ: Between Alto de las Palmas and the top of Cerro de la Horqueta, 2100–2268 m, *Pittier 3267* (F, US). Vicinity of Bajo Chorro, 1900 m, *Woodson & Schery 686* (MICH, holotype; MO, isotype). Cerro Horqueta, cloud forest, 6500 ft, *von Hagen 2129* (MO).

37. **Ardisia microcalyx** Lundell, Wrightia 4: 46. 1968.—Fig. 19.

Trees, to 10 m high, the branchlets slender, at first minutely lepidote. *Leaves* small, petiolate, the petioles marginate, 6–10 mm long; leaf blades chartaceous to subcoriaceous, elliptic, sometimes lanceolate or oblanceolate, 5–10 cm long and 2.2–4.2 cm wide, subabruptly acuminate apically, base cuneate or acutish basally, at first lepidote beneath, the costa sulcate above, elevated beneath, the veins slender, obscurely reticulate. *Inflorescences* terminal, pyramidal, paniculate, 5–8 cm long, sparsely lepidote. *Flowers* 5-merous, umbellate or subcorymbose; pedicels 2–3 mm long; sepals small, ovate or ovate-oblong, ca. 0.75 mm long and 0.6 mm wide, punctate; corolla 5.5 mm long, punctate, the petals connate basally ca. 0.8 mm, narrowly oblong, 5.5 mm long and 1.6 mm wide; stamens 4.5 mm long, the filaments ca. 2 mm long, the anthers slender, lanceolate-linear, 2.3–2.8 mm long, attenuate apically, acutish; ovary ovoid, glabrous, the ovules pluriseriate, numerous, the style slender, 5 mm long.

Native to Panama.

CHIRIQUÍ: Vicinity of El Boquete, 900 m, *Allen 1013* (MO, holotype; BM, F, K, LL, MICH, P, UC, US, isotypes); Boquete (Salta), 5500 ft, *Davidson 777* (F, LL, US).

38. **Ardisia maxonii** Standley, Jour. Washington Acad. Sci. 17: 522. 1927.

A. woodsonii Lundell, Ann. Missouri Bot. Gard. 28: 457. 1941.

Shrubs or small trees, 3–11 m high, the branches stout, terete, rimose, the buds and tips lepidote, densely leafy, with short internodes. *Leaves*

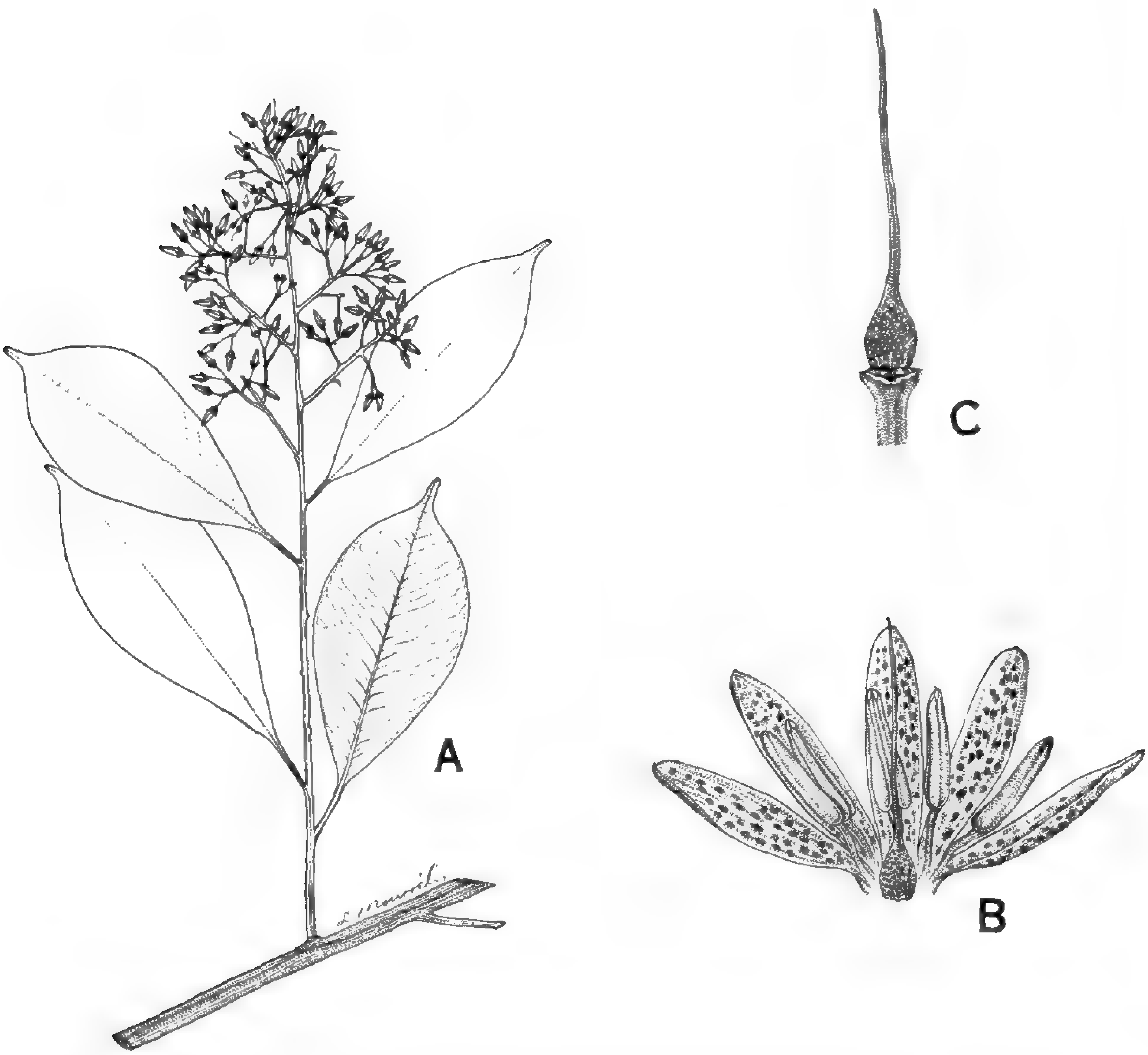


FIGURE 19. *Ardisia microcalyx* Lundell.—A. Habit (× 3/5).—B. Petals, stamens, and gynoecium (× 6).—C. Gynoecium (× 7⅕). [After *Allen 1013* (MO, holotype).]

small, the petioles stout and broad, 2–6 mm long, glabrous, often marginate to the base; leaf blades coriaceous, oblong-obovate, sometimes broadly so, or oblanceolate, 4–6(–10) cm long and 1.5–3.5 cm wide, obtuse or rounded apically, sometimes obtusely subacuminate, broadly obtuse to cuneate basally, entire, glabrous, green and dull above, beneath paler, often brownish, densely and minutely brown-punctate, the costa stout, prominent, the lateral nerves slender, prominent, ascending, connected by the irregular lax reticulation of the ultimate nerves. *Inflorescences* terminal, usually much exceeding the leaves, densely many-flowered, tripinnately paniculate, 8 cm long and wide or smaller, the rachis glabrous, angulate. *Flowers* 5-merous, large, chiefly subumbellate; bracts caducous; pedicels 4–12 mm long; sepals ovate-orbicular, 2–2.5 mm long, connate below, rounded apically, dextrorsely convolute, glabrous, entire, densely punctate with large orange glands; corolla 7–8 mm long, the petals oblong, obtuse, nearly free, symmetric, glabrous, minutely orange-punctate; stamens to 7 mm long, equaling the corolla, the filaments slender, to 3 mm long, the anthers thick, lanceolate-oblong, 3–4 mm long, acute, concolorous; ovary ovoid, smooth, glabrous, the ovules numerous, pluriseriate, the style slender, 6.5 mm long. *Fruit* globose, 6–9 mm in diameter when mature, black-purple.

Native to Panama.

CHIRIQUÍ: Alto de Cuesta, around Camp Aguacatal, E slope of Volcán de Chiriquí, 2100–2200 m, *Pittier 3117* (US). Boquete District, Volcán de Chiriquí, 7000 ft, *Davidson 874* (F, MO, US). Vicinity of Casita Alta, Volcán de Chiriquí, 1500–2000 m, *Woodson et al. 967* (LL, MO). Cerro Horqueta, rain forest, 6500 ft, *von Hagen 2021* (LL), *2067* (MO). Vicinity of Boquete, Finca Collins, 5500 ft, *Stern et al. 1137* (MO), *2008* (MICH, MO). Vicinity of Finca Lérida, 1750 m, *Woodson & Schery 230* (MICH, holotype of *A. woodsonii*; MO, isotype). Between the Río Ladrillo and Los Seguas Camp, S slope of Cerro de la Horqueta, 1200–1700 m, *Maxon 5402* (US, holotype), *Pittier 3167* (US).

39. **Ardisia subsessilifolia** Lundell, Wrightia 4: 48. 1968.

Shrubs or small trees, the branchlets thick, ridged between petioles, glabrous, the leaf buds sparsely and minutely lepidote, the plants entirely glabrous otherwise. *Leaves* sessile or subsessile, the petiole marginate and thick; leaf blades entire, coriaceous to rigidly coriaceous, oblanceolate or elliptic-obovate, 7.5–13 cm long and 3.5–5 cm wide, subabruptly short acuminate apically, the acumen acutish, acutish basally, decurrent, the costa prominent, nearly plane above, conspicuous beneath, the primary lateral veins slender but evident on both surfaces. *Inflorescences* glabrous, terminal, pyramidal, paniculate, 5–12 cm long. *Flowers* 5-merous, glabrous, corymbose; pedicels stout, 5–9 mm long; sepals ovate-oblong, 2–2.5 mm long, thick, conspicuously orange-punctate; corolla drying rugose, orange-punctate, 7 mm long, the petals oblong-elliptic, obtuse, connate ca. 2 mm basally; stamens ca. 7.5 mm long, the filaments slender, ca. 4 mm long, the anthers epunctate, thick, lanceolate, 3.2–3.5 mm long, acutish apically, dehiscent by apical pores; ovary ovoid, the ovules 22, pluriseriate, the style slender, ca. 7.5 mm long. *Fruit* globose, punctate, drying ca. 7 mm in diameter.

Native to Panama.

CHIRIQUÍ: Bajo Chorro, rain forest, 7000 ft, *Davidson 364* (F, holotype; LL, MO, US, isotypes). Cerro Horqueta, cloud forest, 6500 ft, *von Hagen & von Hagen 2040*, *2062* (both MO). Chiquero, 5500 ft, *Davidson 540* (F, MO). Palo Alto, just E of Boquete, cloud forest, 5000 ft, *Stern et al. 1029* (MO, US). Between Pinola and Quebrada Hondo toward summit on Chiriquí Trail, *Kirkbride & Duke 900* (MO).

The interpetiolar ridges are a striking feature of this species.

40. **Ardisia furfuracella** Standley, Ann. Missouri Bot. Gard. 25: 832. 1938.

Trees, the branchlets terete, at first short and slender, minutely furfuraceous with inconspicuous interpetiolar ridges. *Leaves* with canaliculate slender petioles 5–8(–15) mm long; leaf blades chartaceous, paler beneath, entire or subentire, lanceolate or oblong-lanceolate, 6–17.5 cm long and 2.5–5.5 cm wide, acuminate or sub-abruptly acuminate apically, the acumen acutish, acute basally, the costa elevated above, prominent beneath, the primary veins slender but conspicuous on both surfaces, glabrous above, obscurely and minutely lepidote beneath, the scales scarcely discernible. *Inflorescences* terminal and axillary, pyramidal, paniculate, many-flowered, lepidote to sparsely lepidote. *Flowers* 5-merous, umbellate or subcorymbose; sepals in fruit oblong-ovate, 1.2–1.4 mm long, punctate with orange glands, the margin hyaline, obtuse or rounded apically; mature flowers unknown. *Fruit* globose, 5–6 mm diameter.

Native to Panama.

CHIRIQUÍ: Trail from Bambito to Cerro Punta, 1400–2300 m, *Allen 321* (F, LL, MO, UC, US). Cerro Horqueta, 5000–6000 ft, *Dwyer & Hayden 7695* (LL). Vicinity of Finca Lérida, upper S slopes of Quebrada Velo, 5000 ft, *Allen 4739* (MO). Río Chiriquí Viejo valley, near El Volcán, *P. White 215* (GH, LL, MO); between El Volcán and Cerro Punta, *G. White 20* (F, MO), *89* (MO). Valley of the upper Río Chiriquí Viejo, 1300–1900 m, *White & White 8* (F, holotype; MO, isotype).

No flowering material is available. The species is inadequately known, but quite distinctive.

41. **Ardisia antonensis** Lundell, Wrightia 4: 44. 1968.—FIG. 20.

Trees, to 30 m high, the branchlets thick, at first minutely peradpressed lepidote. *Leaves* petiolate, the petioles thick, marginate, 7–12 mm long; leaf blades entire, coriaceous, oblanceolate, 13–22 cm long and 4.5–6.8 cm wide, acuminate apically, obtuse or acutish basally, decurrent, glabrous above, densely and minutely peradpressed lepidote beneath, the costa shallowly sulcate above, thick and elevated beneath, the primary lateral veins slender and evident on both surfaces. *Inflorescences* terminal, rarely appearing axillary, paniculate, 5–8 cm long, glabrous. *Flowers* 5-merous, orange-red punctate, glabrous, umbellate; pedicels slender, 5–7 mm long; sepals ovate, ca. 1.2 mm long, erose, punctate with orange-red glands; petals oblong, 4 mm long and 1.5 mm wide, connate ca. 1 mm basally to form a tube; stamens ca. 2.5 mm long, the filaments ca. 1 mm long, attached at the middle of the corolla tube, the anthers lanceolate-oblong, 2 mm long, subtruncate apically, concolorous, epunctate; ovary glabrous, ovoid, the ovules pluriseriate, numerous, the style slender, 4 mm long.

Native to Panama.

COCLÉ: El Valle de Antón, 1000 m, *Allen 3418* (MO, holotype; F, LL, isotypes).

This is an exceptionally large tree for the genus. The minute lepidote indument of the lower surfaces of the leaves is suggestive of *Ardisia furfuracella* Standl.

42. **Ardisia rigidifolia** Lundell, Ann. Missouri Bot. Gard. 28: 455. 1941.

Shrubs or small trees, the buds and tips of the branchlets dark reddish-brown, lepidote-furfuraceous, the branchlets thick, gnarled, with short internodes. *Leaves* clustered at the ends of the branchlets, the petioles stout, 3–5 mm long, marginate; leaf blades rigidly coriaceous, pallid, paler on the lower surface, minutely punctate, elliptic or rhomboid, 3.5–6.5 cm long and 2–3.2 cm wide, obtuse or obtusely subacuminate apically, broadly cuneate

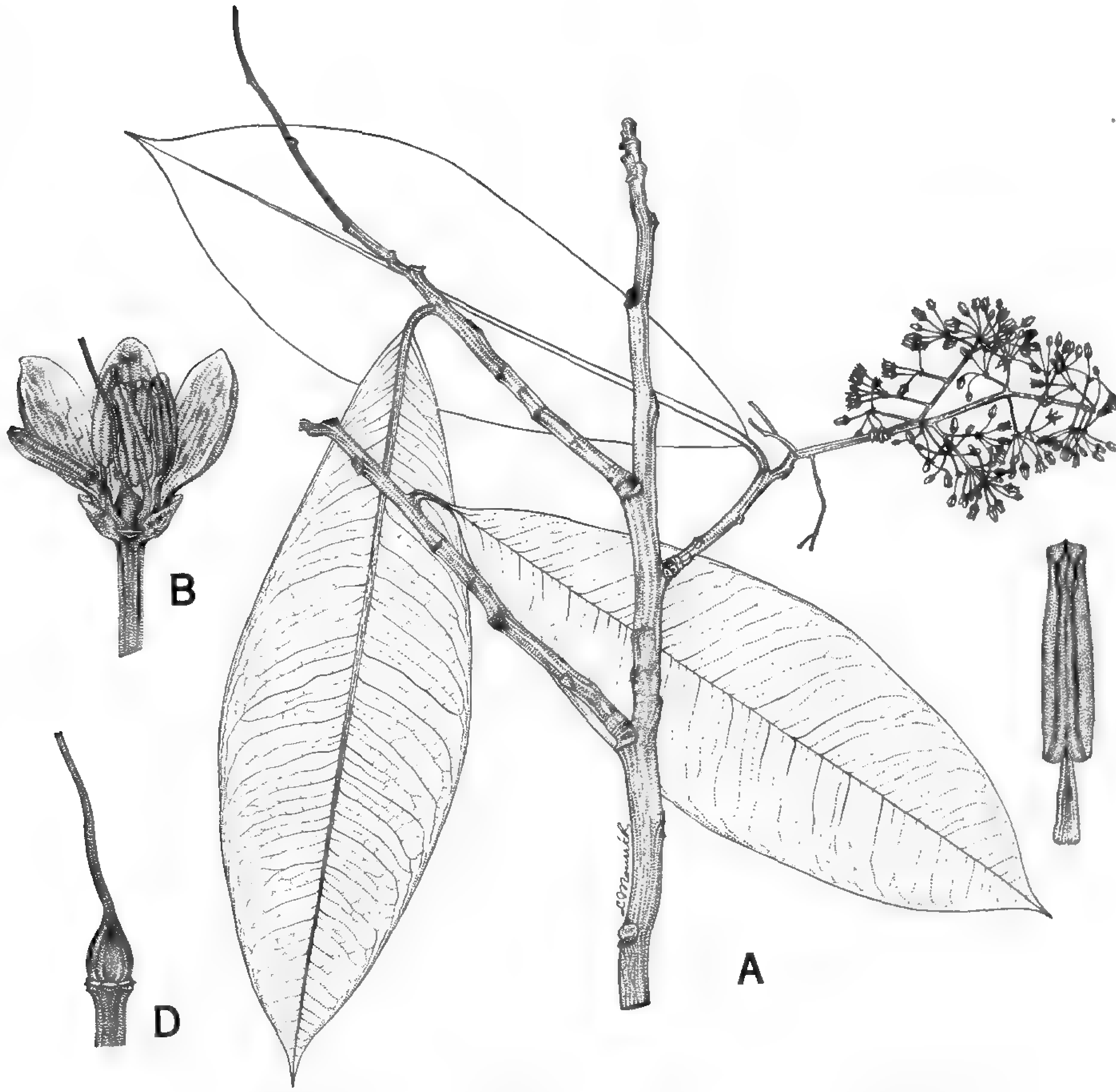


FIGURE 20. *Ardisia antonensis* Lundell.—A. Habit (× ½).—B. Flower (× 5).—C. Stamen (× 7½).—D. Gynoecium (× 6). [After *Allen 3418* (MO, holotype).]

basally, decurrent, the costa plane above, prominent beneath, the primary veins slender, prominulous beneath. *Inflorescences* terminal, tripinnately paniculate, pyramidal, to 7 cm long and wide, furfuraceous-lepidote, many-flowered. *Flowers* 5-merous, white, umbellate; bracts to 1 cm long, lepidote; pedicels 4–5 mm long; sepals ovate, 1–1.3 mm long, punctate with a few conspicuous orange-red glands, the margin scarious, minutely erose; petals oblong, 5 mm long, acutish apically, asymmetrical, punctate with a few inconspicuous glands; stamens ca. 3.5 mm long, the filaments ca. 1 mm long, thick, the anthers thick, lanceolate-oblong, ca. 3 mm long, concolorous, apically dehiscent, not apiculate; ovary glabrous, the ovules numerous, pluriseriate, the style 5.2 mm long.

Native to Panama.

COCLÉ: Vicinity of El Valle, 800–1000 m, *Allen 71* (MICH, holotype; LL, MO, isotypes).

Clearly related to *Ardisia maxonii* Standl., this species differs in its elliptic or rhomboid leaves and much smaller, less punctate flowers.

43. **Ardisia geniculata** Lundell, Ann. Missouri Bot. Gard. 28: 454. 1941.

Trees, 4–5 m high; branchlets slender, furfuraceous, ferruginous. *Leaves* petiolate, the petioles furfuraceous, canaliculate, 3–6 mm long; leaf blades narrowly elliptic or oblanceolate-elliptic, 5.8–11 cm long and 2.5–4.3 cm wide, subabruptly acuminate apically, the acumen obtusish, attenuate basally, decurrent, sparsely lepidote, entire, membranaceous, the costa plane above, prominent beneath, the primary veins 12–16 on each side, conspicuous beneath. *Inflorescences* terminal and axillary, lepidote, bipinnately paniculate, few-flowered, less than 4 cm long; pedicels slender, to 10 mm long. *Flowers* 5-merous, subumbellate, white; sepals broadly ovate, 1 mm long, prominently punctate, the margin scarious, subentire, rounded apically, obscurely emarginate laterally; petals linear-oblong, slightly wider above the middle, 5 mm long, connate 1 mm basally, acutish, orange-punctate; stamens ca. 3.5 mm long, the filaments ca. 1 mm long, the anthers linear-lanceolate, ca. 2.5 mm long, concolorous, abruptly apiculate, dehiscent by apical pores; ovary glabrous, the ovules 25, pluriseriate, the style slender, 4 mm long.

Native to Panama.

CHIRIQUÍ: Vicinity of San Bartolomé, Península de Burica, to 5 m, *Woodson & Schery 944* (MICH, holotype; LL, fragment; MO, isotype).

44. **Ardisia opaca** Lundell, Wrightia 4: 47. 1968.

Trees, to 20 m high, the branchlets slender, at first lepidote. *Leaves* sparsely lepidote at first, glabrate, short-petiolate, the petioles 3–6 mm long, marginate; leaf blades subcoriaceous, opaque, oblong or narrowly oblong-lanceolate, 4.5–10 cm long and 1.3–3.5 cm wide, subabruptly short acuminate apically, the acumen obtuse, obtusish or acute basally, the margin entire, the midvein nearly plane above, elevated beneath, the primary lateral veins slender. *Inflorescences* terminal, many-flowered, pinnately paniculate, sparsely lepidote. *Flowers* 5-merous, subcorymbose, glabrous, the pedicels 3–4 mm long; flower buds ovoid-ellipsoid, 4 mm long, obtuse; sepals thick, opaque, broadly ovate, ca. 1 mm long, obtuse, glabrous; petals opaque, smooth, subcoriaceous, short connate basally, oblong-elliptic, ca. 4 mm long (in bud); stamens ca. 4 mm long (in bud), the filaments ca. 1 mm long, the anthers thick, lanceolate, 3 mm long (in bud), attenuate apically, acutish; ovary glabrous, the ovules numerous, pluriseriate, the style ca. 5.5 mm long.

Native to Panama.

CHIRIQUÍ: Trail from Paso Ancho to Monte Lirio, upper valley of the Río Chiriquí Viejo, 1500–2000 m, *Allen 1487* (US, holotype; LL, MO, isotypes). Valley of the upper Rio Chiriquí Viejo, *White & White 85* (MO).

45. **Ardisia whitei** Lundell, Wrightia 4: 67. 1968.

Trees, branchlets terete, slender, inconspicuously appressed lepidote apically at first. *Leaves* with short stout marginate petioles 3–7 mm long; leaf blades entire, glabrous, subcoriaceous, paler beneath, elliptic or oblong-elliptic, 6–13 cm long and 3–5 cm wide, subabruptly short acuminate apically, the acumen usually obtusish, acutish basally, decurrent, the costa nearly plane above, prominent beneath, the lateral veins 15–17 pairs, slender, but evident on both surfaces. *Inflorescences* terminal, paniculate, pyramidal, to 11 cm long, many-flowered, sparsely lepidote. *Flowers* 5-merous, umbellate or subcorymbose, glabrous; pedicels erect, slender, 3–4 mm long; sepals small, ovate, 1–1.2 mm long, rounded apically, punctate with small rounded orange-red glands; petals elliptic-oblong, 5 mm long, obtuse, asymmetrical, punctate apically with small orange-red glands, connate 1.4 mm basally; stamens 5 mm long, attached ca. 0.5 mm above the base of the corolla, the filaments ca. 2 mm long, the anthers lanceolate-oblong, widest basally, 2.8–3 mm long, dehiscent by apical pores, concolorous, epunctate, minutely apiculate and truncate-rounded apically; ovary ovoid, the ovules 25–29, pluriseriate, the style to 5.5 mm long.

Native to Panama. The vernacular name is "manglia."

CHIRIQUÍ: Río Chiriquí Viejo valley, in Bambita Woods, *White 48* (LL, holotype; MO, isotype).

46. **Ardisia reflexiflora** Lundell, Wrightia 4: 164. 1971.

Trees, branchlets slender, sparsely and minutely lepidote at first, glabrate. *Leaves* sparsely lepidote at first, petiolate, the petioles marginate to the base, 3–6 mm long; leaf blades subchartaceous, drying black-brown, elliptic or rarely obovate-elliptic, 5–9.5 cm long and 2.2–4.7 cm wide, subabruptly acuminate apically, the acumen obtusish, rounded or acutish basally, decurrent, the costa slightly impressed above, elevated beneath, the primary lateral veins slender, 15–16 pairs, scarcely discernible on the upper surface. *Inflorescences* terminal, paniculate, 5.5–9 cm long and to 6 cm wide basally, minutely and sparsely lepidote. *Flowers* 5-merous, umbellate, the pedicels slender, 3–5 mm long; buds elliptic, ca. 4.7 mm long; sepals broadly ovate, 1 mm long, rounded, punctate with a few rounded glands; corolla ca. 4.5 mm long, persistent and reflexed in fruit, the petals connate ca. 1 mm basally, elliptic, with a few small round apical glands, and a few linear glands medially, obtuse-rounded apically, symmetrical; stamens 5 mm long, the filaments slender, attached to the base of the tube, ca. 2.5 mm long, the anthers thick, oblong or lanceolate-elliptic, 2–2.4 mm long, concolorous, dehiscent by apical pores, subtruncate apically; ovary globose, glabrous, the ovules ca. 30, pluriseriate, the style slender, 4 mm long.

Native to Panama.

CHIRIQUÍ: Las Lagunas, 2 mi. SW of El Volcán, 4200 ft, *Tyson 866* (MO, holotype; LL, isotype).

The reflexed corolla, persistent at the base of the developing fruits, is unusual in the genus.

47. **Ardisia obovalifolia** Lundell, Wrightia 4: 162. 1971.

Shrubs or small trees, to 8 m high, the branchlets slender, appressed-lepidote at first. *Leaves* mostly small, drying blackish, petiolate or subsessile, the petioles marginate, to 4 mm long, lepidote at first; leaf blades subcoriaceous, obovate, elliptic-obovate, or elliptic, 3–9.5 cm long and 2–5 cm wide, rounded and abruptly short acuminate apically, the acumen acutish, rounded basally, decurrent, glabrous above and often shiny, paler and glabrate beneath, conspicuously punctate, the glands especially prominent in the young leaves, the midvein rounded and slightly elevated above, prominent beneath, the lateral veins slender, obscurely reticulate. *Inflorescences* terminal, small, tripinnately paniculate, pyramidal, 4–9 cm long, lepidote at first, glabrate. *Flowers* umbellate or subcorymbose, 5-merous, the pedicels rigid, 3–6 mm long; sepals ovate, 1.4–2 mm long, rounded apically, punctate with rounded small glands, these orange and black, minutely erose; petals (in bud) 5.5 mm long, connate ca. 1 mm basally, densely punctate mostly with small rounded orange and red-black glands, the blackish glands dispersed; stamens (in bud) 3.5 mm long, the filaments 1 mm long, the anthers concolorous, lanceolate-oblong, 2.5 mm long; ovary glabrous, the ovules small, numerous, pluriseriate, the style slender, 5 mm long, recurved after anthesis. *Fruit* depressed-globose.

Native to Panama.

PANAMÁ: Cerro Jefe, *Duke 9423* (MO), 2700–3000 ft, *Tyson et al. 3340* (LL, MO); E slope, 2700 ft, *Blum & Duke 2184, 2196* (both MO); summit, 2900 ft, *Dwyer et al. 7281* (LL, holotype), *8078* (LL); 10–13 mi. beyond Goofy Lake, *Duke 8015* (MO).

The species is noteworthy for its densely punctate corolla, the glands being both orange and black.

48. **Ardisia fendleri** Lundell, Wrightia 4: 45. 1968.

Trees, the branchlets thick, at first lepidote. *Leaves* petiolate, the petioles thick, marginate, 5–10 mm long; leaf blades subchartaceous, entire or inconspicuously subentire, oblong-elliptic or elliptic, 10–20 cm long and 4.5–9.5 cm wide subabruptly short acuminate apically, the acumen acutish, smooth and glabrous above, at first sparsely appressed-furfuraceous beneath, glabrate, the costa shallowly sulcate above, elevated beneath, the primary veins slender, 15–19 pairs with intermediaries. *Inflorescences* terminal and axillary, large and open, tripinnately paniculate, to 10 cm long, sparsely lepidote. *Flowers* subcorymbose, 5-merous; pedicels 5–7 mm long; sepals ovate-elliptic, ca. 1.5 mm long, rounded apically, minutely erose, punctate; petals elliptic or oblong-elliptic, 6 mm long and 2–3 mm wide, connate basally, lineate-punctate; stamens 4–4.5 mm long, the filaments ca. 1.5 mm long, the anthers linear-oblong, ca. 3 mm long, subtruncate apically, dehiscent by apical pores; ovary subglobose, glabrous, the ovules pluriseriate, numerous, the style slender, 5.5 mm long. *Fruit* globose, 6–7 mm in diameter.

Native to Panama.

CANAL ZONE: Chagres, *Fendler 314*, Feb. 20, 1850 (K, holotype; F, K, LL, MO, P, US, isotypes); *314*, Mar. 8, 1850 (K). Barro Colorado Island, shore 1 mi. E of lab, *Woodworth & Vestal 481* (F); on shore near end of Chapman Trail, *Wilson 73* (F). COCLÉ: Cerro Pilón, El Valle Site Area WEPCOR, *Kirkbride 1046* (MO). COLÓN: María Chiquita, *Dwyer 4351* (MO).

Ardisia fendleri is very similar to *A. belizensis* Lundell, and it may prove to be conspecific.

49. **Ardisia copeyana** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 886. 1938.

Trees, branchlets stout, with interpetiolar ridges, lepidote at first, glabrate in fruit. *Leaves* with thick marginate petioles 3–10 mm long; leaf blades glabrous, coriaceous or subcoriaceous, punctate, elliptic, oblong-elliptic, or obovate-elliptic, 10.5–20 cm long and 5–9 cm wide, short acuminate apically, sometimes abruptly so, revolute basally, decurrent, acute, the margin obscurely crenulate, essentially entire, drying brownish on both surfaces, the costa thick, nearly plane above, elevated beneath, the primary lateral veins slender. *Inflorescences* terminal, pyramidal, paniculate, essentially glabrous, 4–15 cm long. *Flowers* 5-merous, subcorymbose; pedicels erect, 3–4 mm (in the type), to 8 mm long (*Allen 4023*); sepals broadly ovate, 1.5–2 mm long, rounded apically, punctate with orange glands; petals oblong-elliptic, ca. 7 mm long, connate basally ca. 1.5 mm, asymmetrical apically, inconspicuously punctate with a few orange glands, the medial lineate, the apical rounded; stamens 5 mm long, the filaments thick, ca. 2 mm long, the anthers lanceolate, 3 mm long, acute, dehiscent by small apical pores; ovary subglobose, the ovules many, the placenta pluriseriate, the style 5.5 mm long. *Fruit* globose, ca. 5 mm in diameter, densely punctate.

Costa Rica and Panama.

PANAMÁ: Cerro Campana, 800 m, *Allen 4023* (MO, P).

Stork 1592 (US, holotype; MICH, isotype) is a poor fruiting collection from El Copey, Costa Rica. It has very short fruiting pedicels, and the type is completely glabrous. *Allen 4023*, a flowering specimen, is referred to this species with some question. The pedicels of the Panama plants are longer, but the inflorescence, calyx, and leaves closely resemble those of the Costa Rican taxon. The description of the flowers is based on *Allen 4023.*

50. **Ardisia solanacea** Roxb., Pl. Coast. Coromandel 1: 27. *t. 27.* 1795.

Shrubs, 1–4.5 m high, the branchlets usually thick, glabrous. *Leaves* petiolate, the petioles to 15 mm long, usually shorter, marginate; leaf blades oblanceolate, obovate, or oblong-elliptic, 7.5–15 cm long and 2.5-6 cm wide, widely acuminate or obtusish apically, narrowed and basally acute, decurrent, chartaceous, the venation fine, sometimes conspicuously reticulate, the costa plane or nearly so above, elevated beneath. *Inflorescences* axillary (also see *A. pleurobotrya*), long-pedunculate with 1 corymb apically, few-flowered, glabrous. *Flowers* 5-merous, subcorymbose, the pedicels stout, rigid, 1–3 cm long; flowers at anthesis 7–8 mm long, the buds acute; sepals free, depressed-ovate, suborbicular or reniform, 2–3 mm long, punctate, ciliolate at first; petals connate basally, ovate-elliptic or oblong-elliptic, asymmetrical, punctate with small dispersed glands; stamens ca. 6 mm long, the filaments 1–2 mm long, the anthers lanceolate, to 5.5 mm long, conspicuously black-punctate dorsally, tapered to an acute apex; ovary glabrous, ovoid, the ovules numerous, pluriseriate, the style ca. 6 mm long.

Native to India, Malaya, and China; naturalized and cultivated in the American tropics.

CANAL ZONE: Curundu Heights, *Stimson & Gardner 5439* (MO). Fort Clayton, *Tyson & Dwyer 4469* (MO). Gatún railroad station, *Tyson 3511* (MO). Miraflores Locks area, *Tyson 1133* (MO). Summit Garden, *Dwyer 7166*, *Stimson 5362* (both MO).

INDEX OF LATIN NAMES

Numbers in **bold face** type refer to descriptions; numbers in roman type refer to synonyms; numbers with dagger (†) refer to names incidentally mentioned.

FLORA OF PANAMA[1]

BY ROBERT F. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part IX

FAMILY 165. POLEMONIACEAE

DANIEL F. AUSTIN[2]

Herbs, or less commonly shrubs, vines, or small trees, perennial or annual. *Leaves* alternate or opposite, simple or pinnately-compound; blades pinnately-veined; exstipulate. *Inflorescences* axillary or terminal, solitary or in small cymose clusters of dense heads. *Flowers* medium to large, bisexual, regular or irregular and bilabiate; sepals 5, synsepalous, regular or sometimes irregular, herbaceous or with herbaceous lobes and membranaceous sinuses, imbricate or valvate; petals 5, sympetalous, regular or rarely bilabiate, hypogynous, alternate with sepals, contorted in bud; stamens 5, epipetalous, alternate with the corolla lobes, the point of insertion varying, the anthers 2-loculed, dehiscing longitudinally; ovary superior, inserted on a basal, often 5-lobed disc, (2–)3(–4)-loculed, the placentation axile, the style terminal, simple, filiform, the stigma (2–)3(–4)-lobed. *Fruits* capsular, mostly loculicidal; seeds 1 to many, the endosperm copious and the embryo straight or slightly curved, the seed coat frequently becoming mucilaginous when wet.

A New World family with 18 genera and about 316 species. Mostly found in temperate and subtropical regions, although some genera are confined to tropical montane areas. Two genera occur in Panama: *Cobaea* and *Loeselia*.

a. Lianas with alternate, pinnately-compound leaves, the terminal leaflet modified into a tendril; flowers solitary, terminating long peduncles; corolla 15–20 mm long, regular, campanulate .... 1. *Cobaea*
aa. Shrubs with opposite, simple leaves; flowers clustered in leaf axils, peduncles short; corolla 8–10 mm long, irregular, salverform or funnelform .... 2. *Loeselia*

1. COBAEA

Cobaea Cav., Icon. Descr. Pl. 1: 11. 1791, non Necker (1790).

Rosenbergia Oersted, Vidensk. Meddel. Dansk. Naturhist. Foren. Kjøbenhavn 1856: 30. 1856.

Lianas, stems herbaceous. *Leaves* alternate, pinnately-compound, the terminal leaflet modified into a tendril, the laterals broad. *Inflorescences* solitary, axillary. *Flowers* large, regular; sepals herbaceous, divided to the base, not rupturing in age; corolla campanulate, violet, yellow, brownish-purple, or green, with oval or long-caudate lobes; stamens inserted at the corolla base, the filaments pubescent basally, the anthers dorsifixed, versatile; ovary ovoid, glabrous,

[1] Assisted by National Science Foundation Grant GB-27713 (Duncan M. Porter, principal investigator).

[2] Department of Biological Sciences, Florida Atlantic University, Boca Raton, Florida 33432.

ANN. MISSOURI BOT. GARD. 58: 355–361. 1971.

attenuate to the style. *Capsules* much longer than the persistent calyx, septicidal, 3-locular; seeds numerous, large, flat, broadly winged.

A montane rain forest genus extending from Mexico to Venezuela and continuing in the Andes from Colombia to northern Chile. The approximately 19 species are mostly known from a few localized collections. Many species are known from only the type collection.

The latest revision of the genus was published by Standley (Contr. U. S. Natl. Herb. 17: 448–458. 1914). The species proposed by Standley were, for the most part, recognized by Grant (Natural History of the Phlox Family. The Hague. 1959), but certain of these seem tenuous. A detailed study of the genus is much in order.

Material of only one species from Panama has been examined, but, due to their presence in neighboring Costa Rica and possible occurrence in Panama, three other species are included in the key.

a. Corolla lobes linear or with linear tips.
  b. Calyx lobes densely long-villose; corolla lobes ovate basally, abruptly contracted into a long linear tip .... *C. aschersoniana* (Costa Rica)
  bb. Calyx lobes glabrous or minutely pilose; corolla lobes either linear or gradually tapering from the base.
    c. Corolla yellow; calyx segments villose-ciliate .... *C. gracilis* (Costa Rica)
    cc. Corolla purple or greenish-purple; calyx segments glabrous .... 1. *C. panamensis*
aa. Corolla lobes ovate-triangular to orbicular .... *C. scandens* (Costa Rica)

1. **Cobaea panamensis** Standley, Contr. U. S. Natl. Herb. 17: 452. 1914.—FIG. 1.

Lianas, reaching 7 m in length; main stems becoming woody basally, the young stems herbaceous, glabrous. *Leaves* with subequal, narrowly oblong to oblanceolate leaflets, 4–10 cm long and 1.5–3 cm wide, abruptly acute or acuminate, oblique and rounded to subcordate basally, chartaceous, glabrous, the venation obscure on both sides; petiolules slender, 4–8 mm long, glabrous. *Inflorescences* solitary, axillary, pendulous. *Flowers* with the pedicels 15–35 cm long; sepals connate only basally, linear-lanceolate, long-attenuate, 25–30 mm long, green, glabrous; corolla purple or green with purple or purple-brown stripes, the tube campanulate, 15–20 mm long, with arcuate sinuses, puberulent without, glabrous within, the lobes ca. 6 cm long, 5–6 mm wide basally, tapering to long-attenuate tips; stamens 5, the purple filaments 9–11 cm long, much exceeding the corolla lobes, villose basally, the anthers purple, 13 mm long, versatile; ovary ovoid, glabrous, the style 10–13 cm long, glabrous, the stigmas slender, 8 mm long. *Capsules* 5–6 cm long and ca. 1.5 cm in diameter, light tan, slightly striate, ellipsoidal, acute, glabrous; seeds 2 (*Davidson* 396), oval, with yellowish wings, 2.5–3 cm long and ca. 8 mm wide.

Known to flower March through July.

CHIRIQUÍ. Bajo Chorro, Boquete district, alt. 5500 ft, *Davidson* 396 (MO, US); between El Volcán and Cerro Punta, Río Chiriquí Viejo, *White 12* (MO, US); vicinity of Finca Collins, Boquete, alt. 5800–6700 ft, *Stern et al. 2050* (MO, US); vicinity of Monte Lirio,

→

FIGURE 1. *Cobaea panamensis* Standley, portion of stem with flower (× 0.7). [After *White 12* (US).]

valley of upper Río Chiriquí Viejo, alt. 1300–1900 m, *Seibert 290* (MO); between Río Ladrillo and Los Siguas Camp, *Pittier 3270* (US).

While Grant (*op. cit.*) accepted *Cobaea gracilis* (Oerst.) Hemsl. as a species distinct from *C. panamensis*, this seems doubtful. Specimens from Costa Rica referred to *C. gracilis* (*Austin-Smith A680*; MO, US) differ from *C. panamensis* only in corolla color; both species flower in March. I have not seen the type of *C. gracilis* and therefore will not place *C. panamensis* in synonymy. A close examination of the types will probably show that these two names apply to local variants of the same species.

Cobaea aschersoniana Brand occurs in Esmeralda Province, Costa Rica. There has been some confusion concerning the origin of a supposedly mixed collection by Warscewicz (Standley, *op. cit.*), and this species may also occur in Veraguas, Panama. The types at US are not mixed and clearly belong only to *C. aschersoniana.*

The commonly cultivated *C. scandens* probably also occurs in Panama, but I have seen no collections from there. There are specimens of this species from nearby in Costa Rica (*Worthen*, 1910; MO).

2. LOESELIA

Loeselia L., Gen. Pl. ed. 5. 276. 1754.

Hoitzia Juss., Gen. Pl. 136. 1789.

Shrubs, woody-based perennials and annual herbs. *Leaves* simple, broad, with serrate or dentate margins. *Inflorescences* in cymose axillary clusters or in panicles. *Flowers* medium-sized, regular to bilabiate; sepals lightly irregular, tubular, differentiated into herbaceous lobes and membranaceous sinuses, rupturing in age; corolla salverform to funnelform, white, yellow, blue, or red; stamens inserted on the corolla tube, the filaments glabrous basally, the anthers dorsifixed, versatile; ovary ovoid, glabrous, attenuate to the style. *Capsules* about equal in length to the calyx, often enveloped by the bracts, loculicidal, 3-locular; seeds few per locule, small, flat or plump, broadly or narrowly winged.

A subtropical and tropical genus with about 9 species extending from southern Arizona to Colombia and Venezuela.

a. Leaves mostly ovate, acutely dentate; inflorescence bracts rounded-cordate, the teeth along the margins ending in points which reach 3 mm long; corolla pale yellow .... 1. *L. ciliata*

aa. Leaves laceolate to ovate, serrate; inflorescence bracts linear-lanceolate, the teeth along the margins with short points to 1 mm long; corolla purple .... 2. *L. glandulosa*

1. **Loeselia ciliata** L., Sp. Pl. 628. 1753.—Fig. 2.

L. involucrata G. Don, Gen. Syst. 4: 248. 1838.

Shrubs, becoming suffrutescent basally, to 60 cm high; stems glabrous. *Leaves* ovate, dentate, 3–5 cm long and 2–3 cm wide on the main stem, gradually re-

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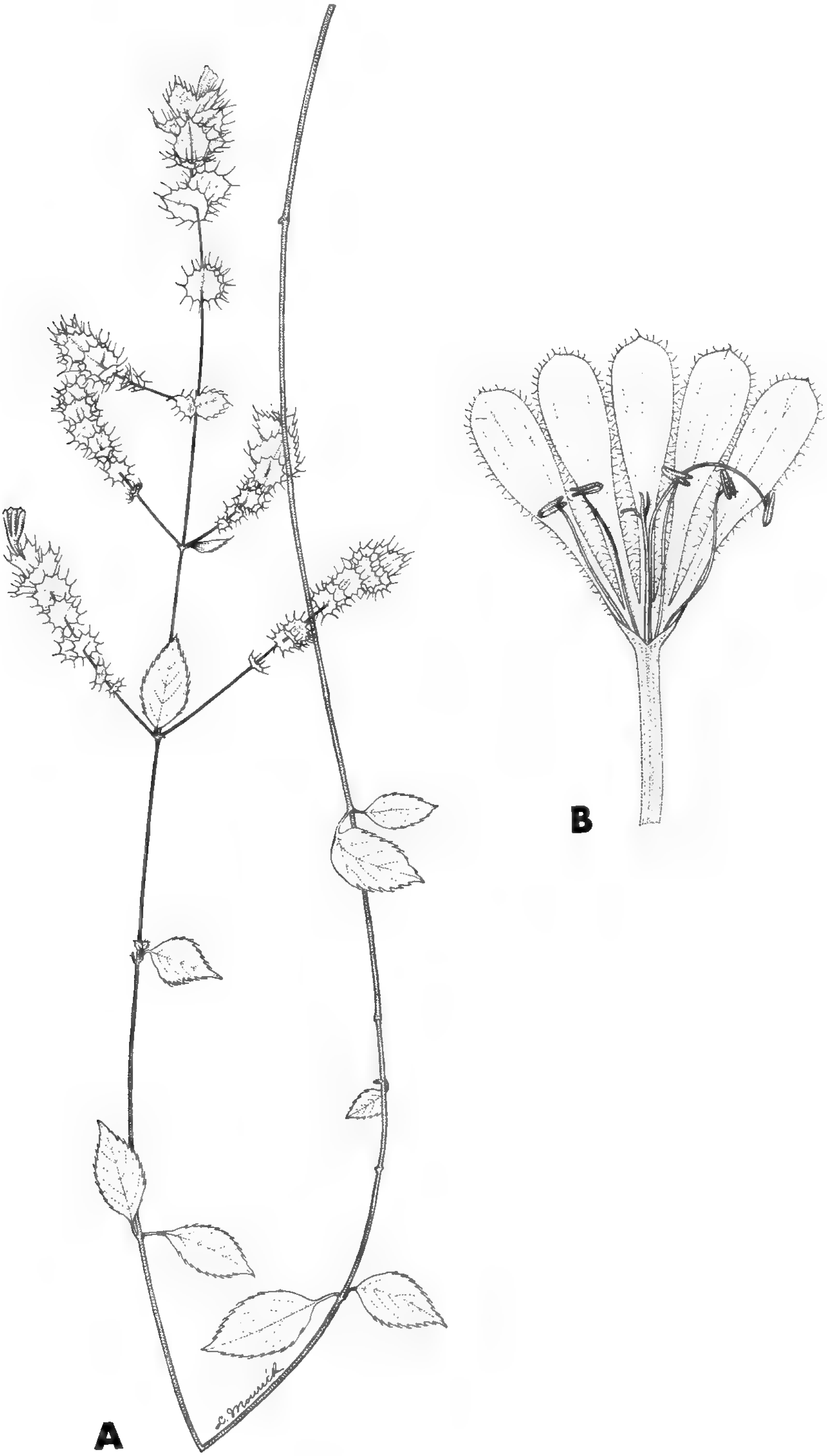
Figure 2. *Loeselia ciliata* L.—A. Habit (× 0.5).—B. Flower (× 2.5). [After *Pittier 5078* (US).]


A
B

duced and becoming bracteoid on the upper branches near the inflorescences, acute, obtuse, or rounded to subcordate, attenuate basally, membranaceous, remotely pubescent above and below, venation obscure above, prominent below; petioles slender, ca. 1 cm long including the attenuate portion, pubescent. *Inflorescences* paniculate, composed of usually solitary flowers axillary in bracts, and scattered along unbranched lateral branchlets which are 3–7 cm long. *Flowers* subsessile; sepals tubular, slightly irregular, lanceolate; corolla white to cream or yellowish, more or less salverform, 10 mm long, glabrous, the free lobes subspathulate, ca. 6 mm long; stamens 5, the white filaments ca. 10 mm long, glabrous, the anthers ca. 1 mm long, versatile; ovary ovoid, glabrous, the style 10 mm long, glabrous, the stigmas filiform, 1 mm long. *Capsules* not seen.
Known to flower December through March.

Found from Baja California, Mexico, to northwestern South America at 100–350 m altitude. The flowers are usually few on the plants from Panama, and the leaves fairly abundant. This usually will distinguish the species from *L. glandulosa*.

CANAL ZONE: Chiva-Chiva Trail, Red Tank to Pueblo Nuevo, *Piper 5744* (US); along old Las Cruces Trail, between Fort Clayton and Corozal, *Standley 29064* (US); 4 mi. S of Los Pozos, *Tyson 2655* (MO). COCLÉ: Vicinity of Olá, *Pittier 5078* (US).

2. **Loeselia glandulosa** (Cav.) G. Don, Gen. Syst. 4: 248. 1838.

Hoitzia glandulosa Cav., Icon. Pl. 4: 45. *pl. 367.* 1797.
Loeselia intermedia Loes., Bull. Herb. Boissier. 7: 567. 1899.

Shrubs, annual but often suffrutescent, to ca. 1 m high; stems pubescent. *Leaves* few on flowering plants, lanceolate to ovate, sharply serrate, 1–2.5 cm long and 0.8–1.2 cm wide, acute, attenuate, obtuse to truncate basally, chartaceous, densely pubescent above, pubescent on the veins below, venation obscure above, prominent below; petioles slender, ca. 3–4 mm long including the attenuate portion, pubescent. *Inflorescences* thyrsiform, with verticils clustered on lateral branches. *Flowers* subsessile; sepals tubular, slightly irregular, lanceolate; corolla blue to purplish, more or less salverform, ca. 8 mm long, glabrous, the free lobes subspathulate, ca. 5 mm long; stamens 5, the filaments white, ca. 6 mm long, the anthers ca. 1 mm long, versatile; ovary ovoid, glabrous, the style ca. 8 mm long, glabrous, the stigmas filiform, 0.5 mm long. *Capsules* not seen.
Known to flower January through March.

Occurring from Baja California, Mexico, to northwestern South America at 1000–1300 m altitude. The flowers on the Panamanian plants are smaller than those reported by Standley (Contr. U.S. Natl. Herb. 23: 1212. 1924) in Mexico. This species apparently occurs at higher altitudes than *L. ciliata*; the altitude and dense-clustered flowers are distinctive.

CHIRIQUÍ: Boquete, *Terry 1260* (MO, US); pastures around Boquete, *Pittier 2884* (US).

Index of Latin Names

Numbers in **bold face** type refer to descriptions; numbers in roman type refer to synonyms; numbers with dagger (†) refer to names incidentally mentioned.

FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part IX

FAMILY 178. PLANTAGINACEAE

W. G. D'ARCY[2]

Ephemeral or perennial *herbs*, rarely shrubs; some with rhizomes or a stout rootstock, a few paludal. *Leaves* estipulate, mostly alternate and in a rosette at the top of the rootstock, rarely opposite or whorled, the venation appearing parallel from the base of the expanded and often clasping petiole which sometimes merges into the blade without distinction. *Inflorescence* an axillary scape, the 1 to many flowers sessile in the axils of sepal-like bracts and aggregated into heads or spikes. *Flowers* 4-merous, mostly bisexual, in some species the plants monoecious or dioecious; sepals 3 or 4, free or nearly so, imbricate, somewhat irregular with a prominent midrib and thin to scarious margins; corolla sympetalous, the tube as long as or rarely much longer than the calyx, with 4 sepal-like lobes often much larger than the tube and sometimes strongly reflexed; stamens (2–)4, alternate with the corolla lobes and inserted below the middle of the tube, the anthers cordate to ovate, exserted on slender filaments and dehiscing longitudinally from the base; ovary superior, 2-carpelled, 1–4-loculed, the ovules 1 to many, tenuinucellate with 1 integument, placentation axile or basal, the style 1, with an elongate stigma. *Fruit* a 2- to many-seeded pyxis or an indehiscent, 1-seeded utricle; seeds with a straight or slightly curved embryo, endosperm fleshy. Pollen[3] spheroidal, ovoidal, or irregular in shape, 18–44 μ in diameter, free; pantoporate, pores 4–20, circular or irregular in shape, with or without an annulus, pore membrane sometimes present with or without granules, operculum present or not; exine & intine thin, 1–2 μ thick; structure verrucate and sculpturing reticulate or microechinate.

The family contains three genera: *Bougeria*, with one diminutive perrenial Andean species; *Littorella*, with three paludal species, two of North Temporate regions and the third from southern Chile; and *Plantago*. *Plantago* includes some 250 species of nearly cosmopolitan distribution, although it is little represented in the lowland tropics.

Two species of *Plantago* are grown in the Old World for the laxative properties of the seed coverings, and in many countries various species are of medicinal repute. In the main the Plantaginaceae has its economic import as a group of noxious weeds, although in Panama, only *P. australis* in the Boquete District is common enough to be a nuisance.

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[1] Assisted by National Science Foundation Grant GB-27713 (Duncan M. Porter, principal investigator).

[2] Washington University and Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.

[3] According to K. J. Basset & C. W. Crompton, Canad. Jour. Bot. 46: 352. 1968.

ANN. MISSOURI BOT. GARD. 58: 363–369. 1971.

Useful reference:

Pilger, R. Plantaginaceae. *In* A. Engler & L. Diels, Das Pflanzenreich 4(269). 1937.

1. PLANTAGO

Plantago L. Sp. Pl. 112. 1753.

Ephemeral or perennial *herbs*, rarely shrubs; some with rhizomes or a stout rootstock. *Leaves* mostly alternate and in a rosette mostly at the top of the rootstock, the venation appearing parallel from the base of the expanded and often clasping petiole which sometimes merges into the blade without disinction. *Inflorescence* an axillary scape, united basally with the subtending leaf, the 1 to many small flowers sessile in the axils of sepal-like bracts and aggregated into heads or spikes. *Flowers* mostly bisexual, but in some species the plants are monoecious or dioecious; sepals 4, free or nearly so, mostly imbricate, somewhat irregular with a prominent midrib and thin to scarious margins; corolla persistent, sympetalous, the tube as long as or rarely much longer than the calyx, with sepal-like lobes often larger than the tube and strongly reflexed; stamens (2–)4, the anthers exserted on slender filaments; ovary superior, 2–4-loculed, the ovules 2-many, the style 1, with an elongate, sometimes pubescent stigma. *Fruit* a 2- to many-seeded pyxis, the number of seeds often characteristic for sections or species, dehiscent near the middle or below, the basal portion remaining mostly empty on the plant and the upper portion falling with the seeds; seeds small, often with characteristic markings, the shape apparently determined by the number present in the capsule and by the shape of the cotyledons.

The genus includes some 250 species widely distributed around the world. The Mediterranean region, the Himalayas, southwestern North America, and the South American mountains have large numbers of species. With the exception of oceanic islands where there are endemic species, the genus is represented in the lowland tropics by only a few cosmopolitan weeds such as *P. major* and *P. lanceolata*, which occur in Panama. Section *Novorbis*, characterised by 2- or 3-seeded capsules, is native to the New World and includes *P. australis* in Panama.

a. Leaves lanceolate, the petiole indistinct from the blade; inflorescence a dense cylinder or head or an elongate spike; seeds 2 or 3, not flattened on one side.

  b. Inflorescence a dense cylinder or head; seeds 2, with a distinct concave depression on 1 side; dried corollas inconspicuous .... 2. *P. lanceolata*

  bb. Inflorescence an elongate spike, the flowers dense or not; seeds 3, lenticular or convex on both sides; dried corollas conspicuous as orange-brown cones on the capsules .... 1. *P. australis*

aa. Leaves rotund, distinctly narrowed into a petiole; inflorescence an elongate spike; seeds more than 8, flattened on one side .... 3. *P. major*

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FIGURE 1. *Plantago.*—A–B. *P. australis* Lam.—A. Habit (× .56).—B. Seeds in dorsal, lateral, and ventral views (× 7.7).—[After *D'Arcy 5441* (MO).]—C. *P. major* L., seeds in dorsal, lateral, and ventral views (× 11). [After *D'Arcy 5485* (MO).]


C
B
A

1. **Plantago australis** Lam., Tab. Encycl. Méth. Bot. 1: 339. 1793.—FIG. 1A–B.

Plantago hirtella Kunth *in* Humb. & Bonpl., Nov. Gen. Sp. Pl. 2: 187. 1817.
Plantago galeottiana Decne. *in* DC., Prodr. 13(1): 726. 1852.
Plantago hirtella var. *galeottiana* (Decne.) Pilg., Bot. Jahrb. Syst. 50: 274. 1913.
Plantago hirtella var. *brachypus* Pilg., *op. cit.* 279. 1913.

Persistent *herb* with a stout rhizome 1–4 cm long and tough fibrous roots. *Leaves* mostly lanceolate, broadest above the middle, narrowed gradually into the petiole, to 30 cm long, the margins entire or with small irregularly spaced teeth, the petiole forming less than half the length; pubescent with spreading whitish trichomes to 1 mm long, especially on the ribs beneath and at the top of the petiole area. *Scape* slender or stout, mostly exceeding the leaves, to 40 cm long, often curved basally, sparsely pubescent when mature, densely so when juvenile, especially near the fertile portion. *Flowers* in a dense or open spike occupying about half the scape; bracts less than one-third the length of or as long as the sepals, strongly keeled with a small hyaline margin; sepals 2–3 mm long, strongly keeled apically, the apex obtuse; corolla lobes open or (Panamanian collections) closed, narrowly deltoid, exceeding the calyx, conspicuous orange-brown when dry. *Pyxis* circumscissile about the middle, well below the sepal tips, the top covered by the closed corolla which falls with the seeds; seeds 3, olive-green, elliptical-lenticular, ca 2 mm long, shining, minutely impressed-punctate.

CHIRIQUÍ: Weed on path, E side of Cerro Pando, ca. 6000 ft, *D'Arcy 5398* (GH, MO). Very common weed, roadside above and NE of Boquete, 4500 ft, *D'Arcy 5441* (C, GH, MO, SCZ). Between Boquete and Monte, *Croat & Porter 15616, 15617* (both MO). Partly disturbed forest of cloud-forest type, Palo Alto, just E of Boquete, 5000 ft *Stern et al. 1008* (MO, US).

This tropical American species has been commonly known as *Plantago hirtella*, but examination of the appropriate types by K. Rahn, University of Copenhagen (personal communication), has shown *P. australis* to be the correct name.

2. **Plantago lanceolata** L., Sp. Pl. 113. 1753.—FIG. 2.

Persistent *herb* with a short, inconspicuous rhizome, the roots tough and appearing fibrous. *Leaves* numerous, lanceolate, to 30 cm long, gradually narrowed into the petiole, strongly ribbed with usually 5 parallel veins, glabrous when mature except for the ribs beneath and a dense tuft of whitish hairs at the base of the petiole. *Scape* slender, longer than leaves, glabrous or pubescent. *Flowers* in a dense, capitate, globose, or cylindrical spike, the lowermost bracts enlarged to form an involucre, flowering proceeding from the bottom upwards giving the spike a very different appearance at different stages; bracts in the inflorescence cucullate, with a light green midrib and hyaline, often erose margins, broadly ovate with an elongate stipe, 4–7 mm long; sepals 3–3.5 mm long, erose-margined, emarginate apically; corolla lobes 2 mm long; anthers

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FIGURE 2. *Plantago lanceolata* L.—A. Habit (× .5).—B. Seeds in dorsal, lateral, and ventral views (× 6.5). [After *D'Arcy 5766*, Missouri (MO).]


B
A

exserted 4–5 mm, elongate with a cordate base; stigma exserted ca. 3 mm. *Pyxis*[4] 3 mm long, ellipsoid, circumscissile near the base; seeds 1–2, elliptical, shining, bright brown, the dorsum with a bright yellow stripe, convex, the hilum face cymbiform-concave.

Plantago lanceolata is presumed to be introduced into Panama and to have originated in Europe. It is now almost worldwide in distribution.

CHIRIQUÍ: Second growth, cultivated areas, and roadsides, vicinity of Boquete to 3 miles N, 3300–4200 ft, *Lewis et al. 643* (MO).

3. **Plantago major** L., Sp. Pl. 112. 1753.—FIG. 1C.

Ephemeral or persistent glabrate *herb* 10–50 cm high at anthesis, developing a short rhizome, but the roots appearing mainly fibrous and shallow. *Leaves* mostly glabrous, except for a tuft of long trichomes at the base of the petiole, green or with some purplish in the petiole, to 50 cm long overall, ovate, elliptic, or reniform, to 20 cm wide, entire or with denticulate margins and narrowed into a ribbon-like or v-shaped petiole which forms about half the length, major veins 3–8 arising at the base of the petiole and forming an elliptical pattern on the blade, in living material the lamina often displaying a wrinkled or crisped appearance. *Scape* longer or shorter than the leaves, fertile in the upper half, the lower portion terete or with longitudinal grooves, glabrate or with a few scattered trichomes. *Flowers* in an elongate spike, congested or somewhat dispersed along the axis, bisexual; bracts about as long as the sepals, with a slender green keel and whitish margins; sepals almost free, elliptic to rotund, 1.5–2.5 mm long with a prominent green keel; corolla-lobes much reduced, to 1 mm long; anthers small, exserted 1–2 mm; stigma short-pilose, exserted 1–2 mm. *Pyxis* 2–3 mm long, slightly larger on larger plants, circumscissile below the middle at about the top of the sepals, the top hemispherical to elliptical, falling with most of the seeds; seeds 9–25 (mostly 14–18 in Panamanian material) 0.8–1.1 mm long, slightly angular but essentially flat on at least one side and not concave, reddish-brown to blackish, the surface with waves of fine, dark tuberculae.

Much of the material of this species from Old World temperate regions has fewer and slightly larger seeds and more conical capsules than in Panama. However, since in assigning the dozens of infraspecific names in this species, workers have given primary attention to the conditon of the leaves or teratological inflorescences, it is not feasable at present to give formal taxonomic recognition to the Panamanian distinctions. These differences from the European plants are present in all the tropical American material seen.

Plantago major is dispersed in most regions of the world and is one of the few species in the genus which occurs in the lowland humid tropics. In the mountains of Chiriquí it grows in wet parts of cultivated areas, where it grows to large size (leaves and scapes 25–50 cm long). Although not plentiful else-

[4] Panamanian material seen is without fruit. Pyxis and seed characters are taken from Pilger, *op. cit.*

where in the country, it may be expected in any locality subject to frequent disturbance.

CANAL ZONE: Cultivated, Curundu, at house #2114, *Tyson 3468* (MO, SCZ). *D'Arcy & Tyson 5485* (MO). CHIRIQUÍ: Along trails, vicinity of Bajo Mona and Quebrada Chiquero, 1500 m, *Woodson & Schery 527a* (MO). Moist roadside ditch in sun, Bambito, 1 mi. SW Cerro Punta, 5600 ft, *Tyson 5616* (MO, SCZ). Street weed above and NE of Boquete, 4500 ft, *D'Arcy 5444, 5445* (both MO). Second growth, cultivated areas, and roadsides, from Boquete to 3 mi. N, 3300–4500 ft, *Lewis et al. 632* (MO). Cerro Punta, ca. 7000 ft, *Blum et al. 2408* (MO, SCZ). In swampy meadows, Finca Lérida to Boquete, ca. 1300–1700 m, *Woodson et al. 1152* (MO). Large plant in low part of vegetable field, Nueva Suisa, 6000 ft, *D'Arcy 5337* (C, GH, MO). HERRERA: Road from La Avena to outskirts of Pesé, ca. 200 ft, *Burch et al. 1287* (MO). WITHOUT LOCALITY: "Llanten," weed along trail, *Duke et al. 13619* (SCZ).

In Central Panama, *Plantago major* is occasionally cultivated as an urban medicinal plant. According to the label on *Tyson 3468*, it was (1966) "said to be brought from Ecuador where it was obtained from Indians; tea from leaves used for kidney infection." The label on *D'Arcy & Tyson 5485* records, "Cultivated by Chinese market gardeners for sale as nursery plants to be grown by Panamanians for medicinal purposes."

While most Panamanian collections are glabrate, *D'Arcy 5445* is pilose on the undersides of the petiole and major veins and on the young scapes. *D'Arcy 5444*, which was growing within a few inches of this collection, is glabrate except for a pilose young scape. Both of these specimens were growing in a weedy field where *Plantago australis* was plentiful, and the pubescence was reminiscent of neighboring *P. australis* plants. Both of these two collections have the characteristic stalked leaves of *P. major* and their ovaries have many ovules.

Index of Latin Names

Numbers in **bold face** type refer to descriptions; numbers in roman type refer to synonyms; numbers with dagger (†) refer to names incidentally mentioned.

PREPARATION OF MANUSCRIPT

The ANNALS publishes original manuscripts in systematic botany and related fields. There is a charge of $25 per printed page to help defray costs of publication. Authors are asked to follow the suggestions below in order to expedite editing and publication. If an author feels that his manuscript presents special problems, he should write the editor concerning the best way to handle these before submitting the manuscript.

Manuscripts must be typewritten on one side of substantial weight paper, 8½ × 11 in. The manuscript should have wide margins and be double spaced throughout, including the abstract, footnotes, legends, tables, lists of specimens, and the bibliography. Tables should be typed separately and placed at the end of the text. Authors should indicate in the margins the approximate places for illustrations and tables. Submission of the original and one carbon or xerographic copy of the manuscript is desirable, and the author should also retain a copy of the final, typed draft.

Acknowledgements to granting agencies, herbaria, illustrators, and technical assistants may be conveniently placed as a footnote on page one. The author's full mailing address should appear as a second footnote.

An abstract must accompany each paper other than "Notes." The abstract should succinctly summarize the findings and conclusions of the paper and should be completely comprehensible itself.

A brief Latin diagnosis for each new taxon is preferred to a complete Latin description. A complete description should be given in English.

The citation of specimens should be concise. Geographic names are put in order of decreasing political magnitude. Only the barest essential data concerning each specific locality should be given. Collectors are cited by family name and collection number. If there is no collection number, the year of collection should be given. Herbaria are designated according to the current edition of *Index Herbariorum.*

Abbreviations should be checked for consistency and to make sure they are unambiguous. Periods are used after all abbreviations except metric measures, compass directions, and herbarium designations.

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37