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THE VEGETATION OF THE SERRANÍA DE MACUIRA, GUAJIRA, COLOMBIA: A CONTRAST OF ARID LOWLANDS AND AN ISOLATED CLOUD FOREST

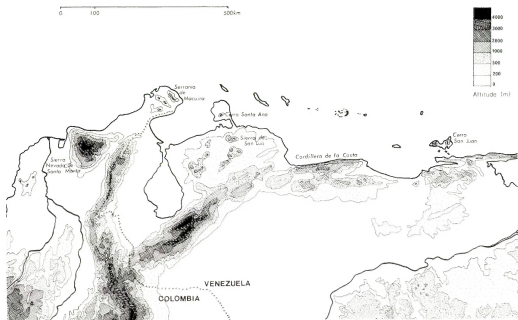
ANDREW M. SUGDEN

IN THE Northeast Trade-Wind Belt on the Caribbean coast of South America, there are a number of small, isolated mountains and ranges of hills that are encompassed by arid lowlands and yet support humid vegetation on their upper slopes and summits. Notable among these are Cerro San Juan,¹ on Isla Margarita, Edo. Nueva Esparta, Venezuela (Johnston, 1909); Cerro Santa Ana, on the Península de Paraguaná, Edo. Falcón, Venezuela (Tamayo, 1941); and the Serranía de Macuira, at the northeastern extremity of the peninsula of Guajira, Colombia (MAP 1). These mountains are geologically distinct from the Andes and the Venezuelan Cordillera de la Costa and are less than 1000 m high.

The summit vegetation of these hills is characterized by its low canopy, generally not exceeding 10 m; its gnarled, stunted trees with coriaceous leaves; and an abundance of vascular epiphytes. Rainfall is more or less restricted to a two-month season, and the vegetation depends upon daily orographic cloud cover resulting from the condensation of water vapor as the air is forced rapidly upward over the mountains by the strong winds. Precipitation is due to interception of wind-borne suspended water droplets by the vegetation and continues throughout the nine- or ten-month dry season prevailing in the surrounding lowlands, where the annual rainfall is less than 1000 mm.

The dependence of these forests on cloud interception (rather than rainfall) and their low altitude combine to produce a very remarkable circumstance. Cloud forests, which can be broadly defined as any montane forests frequently enshrouded by clouds and fog, are generally associated with higher elevations (> 1500 m), particularly in the Andes, and consequently with

¹Presently called Cerro Copey.



MAP 1. Caribbean Colombia and Venezuela.

lower temperatures. Where they do occur at lower altitudes (< 1500 m)—for instance, on the mountains east of the Canal Zone in Panama (Myers, 1969), the Northern Range in Trinidad (Beard, 1946), and the Luquillo Mountains, Puerto Rico (Howard, 1968)—they are surrounded by moist or semimoist lower montane and lowland rain forests rather than by very dry zones. In most places cloud interception is not a primary source of water (Kerfoot, 1968; Rutter, 1975); rather, it has the secondary although important effect of maintaining high humidity during periods of negligible rainfall, thus ensuring the survival of the abundant epiphytes that are almost diagnostic of cloud forest (Walter, 1973; Grubb, 1977; Sugden & Robins, 1979). By contrast, on the low coastal mountains on the Caribbean coasts of Colombia and Venezuela, cloud cover sustains "islands" of moist evergreen forest in the midst of highly seasonal vegetation zones. This paper concerns the summit vegetation of the Serranía de Macuira, the most western of these "islands."

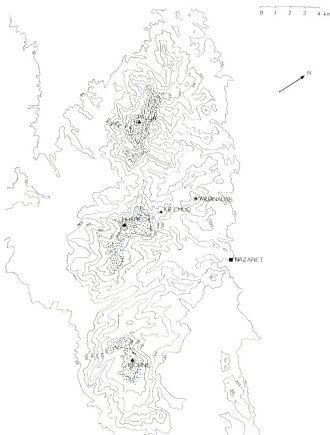
GEOGRAPHY AND GEOLOGY

The peninsula of Guajira is the northernmost extension of the South American continent (MAP 2). It is bounded by the Caribbean Sea to the north and east, the Gulf of Venezuela to the southeast and south, the Montes de Oca and the Sierra de Perijá to the southwest, and the Sierra Nevada de Santa Marta to the west. Except for a strip of the southeastern coast, which is Venezuelan territory, the peninsula lies within the borders of Colombia. It is as yet a largely undeveloped region because of its aridity and the scarcity of fresh water. Indians of the Guajiro tribe are the almost exclusive inhabitants of the peninsula. Previously nomadic pastoralists, they are now more sedentary as a result of improved communications, profitable commercial enterprises, and more reliable water supplies due to the advent of wind-pumps.



MAP 2. The Guajira Peninsula, Colombia (contours in meters).

Guajira is predominantly flat, rising only a few meters above sea level, and is covered by Quaternary sand deposits. The flat plains are interrupted in the Alta Guajira (the bulging northeastern end of the peninsula) by three ranges of hills: the Serranía de Cocinas, the Serranía de Jarara, and the Serranía de Macuira (MAP 2). The Serranía de Macuira is the highest of the



MAP 3. The Serranía de Macuira. Stippled areas represent approximate extent of Cloud Forest (contours in meters).

three, attaining a maximum elevation of 865 m. It was uplifted during the Late Cretaceous and consists mainly of metamorphic micaceous schists and granodiorites (Macdonald, 1964). Cretaceous limestones cap some of the outlying hills on the northeastern flanks of the range. The Serranía de Macuira is about 30 km long and 10 km across at its widest point, with the long axis lying northeast to southwest (MAP 3).

The slopes of the Serranía de Macuira are characteristically very steep. The highest peaks, Jiborne (735 m), Huarech (853 m), and Palua (865 m), are separated from each other by several kilometers of deeply dissected terrain (MAP 3). In the immediate vicinity of these peaks, the ground is more finely divided into a labyrinth of miniature valleys that run in a bewildering variety of directions and eventually flow together to descend into the deep valleys leading to the surrounding plains. The wide watercourses that flow from the Serranía are dry for most of the year, becoming impassable torrents several meters deep during and immediately after the brief rains. On the northeastern flank the slopes are largely covered with deposits of sand up to 100 m deep, borne from the surrounding desert by the prevailing northeasterly winds (Chaves, 1953; Macdonald, 1964).

CLIMATE

The peninsula lies entirely within the anomalous South Caribbean Dry Zone, which extends from Trinidad westward as far as Cartagena, Colombia (MAP 4). The zone includes all parts of the coastal region where annual rainfall is less than 1000 mm (Lahey, 1958; Snow, 1976). The aridity of Guajira is caused by the combination of persistent northeasterly winds and a relatively cool sea surrounding the peninsula (Chaves, 1953). The coolness of the sea is due to upwelling of cold water from the depths to the north and east (Snow, 1976). The atmospheric humidity is too low for cloud formation, except where the airstream is forced up by the steep slopes of the Serranía de Macuira. Since the wind velocity is high and the clouds are rapidly formed on the windward side of the hills and equally rapidly dissipated on the lee-



MAP 4. Southern limit of South Caribbean Dry Zone (adapted from Lahey (1958) and Snow (1976)).

ward side, rainfall is a rare event. From mid-September to mid-November, however, the Trade-Wind Belt is at its maximum northern displacement and the peninsula is embraced by the Equatorial Zone of atmospheric convergence. During this season the winds are mostly southwesterly, humid, and moderate; there is extensive cloud formation and considerable precipitation over the entire peninsula (FIGURE 1), transforming large tracts of land into impassable quagmires. The mean annual precipitation in the lowlands is 355 mm and is quite variable; a total of 100 mm fell in 1941, followed by 680 mm in 1942 (Chaves, 1953). The mean monthly temperature is 28°C and varies little throughout the year. Absolute minima and maxima recorded by Chaves (1953) were 14 and 40°C , respectively.

There are virtually no climatic records from the upper slopes of the Serranía de Macuira. The few data presented by Sugden and Robins (1979) suggest a temperature lapse rate of ca. 1°C per 100 m, with a mean tem-

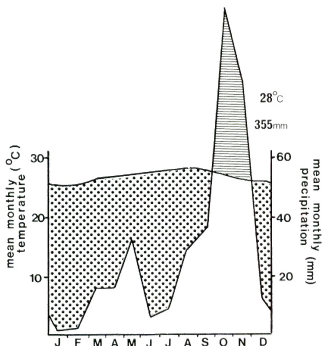


FIGURE 1. Climatic diagram for Guajira, drawn from the data of Chaves (1953).

perature of ca. 22.5° C at 500 m. The important point is that, according to my experience and that of reliable local informants, rainfall occurs on the upper slopes only when also occurring in the surrounding lowlands, although it is not known whether the quantity differs. Otherwise, the only precipitation is through cloud interception by the vegetation.

Small, fair-weather cumulus and lenticular clouds are present over the Serranía de Macuira during the day, but they rarely envelop the peaks. During early evening, however, nimbostratus develops on the windward side of the hills, often some kilometers toward the coast, and by sunset on most days the slopes above 600 m are cloaked in a thick layer of low cloud. The cloud base is always lower on the windward side of the hills, and at dawn it is often down to 350 m. TABLE 1 shows the results of observations made during March, April, and May, 1977, of the cloud cover on two prominent (565 and 710 m high) peaks. If it is assumed that the clouds do not disperse during the night and reform by dawn (an assumption that is supported by the experience of a month of soaking nights in a camp at 600 m), it can be concluded that the clouds remain for at least 12.5 hours at 550 m on 77 percent of the nights observed, and for at least 12.5 hours at 700 m on 95 percent of nights. The gaps in the records in TABLE 1 are due to nights when the clouds descended after dark; on most such occasions, however, clouds were present on the slopes at dawn the following day—only twice were they entirely absent. The highest peaks, Palua and Huarech, were occasionally observed to remain in cloud for up to 36 hours.

VEGETATION

The dry vegetation types of Guajira have been described by Espinal and Montenegro (1963) and by Rieger (1976). Espinal and Montenegro, using the Holdridge Life Zone system of classification, divided the vegetation of the peninsula into two main zones: an inland zone of Tropical Thorn Woodland (Monte Espinoso Tropical), extending from the base of the peninsula and encompassing the three serranías; and a coastal zone of drier Desert Scrub (Maleza Desertica). In their ecological map of the region, they depicted a small zone of Very Dry Tropical Forest (Bosque Muy Seco Tropical) on the slopes of the Serranía de Macuira and the northeastern flanks of the Serranía de Jarara, and a zone of Subtropical Humid Forest (Bosque Húmedo Subtropical) on the summits of the Serranía de Macuira (TABLE 2).

Rieger (1976), in a more detailed analysis using Braun-Blanquet phytosociological techniques, divided the dry vegetation of the peninsula into twenty associations falling into six major groups. In a transect across Jiborne, the southernmost high peak of the Serranía de Macuira, he recognized seven associations (TABLE 2).

My view of the vegetation is somewhat different in its details from the descriptions of these authors, partly because I had the opportunity to spend more time exploring the Serranía. Qualitative observations made during July, August, and September of 1975 and March, April, May, July, and August

TABLE 1. Period of cloud cover* on consecutive nights at different altitudes on the Serranía de Macuira.

DATE	ALTITUDE		DIFFERENCE
	550 m	700 m	
March 22/23	14.5	18.0	3.5
	12.5	14.0	1.5
	13.0	14.5	1.5
	13.0	16.0	3.0
	17.0	19.0	2.0
	13.0	15.5	2.5
	—	14.0	—
	12.5	15.0	2.5
	14.0	15.5	1.5
	14.0	15.5	1.5
	15.5	17.0	1.5
	—	14.5	—
	—	14.0	—
	15.0	20.0	5.0
April 3/4	14.5	17.0	2.5
April 6/7	13.0	14.5	1.5
	13.0	14.5	1.5
	15.0	19.0	4.0
	15.0	16.5	1.5
	—	15.0	—
	15.0	19.0	4.0
	14.5	18.0	3.5
	14.0	17.0	3.0
	16.0	18.0	2.0
	16.0	17.5	1.5
	14.5	16.5	2.0
	—	14.5	—
	13.5	15.0	1.5
	13.0	14.5	1.5
	14.0	18.0	4.0
	—	14.0	—
	12.5	14.5	2.0
	—	15.5	—
	13.5	16.0	2.5
	13.0	15.0	2.0
	13.0	15.0	2.0
	—	13.5	—
	—	—	—
	—	—	—
	13.0	15.0	2.0
	14.0	15.5	1.5
	15.5	17.0	1.5
	15.5	18.5	3.0
May 6/7	13.5	14.0	0.5

*Measured in hours.

TABLE 2. Vegetation types of the Serranía de Macuira: comparison of different classifications.

ESPINAL & MONTENEGRO (1963)	SUGDEN (present paper)	RIEGER (1976)*
Monte Espinoso Tropical	Thorn Woodland	<i>Bursera glabra</i> woodland
Bosque Muy Seco Tropical	Very Dry Deciduous Woodland	<i>Lonchocarpus punctatus</i> forest <i>Astronium</i> <i>graveolens</i> - <i>Tabebuia</i> <i>bilbergii</i> woodland <i>Bursera graveolens</i> wood- land
	Dry Evergreen Forest	Evergreen thicket domi- nated by <i>Capparaceae</i> <i>Eugenia umbellulifera</i> woodland
(No equivalent)	Riparian Vegetation	<i>Vitex cymosa</i> - <i>Libidibia</i> <i>coriaria</i> woodland
Bosque Húmedo Subtropical	Cloud Forest	<i>Rapanea guianensis</i> woodland (Elfin Woodland)

*This comparison is not intended to contest the validity of Rieger's associations; these are recognizable subdivisions of the major vegetation types described in this paper.

of 1977 indicate that there are four principal vegetation types on the lower slopes of the Serranía, which may be distinguished by their physiognomy, their leaf morphology and phenology, and the presence or absence of certain indicator species. These are Thorn Woodland, Very Dry Deciduous Woodland, Riparian Vegetation, and Dry Evergreen Forest (TABLE 2), occurring respectively on well-drained sand deposits, on steep, micaceous schist slopes on outlying hills, on the banks and beds of arroyos (seasonal streams and rivers), and on the sheltered slopes of the larger (to 500 or 600 m) hills. Rieger's (1976) associations are subdivisions of some of these categories (TABLE 2). The characterization of vegetation types is particularly difficult because of the extent of human activity in the region and the abundance of secondary vegetation types.

THORN WOODLAND

Most of Guajira is covered with this type of vegetation. In the Serranía de Macuira it occurs on the deep deposits of sand that cover the northeastern slopes and is characterized by evergreen, leptophyllous (*sensu* Raunkiaer, 1934), flat-topped, leguminous trees 5-10 m tall (e.g., *Prosopis juliflora* (Sw.) DC. and *Libidibia coriaria* (Jacq.) Schlechter) and by deciduous trees such as *Bursera glabra* Triana & Planchon. The canopy varies from quite

open to dense and is frequently interrupted and overtopped by large cacti, especially *Lemaireocereus griseus* (Haw.) Britton & Rose. The undergrowth is variable and is generally thicker where the canopy is broken. *Croton rhamnifolius* H.B.K. and *Cordia curassavica* (Jacq.) Roemer & Schultes are the most frequent species, the former favoring the more shaded habitats and often forming pure stands. Scattered individuals of the evergreen shrubs *Bunchosia odorata* (Jacq.) H.B.K., *Calotropis procera* R. Br., *Hippocratea verrucosa* H.B.K., and *Melochia tomentosa* L. occur throughout the formation. There is virtually no ground cover apart from small individuals of *Opuntia* spp. With the exception of rare colonies of *Tillandsia flexuosa* Sw., epiphytes are absent. Woody lianas such as *Arrabidaea mollissima* (H.B.K.) Bur. & K. Schum. and *Banisteriopsis jasminellum* A. Juss. are, on the other hand, quite frequent.

There is no doubt that this vegetation is highly disturbed by human activity. The Guajiro favor the extensive ridges and hummocks of sand between the watercourses as dwelling places for several reasons: the sand has the right combination of softness and firmness for the foundations of wood-pile huts, and there is relative ease of access to water, safety from the annual floods, and freedom from mosquitoes. Because water is less scarce than it is elsewhere in Guajira, the human population is quite dense, and the Thorn Woodland has therefore suffered the depredation of domestic animals, particularly goats. Additionally, trees are frequently felled for the construction of corrals and enclosures. There appears to be little regeneration of canopy species; the prevalence of *Cordia curassavica* and *Croton rhamnifolius* in the undergrowth may be due to their unpalatability to goats.

VERY DRY DECIDUOUS WOODLAND

The boundary between Thorn Woodland and Very Dry Deciduous Woodland (FIGURE 2) is usually marked by an abrupt change in topography and substrate. Wherever the steep, micaceous schist slopes of the Serranía emerge from the blanket of sand, whether at 50 or 200 m, the leptophyllous, evergreen, leguminous trees are replaced by taller, microphyllous or mesophyllous species. The canopy is variable in height, reaching a maximum of ca. 20 m in sheltered sites and decreasing to as little as 5 m on windward slopes. Some more common species of canopy trees in this vegetation are *Astronium graveolens* Jacq., *Bursera simaruba* (L.) Sarg., *Cochlospermum vitifolium* (Willd.) Sprengel, *Lonchocarpus punctatus* H.B.K., and *Sapindus saponaria* L. Most canopy species produce a flush of leaves at the beginning of the rainy season or a few weeks before and shed them between January and March, remaining leafless for six to eight months of the year.

There is a very broken understory of evergreen Capparaceae, including several species of *Capparis*. The leaves of *C. coccobifolia* Martius ex Eichler and *C. pachaca* H.B.K. are coriaceous and glabrous, while those of *C. tenuisiliqua* Jacq. are chartaceous and pubescent; those of *C. linearis* Jacq. are narrowly linear and coriaceous. The ground layer is very sparse, consisting of scattered individuals of *Opuntia* sp., *Elytraria imbricata* (Vahl) Pers., *Isocarpha oppositifolia* (L.) R. Br., and *Ruellia inundata* H.B.K.; the



FIGURE 2. Very Dry Deciduous Woodland, ca. 200 m alt.

stems of a scandent *Philodendron* are frequently found trailing across the substrate toward the upper limit (ca. 400 m) of the Very Dry Deciduous Woodland. Climbers and epiphytes are rare; colonies of epiphytic *Tillandsia flexuosa*, *Brassavola nodosa* Lindley, and *Schomburgkia humboldtii* Reichenb. f. were each seen on two occasions.

The soil is hard and shallow, and much of the surface consists of bare rock and compacted or loose stone fragments. Organic matter generally accumulates in crevices and gullies. Most of the dry litter is washed away during the annual rains due to the steeply sloping terrain.

It appears that little regeneration of canopy species is occurring, once again due to the ravages of goats, which are allowed to wander some distance from the farmsteads. *Jatropha urens* L., a stinging, unpalatable shrub, is avoided by goats and is consequently common in the Very Dry Deciduous Woodland.

The upper and lower limits of this formation are variable. On the smaller (300–600 m) outlying hills it extends to the summits. (On the neighboring Serranía de Jarara it covers the hills entirely.) On the higher, more extensive central hills around the principal peaks, the transition to Dry Evergreen Forest (see below) may occur as low as 250 m, especially in sheltered situations. The lower limit is contiguous with the upper limit of the sand deposits.

RIPARIAN VEGETATION

The numerous wide arroyos flowing through the foothills of the Serranía de Macuira are fringed by vegetation distinctly greener and more luxuriant than the dry types described above. Although these rivers are dry for most of the year, groundwater is always close to the surface and emerges at in-

tervals (usually where the basement rock outcrops and the layer of sand is thin or absent) as small streams. The streams disappear wherever the bed consists of deep sand or boulders.

While the Riparian Vegetation (FIGURE 3) is of limited extent compared to the other vegetation types, it warrants separate consideration because of the considerable number of species it contains that are absent elsewhere. Prominent among the woody species are *Anacardium excelsum* (Bert. & Balbis) Skeels, *Crateva tapia* L., *Vitex cymosa* Bert., and *Sapium aucuparium* Jacq., the first reaching a diameter of more than 1 m and a height of 25 m. Trees characteristic of Thorn Woodland and Very Dry Deciduous Woodland are quite frequent; *Prosopis juliflora*, *Astronium* spp., and *Lonchocarpus* spp. all grow to a greater size here than they do on the dry slopes and tend to retain their leaves longer. *Anacardium excelsum* and *Sapium aucuparium* are evergreen, with fairly coriaceous leaves, while *Crateva tapia* and *Vitex cymosa* have more or less membranaceous leaves that flush in February and March, when the dry season is already well advanced.

In the shade of these trees grows an understory of evergreen shrubs, especially *Annona glabra* L., *Hamelia patens* Jacq., and *Tabernaemontana amygdalifolia* Jacq.—species that are exclusive to this habitat. Lianas are more abundant here than in any other vegetation type in the Serranía; *Arabidaea mollissima*, *Cardiospermum corindum* L., *Funastrum clausum* (Jacq.) Schlechter, *Momordica charantia* L., *Passiflora pulchella* H.B.K., and *Plumbago scandens* L. are all common. Epiphytes are very rare, as they are in the other low-altitude vegetation types.

Riparian Vegetation extends only a very short distance back from the banks



FIGURE 3. Riparian Vegetation, ca. 100 m alt.

of the arroyos—usually no more than 20 m and often much less if the banks are steep. Apart from the woody flora on the banks, there is also a characteristic flora of herbaceous annuals or ephemerals that grow in the riverbeds themselves during the dry season; these are evidently both moisture loving and heliophilic since they are mostly absent from the densely shaded banks. Grasses (e.g., *Chloris inflata* Link), sedges (*Eleocharis geniculata* (L.) Roemer & Schultes, *Mariscus rufus* H.B.K.), and composites (*Egletes prostrata* (Sw.) Kuntze, *Pluchea symphytifolia* (Miller) Gillis) are particularly abundant. Several ferns (*Adiantum concinnum* Willd., *Thelypteris* spp.) are commonly found on the shaded edges of permanent rock pools higher (300–500 m) in the mountains.

The obvious potential for cultivation in this habitat has been realized by the local people, who grow mangoes, coconuts, maize, papayas, tobacco, and other crops on the banks and in the beds of the arroyos. Livestock, especially cattle and swine, are watered and grazed. As a result, there is a great deal of disturbance, and it is certain that none of the Riparian Vegetation is primary except in the more inaccessible gullies.

DRY EVERGREEN FOREST

This vegetation (FIGURE 4) occurs on the larger central hills from ca. 250 to 550 m (600–650 m on the leeward side of the Serranía). The dominant trees are evergreen; the leaves (microphylls and mesophylls) are chartaceous to coriaceous and mostly simple. Common canopy trees are *Morisonia americana* L., *Clusia* sp., *Eugenia umbellulifera* (H.B.K.) Krug & Urban, *Ficus prinoides* (Humb. & Bonpl.) Willd., *Coccoloba* sp., and *Jacquinia revoluta*



FIGURE 4. Dry Evergreen Forest, ca. 350 m alt. Large bole left of center has d.b.h. of ca. 40 cm.

H.B.K., which attain heights of 8–15 m. The canopy is generally quite closed and shading. There is a well-developed understory containing small trees and shrubs 2–4 m tall; frequent species are *Acalypha diversifolia* Jacq., *Amirys sylvatica* Jacq., *Actinostemon concolor* (Sprengel) Mueller-Arg., *Aphelandra pulcherrima* (Jacq.) H.B.K., *Capparis baduica* L., *C. verrucosa* Jacq., *Hippocratea verrucosa*, *Psychotria microdon* (DC.) Urban, *Rauvolfia ligustrina* Roemer & Schultes, and *Ruellia macrophylla* Vahl. The ground layer is quite sparse, consisting mainly of *Petiveria alliacea* L. and occasional individuals of *Bromelia chrysantha* L. and *Elytraria imbricata*; seedlings and saplings of trees are quite common, indicating that there is less disturbance from man and livestock. Epiphytes are as rare as they are in the other dry formations, and lianas are infrequent.

The soil supporting the Dry Evergreen Forest is undoubtedly richer and better developed than that supporting the Very Dry Deciduous Woodland. There is a layer of dry litter several centimeters deep and a thin humus layer overlying a gray, crumbly mineral soil that varies in depth according to the proximity to the surface of the parent rock.

THE CLOUD FOREST

At 500–550 m on the windward side of the hills and 600–650 m on the leeward side, the dry formations give way to the Cloud Forest (FIGURE 5), which differs in nearly every respect from the surrounding vegetation. It has a different complement of species (including bryophytes and an abundance of vascular epiphytes), a smaller leaf size, a notable absence of compound leaves, and an often luxuriant undergrowth. The transition from dry seasonal vegetation to Cloud Forest is very abrupt, and the sudden increase in verdure and dampness is striking. The substrate is damp, and moisture drips from the vegetation, particularly in the morning after the clouds have lifted.

This vegetation is present on each of the three main peaks of the Serranía de Macuira, giving a total area of ca. 15 km² (MAP 3). Of all the vegetation types in the Serranía, it is the least disturbed by human activity. In 1977 the total area cleared for the grazing of cattle constituted only a small fraction of the Cloud Forest, and an estimated 95 percent of the vegetation was primary.

The vascular flora of the Cloud Forest is listed in TABLE 3 and is categorized into canopy trees, understory woody shrubs and coarse herbs, ground-cover herbs, epiphytes, ground-rooted climbers and scramblers, and hemiparasites. A total of 126 species were encountered, 14 of which are as yet incompletely identified; several species were encountered only once. TABLE 3 includes only those species collected during the course of the present study since the notes accompanying the small number of specimens collected by previous workers in the Cloud Forest do not accurately define the habitat of provenance. Species recorded by other collectors would increase the number of species in the table by a maximum of six. A few individuals of species common in the surrounding Dry Evergreen Forest (e.g., *Capparis baduica* and *Hippocratea verrucosa*) were encountered in the Cloud Forest but are not included in the table. Only four species (*Acalypha diversifolia*, *Actinos-*



FIGURE 5. Cloud Forest, 650 m alt., showing abundance of vascular epiphytes.

TABLE 3. Ferns and flowering plants of the Cloud Forest.

I. WOODY PLANTS OF THE CANOPY*

Pteridophyta	Blechnaceae	<i>Blechnum arborescens</i> (Klotzsch & Karsten) Hieron.
Dicotyledones	Cyatheaceae	<i>Cyathea arborea</i> (L.) J. E. Smith
	Apocynaceae	<i>Stemmadenia minima</i> A. Gentry
	Araliaceae	<i>Dendropanax arboreus</i> (L.) Dene. & Planchon
	Boraginaceae	<i>Cordia macuirensis</i> Dugand
	Clusiaceae	<i>Clusia rosea</i> Jacq.
	Compositae	indet.
	Euphorbiaceae	<i>Euphorbia cotinifolia</i> L.
		<i>Margaritaria nobilis</i> L. f.
	Lauraceae	<i>Persea caerulea</i> (Ruiz & Pavon) Mez
	Melastomataceae	<i>Conostegia icosandra</i> (Sw.) Urban
		<i>Miconia acinodendron</i> (L.) Sweet
		<i>Miconia laevigata</i> (L.) DC.
		<i>Mouriri rhizophoraefolia</i> (DC.) Triana
	Moraceae	<i>Cecropia</i> sp.
		<i>Ficus perforata</i> L.
	Myrsinaceae	<i>Rapanea guianensis</i> Aublet
	Myrtaceae	<i>Myrcia fallax</i> (Rich.) DC.
		<i>Myrcia splendens</i> (Sw.) DC.
		<i>Myrcianthes fragrans</i> (Sw.) McVaugh
	Nyctaginaceae	<i>Guapira fragrans</i> (Dum.-Cours.) Little
	Ochnaceae	<i>Oureatea nitida</i> (Sw.) Engler
	Polygonaceae	<i>Coccoloba coronata</i> Jacq.
	Rubiaceae	<i>Genipa spruceana</i> Steyerf.
		<i>Randia formosa</i> (Jacq.) Schum.
		<i>Rudgea marginata</i> Standley

II. UNDERSTORY SHRUBS AND COARSE HERBS

Pteridophyta	Equisetaceae	<i>Equisetum giganteum</i> L.
Cycadales	Zamiaceae	<i>Zamia muricata</i> Willd.
Monocotyledones	Araceae	<i>Dieffenbachia</i> sp.
	Gramineae	<i>Gynerium sagittatum</i> (Aublet) Beauv.
		<i>Olyra latifolia</i> L.
	Marantaceae	<i>Maranta divaricata</i> Roscoe
		<i>Stromanthe lutea</i> (Jacq.) Eichler
	Musaceae	<i>Heliconia bihai</i> L.
		<i>Heliconia latispatha</i> Bentham
	Zingiberaceae	<i>Costus guanaiensis</i> Rusby
		<i>Costus villosissimus</i> Jacq.
		<i>Renealmia occidentalis</i> (Sw.) Sweet
Dicotyledones	Acanthaceae	<i>Aphelandra pulcherrima</i> (Jacq.) H.B.K.
		<i>Ruellia macrophylla</i> Vahl
	Amaranthaceae	<i>Alternanthera pubiflora</i> (Bentham) Kuntze
		<i>Chamissoa altissima</i> H.B.K.

TABLE 3 (continued).

	Compositae	<i>Baccharis trinervis</i> Pers.
	Euphorbiaceae	<i>Acalypha diversifolia</i> Jacq. <i>Actinostemon concolor</i> Mueller-Arg. <i>Croton margaritensis</i> J. R. Johnston
	Malvaceae	<i>Malvaviscus arboreus</i> Cav.
	Melastomataceae	<i>Clidemia hirta</i> (L.) D. Don
	Piperaceae	<i>Piper</i> sp.
	Portulacaceae	<i>Talinum paniculatum</i> (Jacq.) Gaertner
	Rubiaceae	<i>Chiococca alba</i> (L.) Hitchc. <i>Guettarda divaricata</i> (Humb. & Bonpl.) Standley <i>Psychotria alba</i> Ruiz & Pavon <i>Psychotria barbiflora</i> A. DC. <i>Psychotria nervosa</i> Sw. <i>Spermacoce suffrutescens</i> Jacq.
	Solanaceae	<i>Cestrum alternifolium</i> (Jacq.) O. E. Schulz <i>Solanum hirtum</i> Jacq.
III. GROUND LAYER		
Pteridophyta	Adiantaceae	<i>Adiantum latifolium</i> Lam. <i>Adiantum petiolatum</i> Desv.
	Aspleniaceae	<i>Asplenium cristatum</i> Lam. <i>Asplenium myriophyllum</i> (Sw.) Presl
	Blechnaceae	<i>Blechnum occidentale</i> L.
	Aspidiaceae	<i>Polybotrya cervina</i> (L.) Kaulf. <i>Tectaria incisa</i> Cav.
	Lycopodiaceae	<i>Lycopodium cernuum</i> L.
	Monocotyledones	<i>Zephyranthes tubispatha</i> Herb.
	Araceae	<i>Anthurium crassinervium</i> (Jacq.) Schott
	Cyperaceae	<i>Rhynchospora comata</i> (Link) Schultes <i>Scleria secans</i> (L.) Urban
	Gramineae	<i>Acroceras zizanioides</i> (H.B.K.) Dandy <i>Coix lacryma-jobi</i> L. <i>Ichnanthus pallens</i> (Sw.) Munro indet.
	Haemadoraceae	<i>Xiphidium caeruleum</i> Aublet
Dicotyledones	Orchidaceae	<i>Campylocentrum micranthum</i> (Lindley) Rolfe <i>Encyclia fragrans</i> (Sw.) Lemée
	Acanthaceae	<i>Ruellia malacosperma</i> Greenman indet.
	Compositae	<i>Erigeron bonariensis</i> L. <i>Erechtites hieracifolia</i> Raf. <i>Liabum asclepiadeum</i> Schultz Bip.
	Labiatae	<i>Scutellaria verecunda</i> Epling
	Leguminosae	<i>Desmodium axillare</i> (Sw.) DC.
	Passifloraceae	<i>Passiflora</i> sp.
	Solanaceae	<i>Solanum dulcameroides</i> Dunal
	Urticaceae	<i>Pilea microphylla</i> (L.) Liebm.

TABLE 3 (continued).

IV. EPIPHYTES

Pteridophyta	Grammitidaceae	<i>Grammitis blepharolepis</i> (C. Chr.) Morton
	Hymenophyllaceae	<i>Hymenophyllum hirsutum</i> (L.) Sw.
	Lomariopsidaceae	<i>Elaphoglossum</i> sp.
	Oleandraceae	<i>Nephrolepis rivularis</i> (Vahl) Mett.
	Polypodiaceae	<i>Microgramma lycopodioides</i> (L.) Copeland
		<i>Microgramma piloselloides</i> (L.) Copeland
		<i>Polypodium maritimum</i> Hieron.
		<i>Polypodium phyllididis</i> L.
		<i>Anthurium scandens</i> (Aublet) Engler
		<i>Guzmania cylindrica</i> L. B. Smith
Monocotyledones	Araceae	<i>Guzmania lingulata</i> (L.) Mez
		<i>Guzmania monostachya</i> (L.) Rusby ex Mez
		<i>Guzmania sanguinea</i> (André) André ex Mez
		<i>Guzmania</i> sp.
		<i>Tillandsia anceps</i> Lodd.
		<i>Tillandsia bulbosa</i> Hooker
		<i>Vriesea heterandra</i> (André) L. B. Smith
		<i>Vriesea splendens</i> (Brongn.) Lemée
		<i>Dichaea</i> sp.
		<i>Eleocharis arpophyllostachys</i> Reichenb.
	Orchidaceae	<i>Epidendrum agathosmicum</i> Reichenb. f.
		<i>Epidendrum stenopetalum</i> Hooker
		<i>Jacquinella globosa</i> (Jacq.) Schlechter
		<i>Maxillaria sophronitis</i> (Reichenb.) Garay
		<i>Pleurothallis ruscifolia</i> R. Br.
Dicotyledones	Lentibulariaceae	<i>Polystachya foliosa</i> (Lindley) Reichenb. f.
		<i>Stelis</i> sp.
		<i>Utricularia alpina</i> Jacq.
		<i>Peperomia glabella</i> (Sw.) A. Dietr.
		<i>Hillia costanensis</i> Steyerf.

V. GROUND-ROOTED CLIMBERS AND SCRAMBLERS

Monocotyledones	Araceae	<i>Monstera</i> sp.
		<i>Philodendron erubescens</i> C. Koch & Augustin
Dicotyledones	Amaranthaceae	<i>Iresine argentata</i> (Martius) D. Dietr.
	Apocynaceae	<i>Mandevilla bella</i> (Pittier) Woodson
	Asclepiadaceae	<i>Cynanchum atrovirens</i> (Rusby) Sugden†

TABLE 3 (continued).

Bignoniaceae	<i>Schlegelia fuscata</i> A. Gentry
Leguminosae	<i>Machaerium humboldtianum</i> Vogel
Passifloraceae	<i>Passiflora</i> sp.

VI. HEMIPARASITES

Dicotyledones	Loranthaceae	<i>Phoradendron</i> sp.
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*Each species is listed under the category (I-VI) in which it most commonly occurs; not all species are exclusive to one category. For instance, a number of the epiphytic species are sometimes found growing on the ground, and some of the understory shrubs occasionally reach the canopy.

†*Cynanchum atrovirens* (Rusby) Sugden, comb. nov.

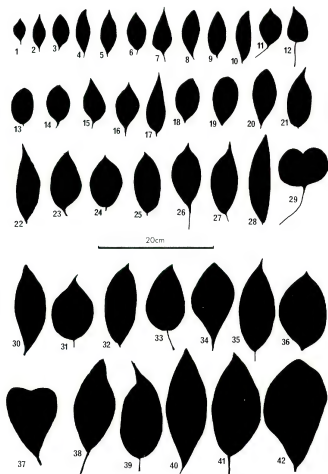
BASIONYM: *Metastelma atrovirens* Rusby, Descr. 300 New Sp. S. Am. Pl. 95, 1920.

temon concolor, *Aphelandra pulcherrima*, and *Ruellia macrophylla*) were frequent in both formations.

Guapira fragrans, *Rapanea guianensis*, and *Myrcianthes fragrans* are the most frequent species in the canopy flora, accounting respectively for 41, 28, and 10 percent of the woody stems with d.b.h. greater than 1.5 cm. Most other species account for less than 1 percent of the woody stems in any size class. The three dominant species are morphologically similar in several respects, especially leaf size, texture, shape, and arrangement. The leaves are simple, glabrous, and elliptic to oval with cuneate bases; they have indistinct venation with the exception of the prominent midrib; they are tough, thick, and leathery, with a shiny cuticle on the adaxial surface only; the adaxial surface is much darker than the abaxial; and the petioles and internodes are short. The leaves of the less common canopy species are similar in most respects, although many are not as coriaceous as those of the dominant species. The spectrum of leaf size and the diversity of leaf shape of the woody species (canopy and understory) of the Cloud Forest are illustrated in FIGURE 6.

Rapanea guianensis has monopodial growth, and in sheltered sites the boles are usually quite straight and vertical (maximum d.b.h., 17.5 cm), branching only in the canopy. *Guapira fragrans* (maximum d.b.h., 35 cm) and *Myrcianthes fragrans* (maximum d.b.h., 27 cm) grow sympodially and are characteristically twisted and gnarled, branching at all levels and forming wider crowns than *R. guianensis*. The largest tree encountered in the Cloud Forest was an individual of *Dendropanax arboreus* with a d.b.h. of 41.5 cm.

The most frequent understory shrub is *Actinostemon concolor*, which occasionally reaches the canopy. Young individuals of the dominant canopy species are very frequent, as are the rubiaceous shrubs *Psychotria alba*, *P. nervosa*, *Guettarda divaricata*, and *Spermacoce suffrutescens*. The leaves of plants in the shrub layer are more variable than those of the canopy trees, and the internodes are longer. There is a greater range of size (FIGURE 6), less difference in color between the upper and lower surfaces, and a greater



range in texture—from membranaceous (*Psychotria alba*) to coriaceous (*Actinostemon concolor*). As in the canopy, drip-tips and compound leaves are absent, and species with pubescent leaves (e.g., *Psychotria nervosa*) are few.

Other common components of the undergrowth are the cycad *Zamia muricata*, which has an underground stem and fronds up to 1 m long, and several large monocotyledons, particularly *Costus guanaiensis*, *Heliconia latispatha*, *Maranta divaricata*, and *Stromanthe lutea*. The occasional small swamps are populated by large heliophiles, especially *Dieffenbachia* sp., *Costus villosissimus*, and *Gynierium sagittatum*. Ground cover is provided by sparse grasses, sedges, ferns, bromeliads, a few herbaceous dicotyledons (e.g., *Scutellaria verecunda*), and the seedlings of trees and shrubs. The cover is by no means continuous, and there are large patches of bare soil and litter and frequent mossy boulders.

The epiphytes of the Cloud Forest have been discussed in detail by Sugden and Robins (1979) and by Sugden (in press). Although orchids are quite diverse (TABLE 3), bromeliads are the most conspicuous element of the vascular epiphytic flora, both in number of individuals and in biomass. Species of *Guzmania* grow on the boles and lower branches of the trees, while *Vriesea heterandra*, which is a smaller, more xeromorphic species, abounds in the canopy. On an individual of *Guapira fragrans* with a d.b.h. of 25 cm, 1035 bromeliads were counted, ranging in size from small juveniles 5 cm high to adult specimens of *Guzmania cylindrica* with leaves up to 1 m long (FIGURE 5). Mosses and hepatics are not prominent and do not festoon the branches as they do in similar vegetation in the Antilles (Beard, 1949). There is nevertheless a sparse growth of hepatics such as *Ceratolejeunea* spp., *Lep-tolejeunea* spp., and *Cololejeunea* spp. on the upper branches and in the canopy, and cushion-forming mosses are frequent on the boles close to the ground, especially on the highest peaks. Epiphylls are rare.

Ground-rooted climbers are few. *Philodendron erubescens* is frequent, as is a species of *Monstera*; occasional individuals of *Passiflora* sp. were observed. Only one species of parasite, *Phoradendron* sp., was encountered, at infrequent intervals.

FIGURE 6. Leaf size and shape in woody species of the Macuira Cloud Forest (silhouettes represent largest leaves on herbarium specimens of adult individuals): 1, *Myrcianthes fragrans*; 2, *Spermacoce suffrutescens*; 3, *Randia formosa*; 4, *Guettarda divaricata*; 5, *Chiococca alba*; 6, *Ficus perforata*; 7, *Iresine argentata*; 8, *Cordia maculensis*; 9, *Cestrum alternifolium*; 10, *Stemmadenia minima*; 11, *Dendropanax arboreus*; 12, *Croton margaritensis*; 13, *Mouriri rhizophoraefolia*; 14, *Guapira fragrans*; 15, *Chamissoa altissima*; 16, *Mandevilla bella*; 17, *Alternanthera pubiflora*; 18, *Machaerium humboldtianum* (single leaflet of compound leaf); 19, *Rudgea marginata*; 20, *Rapanea guianensis*; 21, *Myrcia fallax*; 22, *Psychotria alba*; 23, *Psychotria barbiflora*; 24, *Coccoloba coronata*; 25, *Margaritaria nobilis*; 26, *Conostegia icosandra*; 27, *Miconia acinodendron*; 28, *Piper* sp.; 29, *Euphorbia cotinifolia*; 30, *Actinostemon concolor*; 31, *Clidemia hirta*; 32, *Ouratea nitida*; 33, *Solanum hirtum*; 34, *Psychotria nervosa*; 35, *Miconia laevigata*; 36, *Hillia costanensis*; 37, *Clusia rosea*; 38, *Ruellia macrophylla*; 39, *Acalypha diversifolia*; 40, *Aphelandra pulcherrima*; 41, *Persea caerulea*; 42, *Genipa spruceana*.

DIVERSITY OF HABITAT IN THE CLOUD FOREST. The overall impression given in the foregoing paragraphs is somewhat generalized. There is, in fact, considerable variation within the Cloud Forest, although not enough to warrant the division of the vegetation into anything more than minor subcategories, since the dominant trees are present throughout. Because of the dissection of the Serranía de Macuira into a labyrinth of small, steep valleys and ridges, levels of exposure to wind vary greatly according to aspect. The height of the canopy varies from 10 m in the most sheltered gullies to less than 1 m on the highest windswept peaks of Huarech and Palua. On the windward slopes boles and branches lean strongly uphill, often almost parallel to the ground (FIGURE 7), internodes are very short, and the low canopy has the appearance of a matted mass of tight rosettes. It is impossible to see the ground, and progress through this thicket is made only by clambering over the trees. This form of canopy continues over to the immediate sheltered sides of the sharp ridges, although the ground is in fact sloping the other way (FIGURE 7). Thus there is space for the growth of an understory, which is sheltered and heavily shaded as a result of the thick canopy. Further down the leeward slopes the canopy is more open since there is less disturbance from wind, and the trees are taller. Maximum canopy height is attained in the gullies, which afford more luxuriant and thicker growth than the leeward slopes, presumably because of the noticeably higher soil moisture content and the accumulation of organic matter and leached nutrients.

The relative rarity of the majority of woody species in the Cloud Forest

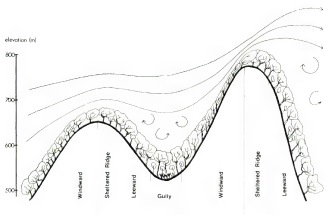


FIGURE 7. Schematic representation of habitat diversity within the Macuira Cloud Forest.

creates difficulties in the quantification of any habitat preferences that might exist because a very large area would have to be surveyed to obtain a large enough sample. Additionally, the types of habitat outlined above (i.e., windward slope, sheltered ridge, leeward slope, and gully) are not always clearly demarcated; the variety of slope and aspect and the vagaries of topographical effects on the airstream ensure the existence of a range of intermediate habitats. In a quantitative survey in which all woody stems with d.b.h. greater than 1.5 cm were counted in 14 plots, each 98 m², the only clear result was that *Rapanea guianensis* was more abundant on windward than on leeward slopes.

Most of the larger herbaceous monocotyledons are more or less confined to the damp, shaded gullies; *Xiphidium caeruleum*, the two species of *Heliconia*, and *Stromanthe lutea* are good examples of species showing a strong preference for this habitat. The species of the few small swamps have already been mentioned.

The variation of habitat within the Cloud Forest is most strikingly shown by the vascular epiphytes. The most dense epiphytic populations occur on sheltered ridges (Sugden & Robins, 1979), and within this habitat there is an increase in both population density and species diversity with increasing altitude. Leeward slopes and gullies between 550 and 650 m support fewer species and smaller populations than do either sheltered ridges or windward slopes in the same altitudinal range. Windward slopes at higher altitudes are more impoverished than those at lower altitudes. These differences can be attributed to the variation with altitude of the daily period of cloud cover (TABLE 1), and to the variation with aspect of the cloud flux or throughput (Sugden & Robins, 1979; Sugden, in press a).

OUTLYING AREAS OF CLOUD FOREST. In addition to the three principal areas of Cloud Forest, there are at least two outlying peaks about 550 m high, each of which supports less than 1 ha of Cloud Forest on its summit. The two that were visited during the course of this study were Cerro Yauanauas and Cerro Ke'chuo (MAP 3). The former is separated from the Palua Cloud Forest, which is ca. 2 km away, by a steep-sided valley; the latter is separated from the Huarech Cloud Forest by a gentle saddle 0.5 km long, which dips to an elevation of ca. 450 m and is covered by Dry Evergreen Forest. The Cloud Forest species present on Cerro Yauanauas and Cerro Ke'chuo total 25 and 30, respectively; the two peaks have 16 species in common. Most of the commoner woody species of the Cloud Forest, including the dominant trees, are present on one or both of the peaks, while the herbaceous and epiphytic species are poorly represented.

The physiognomic and floristic transition from Dry Evergreen Forest to Cloud Forest is as abrupt on these hills as it is on the larger massifs. In both instances, the small patch of Cloud Forest is on the windward side of the peak, giving way to Dry Evergreen Forest on the leeward side within a few meters of the crest. It is probable that similar small patches of Cloud Forest are to be found on other outlying peaks over 500 m high (MAP 3), but these remain to be visited.

DISCUSSION

The important general features of the Macuira Cloud Forest are its isolation by surrounding arid lowlands and its clear dependence on cloud interception for its existence. Isolation from other moist regions poses interesting biogeographic questions concerning the origin and dispersal of the flora; these issues are discussed in separate papers (Sugden, in press b, 1982). Dependence on clouds is significant in the context of the classification of the Macuira Cloud Forest and may increase our understanding of the effects of cloud cover on tropical montane vegetation.

The Cloud Forest is similar in many respects to the Elfin Woodlands of Beard (1944, 1949, 1955) and Howard (1968, 1970, 1973), and to the Upper Montane Rain Forest of Richards (1952). The characteristics of Upper Montane Rain Forest, as tabulated by Grubb and Tanner (1976, *table 1*) and by Grubb (1977, *table 1*), include canopy height of 1.5–18 m, predominance of microphylls; usual absence of buttresses, cauliflorous trees, and drip-tips; paucity of compound leaves and climbers; and frequent occurrence of vascular epiphytes. The Macuira Cloud Forest has all of these features, although its abundance of vascular epiphytes is more characteristic of Lower Montane Rain Forest (see Grubb, 1977). The Elfin Woodlands of the summits of Antillean mountains (Howard, 1968) also fall into the broad category of Upper Montane Rain Forest, although the Macuira Cloud Forest differs from these at least in the relatively poor development of its bryophyte community. Both Howard (1968), in his extensive review of elfin vegetation, and Beard (1949) have stressed the abundance of bryophytes in Elfin Woodlands, where mosses and liverworts festoon the branches and often cover the forest floor. The Macuira Cloud Forest also lacks the aerial roots that were found to be common in an Elfin Forest on Pico del Oeste, Luquillo Mountains, Puerto Rico (Gill, 1969), and does not suffer the high level of leaf damage recorded in the same forest by Howard (1969); nevertheless, the two forests are similar in stature, leaf size and shape, and diversity of woody species.

Physiognomically, the Macuira Cloud Forest resembles the summit vegetation of Cerro Santa Ana (850 m), Edo. Falcón, Venezuela, and Cerro San Juan (930 m), Isla Margarita, Venezuela, more closely than any others (see above). The qualitative descriptions of these two mountains (by Tamayo (1941) and Johnston (1909), respectively) closely parallel that of the Serranía de Macuira. Both authors noted the importance of cloud interception on these mountains. The daily pattern of cloud cover and the contribution of direct rainfall to the precipitation on Cerro San Juan (Johnston, 1909) are apparently much the same as on the Serranía de Macuira.

In terms of the rapid transition from dry to moist vegetation, the Serranía de Macuira also resembles the Sierra de San Luis (1500 m), Edo. Falcón, Venezuela, which stands to the south of the Península de Paraguaná. The cloud forest on the Sierra de San Luis, however, begins at 1200 m (Steyermark, 1975) and has more diverse habitats and taller trees than does the Macuira Cloud Forest. Also, direct rainfall is of greater consequence; annual precipitation of up to 3000 mm has been recorded (Steyermark, 1975).

The Macuira Cloud Forest cannot be placed in any of the Life Zones of Holdridge (1967) and Holdridge *et al.* (1971). Mean temperatures of about 22° C and annual precipitation between 1000 and 5000 mm (which can be considered as reasonable lower and upper limits of precipitation in the driest and wettest parts of the Macuira Cloud Forest) are, according to the Holdridge model, the climatic conditions that support "subtropical" or "premontane" moist and wet forests. These forests bear no physiognomic resemblance to the Macuira Cloud Forest; rather, they are characterized by a canopy at least 20 m high, trees with spreading crowns, a well-developed understory layer, and few epiphytes. For this reason, Espinal and Montenegro's (1963) classification of the Macuira Cloud Forest as "Bosque Húmedo Subtropical" must be considered as erroneous.

Myers (1969) has also found the Life Zone model inadequate for the classification of Panamanian cloud forests. This may well be due to the fact that the model does not take into account the effect of clouds. Holdridge and colleagues (1971) admitted that cloud interception may significantly augment the total precipitation in a forest and noted that its quantity is dependent on the physiognomy and foliage characteristics of the vegetation. Nevertheless, undoubtedly because of the difficulty of quantifying cloud moisture interception, "it does not enter into the computation of mean annual precipitation of the Life Zone itself" (Holdridge *et al.*, 1971, p. 47) but may be important in distinguishing vegetation associations within a Life Zone. In the case of the Serranía de Macuira, it is clear that cloud interception is of far greater importance than this.

The measurement of cloud interception by vegetation is troublesome. Kerfoot (1968) and Rutter (1975) have reviewed and summarized the many efforts to assess the levels of mist and cloud precipitation in various habitats, mostly in temperate regions. Shuttleworth (1977) has produced some theoretical considerations of the question. The essential problem is that since the magnitude of interception and subsequent precipitation is dependent on the stature and form of the vegetation, physical measurement using standard fog recording apparatus, such as gauze screens set above rain gauges, can give an idea only of the potential precipitation. Kerfoot (1968) concluded that the absolute values for cloud and mist interception were as yet conjectural, and it would appear that this state of affairs still prevails, especially in the neotropics.

Grubb and Whitmore (1966), in an extensive consideration of the importance of cloud cover in a montane forest in Ecuador, noted that droplet interception is likely to make a considerable contribution to overall precipitation but admitted the virtual impossibility of quantifying it. Baynton (1968, 1969) made a relative measurement of the amount of water extracted from impinging cloud on the summit of Pico del Oeste, Puerto Rico, but concluded that the interpretation to be placed on the measurement was not self evident; nevertheless, he estimated that cloud interception augmented the annual precipitation of 4530 mm by about 10 percent. In both localities difficulty in recording cloud interception was a consequence of the problem of distinguishing it from true rainfall. This problem is recognized by Rutter (1975)

as being one of the principal barriers to effective measurement.

Other effects of clouds, apart from precipitation, have also proved difficult to assess. Cloud cover is accompanied by high humidity and, during the daytime, low incident radiation; the water vapor pressure deficit, the light intensity, and the surface temperature are thereby reduced. These factors, and sometimes high winds, have been proposed by many authors to account directly or indirectly for many of the physiognomic features of wet montane forests.

High winds and low rates of transpiration, the latter resulting from the saturation of the air and the lowering of leaf temperature, have been suggested as major causes of stunted growth in cloud forests. Low rates of transpiration have been demonstrated in woody species of the Elfin Forests on the summits of Pico del Oeste (Gates, 1969) and Pico del Este (Weaver *et al.*, 1973), Luquillo Mountains, Puerto Rico. Weaver and colleagues suggested that this decreased the efficiency of base-pumping and ion uptake, thus lowering growth rates and causing stunting. Leigh (1975) also considered that the blocking of transpiration by the combination of atmospheric saturation and high winds (resulting in low rates of mineral uptake) is important in reducing the stature of montane forests subject to frequent cloud cover.

Grubb (1977) has disputed the importance of low transpiration rates, suggesting that the decrease in stature, biomass, and productivity in montane rain forests can be attributed primarily to lower temperatures and lower rates of photosynthesis, which are the expected results (Gates, 1969) of frequent cloud cover. Grubb pointed out that the primary factor limiting ion uptake is the availability of photosynthate for fueling active transport in the roots; the rate of transpiration does not affect the uptake of ions when they are at concentrations as low as those typical of most montane forest soils (Grubb, 1977). The slow rates of breakdown of organic material in the soil due to waterlogging, limited aeration, and the inherently slow rate of decay of coriaceous leaves (Grubb, 1971, 1977; Leigh, 1975) may also limit nutrient supply to the roots. Reduced rates of root respiration due to poor soil aeration may be an additional factor limiting uptake (Holdridge, 1967). Grubb (1977) also noted that the translocation of nutrients to young shoots, which takes place via the phloem, is not influenced by the rate of transpiration, although it can be expected to be affected by the availability of photosynthate. Leaching of minerals from the soil, particularly from ridges, may also contribute to stunting and slow growth rates (Baynton, 1969).

Tanner (1980b) suggested that the immediate cause of low stature in Upper Montane Rain Forest could be the reduced rate of wood production. In Mor Ridge forest in Jamaica (see Grubb & Tanner, 1976), he found that the annual biomass increment was very low, while the biomass of the standing crop of leaves was not very much lower than that in taller Lower Montane Rain Forests (Tanner, 1980a). He concluded that lower temperatures or water stress could not explain the stunting and impoverishment of Jamaican Upper Montane Rain Forests (Tanner, 1980b), favoring instead the low levels of nutrients and/or low levels of insolation as limiting factors (Tanner, 1980a).

The mechanical effects of high winds have been invoked as a further cause of the reduced stature of many cloud forests, particularly elfin forests on ridges and summits (Gleason & Cook, 1926; Leigh, 1975). While wind-pruning may be important on exposed ridges and slopes (Howard, 1970; Weaver *et al.*, 1973; Grubb & Tanner, 1976), gnarling and stunting also occur on sheltered slopes and gullies.

The tendency in Upper Montane Rain Forests toward coriaceous pachyphylls (see Grubb (1977) for definition of this term) with thick cuticles has been interpreted as a defense against the loss of minerals as a result of leaching from the leaves (Whitmore, 1975)—a likely consequence of frequent wetting by clouds and fog. It has also been suggested (Grubb, 1977) that the thickened palisade layer in tropical montane pachyphylls should result in high rates of photosynthesis per unit area, thus offsetting the effect of periods when cloud cover reduces light intensity and surface temperatures. The xeromorphy of these leaves may also enable them to withstand the fluctuations in humidity and incident radiation that occur as a result of the alternation of cloudy and cloud-free periods (Leigh, 1975). Pachyphylls does not, however, appear to confer any drought-resistant properties, since under controlled conditions these leaves dry out at rates similar to those of thinner, lowland rain forest leaves (Buckley *et al.*, 1980); this is in accord with Tanner's (1980b) contention that Upper Montane Rain Forests are not water stressed.

The relative abundance of epiphytes (both vascular and nonvascular) in cloud forests is due to regular bathing in clouds, which causes frequent precipitation and atmospheric saturation (Richards, 1952; Grubb & Whitmore, 1966; Johansson, 1974; Leigh, 1975; Grubb, 1977; Sugden & Robins, 1979). The epiphytic habit entails independence of the substrate for water and nutrients; the growth of epiphytes—especially those that are not xeromorphic or drought tolerant (Johansson, 1974)—is therefore favored by frequent precipitation and low saturation deficit. Cloud cover ensures the water supply during periods of negligible rainfall.

In the Serranía de Macuira it was possible to assess the distribution of epiphytic species in terms of cloud flux (Sugden & Robins, 1979; Sugden, in press a) simply because other factors—especially rainfall and the minimal variation in temperature due to the narrow altitudinal range of the Cloud Forest—did not complicate the interpretation of the results. While the Macuira Cloud Forest shares the characteristics of many stunted montane wet forests, it is not subject to low temperatures, high rainfall, and prolonged daytime cloud cover, and it therefore represents an excellent opportunity to resolve some of the outstanding questions concerning the effects of clouds on montane vegetation. On the basis of the present evidence, it would appear that the Upper Montane Rain Forest characteristics of the Macuira Cloud Forest do not result from low temperature (because of the low altitude), low insolation, or high winds. Water stress appears to affect the distribution of vascular epiphytes (Sugden, in press a), but not of woody species, in the Macuira Cloud Forest. Soils and mineral nutrition are therefore likely to be of key significance, and these aspects of the Macuira Cloud Forest now require investigation.

The new status of the Serranía de Macuira as a Colombian National Park will hopefully create favorable opportunities for future research oriented toward topics not covered in the present descriptive study. Conservation of the Cloud Forest is essential not only because of its intrinsic scientific interest but also to ensure continued irrigation, production, and prosperity in the valley and foothill settlements of the Serranía. The permanent groundwater in the arroyos is the direct result of cloud interception on the upper slopes, and one may confidently predict that extensive felling in the Cloud Forest would endanger this water supply. Felling for pasture may become a serious threat if regeneration in the surrounding dry vegetation continues to be prevented by overgrazing of goats.

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THE ECOLOGICAL, GEOGRAPHIC, AND TAXONOMIC
RELATIONSHIPS OF THE FLORA OF AN ISOLATED
COLOMBIAN CLOUD FOREST, WITH SOME IMPLICATIONS
FOR ISLAND BIOGEOGRAPHY

ANDREW M. SUGDEN

IN A companion paper (Sugden, 1982) I have described the Cloud Forest on the Serranía de Macuira (865 m), Guajira, Colombia. This forest, because of its isolation in the midst of arid lowlands, poses some interesting biogeographic problems. The Cloud Forest extends from an abrupt ecotone with dry vegetation at 550 m to the summits of the hills, forming an "archipelago" consisting of three main "islands," each approximately 5 km² in area, and a few outliers of less than 1 ha. The vascular flora of the Cloud Forest consists of 126 species, and the three main areas are floristically similar. Only six of these species occur frequently on the surrounding dry slopes, and none has been recorded from the lowlands of Guajira (Sugden & Forero, in prep.). The nearest moist regions (the Sierra Nevada de Santa Marta and the Sierra de Perijá) lie 250 km to the southwest. The great majority of the Cloud Forest species, including all the dominants, could have arrived in the Serranía de Macuira by long-distance dispersal (Sugden, in press a).

The purpose of this paper is to determine the origin and relationships of the Macuira Cloud Forest flora and the effects of isolation on its composition, by considering the geographic distribution, ecology, and taxonomic relationships of each species in the flora. A survey of the distributions of the species in the flora determines the geographic affinities and possible sources of recruitment; it also reveals the level of endemism in the flora, which may sometimes be a measure of the individuality of the habitat or of the extent of geographic isolation. A survey of the autecology of each species throughout its range reveals the extent to which the flora is specialized or unspecialized. Clearly, the results of each survey are of less value on their own than in relation to others; to complement and evaluate the distributional and ecological findings, it is also desirable to understand the taxonomic relationships of the species concerned and the extent to which they vary infraspecifically (White, 1971).

Because of the broad scope of this paper, a few explanatory notes on the course of the text may be useful. The methods used are briefly discussed first, followed by the general results of the surveys of distribution, ecology, and taxonomy of the Cloud Forest flora; taxonomic details for most of the species are given in the appendix. The first section of the Discussion deals

with the extent to which the flora is unique, with regard to species composition, by comparing it with published floristic data from other forests with similar climate and physiognomy. A hypothesis is then advanced for the origin of the Cloud Forest, taking into account its probable age and geographic affinities and the ecological preferences and taxonomic characteristics of its species. Finally, this hypothesis is discussed and developed in relation to some of the recent ideas and theories concerning island biology and vegetation succession, and some suggestions are made for future work.

Authors for all the species mentioned in the text are given in the companion descriptive paper (Sugden, 1982).

METHODS

Specimens of all the species of the Macuira Cloud Forest flora were examined at the herbaria of Kew (K), Oxford (FHO), the New York Botanical Garden (NY), the Missouri Botanical Garden (MO), the Smithsonian Institution (US), and the Instituto de Ciencias Naturales, Bogota (COL). In the absence of reliable published information on the majority of species, this is the only method available for determining geographic and ecological ranges. It is, however, not always satisfactory, since the labels accompanying specimens tend not to provide adequate information concerning locality or habitat. Often the degree square in which a specimen was collected cannot be determined with confidence; likewise, habitat data are of very variable quality, and altitude is frequently unrecorded. Details of habitat, if present at all, are frequently meaningless or uninformative. It was finally possible to locate about 70 percent of the specimens examined to the nearest degree square, and reliable habitat data were present on about 20 percent. Clearly, contemporary collectors must improve this situation. Altogether, some 4000 specimens were examined.

A further problem affecting the production of reliable distribution maps is that some regions are much better collected than others. Records are particularly concentrated around capital cities such as Bogota and Caracas, and in places such as Puerto Rico and the Canal Zone in Panama, where North American influence has been strong. The individual species distribution maps are not published here, but copies may be obtained from the author.

RESULTS

GEOGRAPHIC ELEMENTS

The elements of the Macuira Cloud Forest flora have been considered primarily in relation to the geographic position of the Serranía de Macuira, rather than to general patterns of distribution in the neotropical flora, not least because the latter have yet to be fully established. Thus, in the case of a species with a disjunct distribution in northern Venezuela, the Lesser Antilles, and southeastern Brazil (e.g., *Actinostemon concolor*), the Brazilian population is considered irrelevant for present purposes.

To assign species to geographic elements is not always simple, especially when the distributional records are patchy. Some species (see below) have dubious taxonomic status, and their true distribution is therefore uncertain. Also, there are inevitably some borderline cases that could be placed with justification in either of two elements. Distributions are not always as tidy as the plant geographer might wish, and there are some cases that defy categorization. The aim is simply to define some basic patterns or themes, within which there may be considerable variation.

The Macuira Cloud Forest flora has been divided into six basic elements that include all but six of the identified species. These remaining species (*Euphorbia cotinifolia*, *Iresine argentata*, *Ruellia malacosperma*, *Solanum dulcameroides*, *S. hirtum*, and *Zephyranthes tubispatha*) have not been included due to very inadequate data or uncertain taxonomy, or because their distribution has been obscured by cultivation. Of the six basic elements, five have been delimited according to large-scale differences in geographic distribution. These elements all contain species with wide distributions, while the sixth element contains species with narrow distributions. The elements are as follows:

- 1) Ten species, distributed throughout the neotropics and also occurring in other regions. This element can be divided into four sections according to the extra-neotropical distributions of the species: a) pan-tropical—*Coix lacryma-jobi*,¹ *Lycopodium cernuum*, *Microgramma lycopodioides*; b) tropical Africa—*Acroceras zizanioides*, *Gynerium sagittatum*, *Olyra latifolia*; 3) Malesia—*Clidemia hirta*;¹ and d) temperate America—*Erechtites hieracifolia*, *Erigeron bonariensis*, and *Baccharis trinervis*.
- 2) Forty-one species, widespread in the neotropics. This element can be divided into two sections: a) species widespread in the Caribbean area and tropical South America—*Adiantum latifolium*, *A. petiolatum*, *Chamissoa altissima*, *Desmodium axillare*, *Encyclia fragrans*, *Ichnanthus pallens*, *Jacquinella globosa*, *Margaritaria nobilis*, *Myrcia fallax*, *M. splendens*, *Nephrolepis rivularis*, *Polystachya foliosa*, *Randia formosa*, *Scleria secans*, *Talinum paniculatum*, and *Tillandsia bulbosa*; and b) neotropical species, with continental South American range mainly restricted to the Andean and/or Guayanian regions—*Anthurium scandens*, *Asplenium cristatum*, *A. myriophyllum*, *Blechnum occidentale*, *Campylocentrum micranthum*, *Cestrum alternifolium*, *Chiococca alba*, *Costus guanaiensis*, *Equisetum giganteum*, *Guzmania lingulata*, *Guzmania monostachya*, *Heliconia bihai*, *H. latispatha*, *Hymenophyllum hirsutum*, *Malvaviscus arboreus*, *Peperomia glabella*, *Pilea microphylla*, *Pleurothallis ruscifolia*, *Polypodium phyllitidis*, *Rapanea guianensis*, *Renalmia occidentalis*, *Spermacoce suffrutescens*, *Tectaria incisa*, *Utricularia incisa*, and *Xiphidium caeruleum*. Three of the

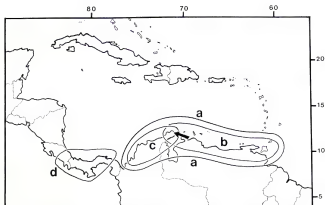
¹Distributions due to introductions by man.

species in this element (*Randia formosa*, *Heliconia bihai*, and *Utricularia alpina*) are absent from Central America.

- 3) Seven species, mainly restricted to Central America and continental tropical South America: *Acalypha diversifolia*, *Alternanthera pubiflora*, *Liabum asclepiadeum*, *Persea caerulea*, *Psychotria alba*, *Stromanthe lutea*, and *Tillandsia anceps*.
- 4) Twelve species, mainly restricted to continental tropical South America: *Aphelandra pulcherrima*, *Blechnum arborescens*, *Costus villosissimus*, *Epidendrum stenopetalum*, *Genipa spruceana*, *Grammitis blepharolepis*, *Guzmania sanguinea*, *Maranta divaricata*, *Miconia acinodendron*, *Psychotria barbiflora*, *Rhynchospora comata*, and *Vriesea heterandra*.
- 5) Twelve species, mainly restricted to the Caribbean region: *Clusia rosea*, *Conostegia icosandra*, *Cyathea arborea*, *Dendropanax arboreus*, *Ficus perforata*, *Guapira fragrans*, *Miconia laevigata*, *Microgramma piloselloides*, *Myrcianthes fragrans*, *Ouratea nitida*, *Polybotrya cervina*, and *Psychotria nervosa*.
- 6) Twenty-three species with narrow distributions in Caribbean Venezuela and/or Colombia. This element can be divided into five geographic subcategories, the limits of which are shown in MAP 1. The largest subcategory consists of 11 species with the Serranía de Macuira as the westernmost limit of their range: *Actinostemon concolor*, *Croton margaritensis*, *Epidendrum agathosmicum*, *Elleanthus arpophylostachys*, *Guzmania cylindrica*, *Hillia costanensis*, *Mandevilla bella*, *Maxillaria sophronitis*, *Mouriri rhizophoraefolia*, *Vriesea splendens*, and *Zamia muricata*. To date, none of these species has been recorded from other parts of Colombia. The distributions of these species east of the Serranía de Macuira vary in extent, the widest being that of *Vriesea splendens*, which occurs as far east as Guyana and Trinidad. They also show varying degrees of continuity and disjunction; *Croton margaritensis* has the most disjunct distribution, with one population on the Serranía de Macuira and another on Cerro San Juan,² Isla Margarita, 1000 km to the east.

The second subcategory in element 6 consists of six species (*Anthurium crassinervium*, *Coccoloba coronata*, *Guettarda divaricata*, *Machaerium humboldtianum*, *Philodendron erubescens*, and *Ruellia macrophylla*) distributed to either side of the Serranía de Macuira in northern Colombia and Venezuela. Of these, *Coccoloba coronata* has the widest distribution, with limits in eastern Panama and the southern Lesser Antilles. *Ruellia macrophylla* also has small disjunct populations in Cuba, Jamaica, and Peru and is included in this element only because

²Presently called Cerro Copey.



MAP 1. Approximate limits of subcategories of geographic element 6. a: *Anthurium crassinervium*, *Coccoloba coronata*, *Guettarda divaricata*, *Machaerium humboldtianum*, *Philodendron erubescens*, *Ruellia macrophylla*. b: *Actinostemon concolor*, *Croton margaritensis*, *Epidendrum agathosmicum*, *Elleanthus arpophyllostachys*, *Guzmania cylindrica*, *Hillia costanensis*, *Mandevilla bella*, *Maxillaria sophronitis*, *Mouriri rhizophoraefolia*, *Vriesea splendens*, *Zamia muricata*. c: *Cynanchum atrovirens*, *Rudgea marginata*, *Scutellaria verecunda*. d: *Stemmadenia minima*, *Schlegelia fuscata*. Arrow, Serrania de Macuira.

the Colombian and Venezuelan parts of its range are clearly the most substantial.

The third subcategory consists of three species (*Cynanchum atrovirens*, *Rudgea marginata*, and *Scutellaria verecunda*) that are restricted to northern Colombia, with the Serrania de Macuira as their northernmost limit.

The fourth subcategory consists of two species (*Stemmadenia minima* and *Schlegelia fuscata*) that have not previously been recorded outside eastern Central America; before this disjunction can be proved genuine, however, further collections are required from the intervening Sierra Nevada de Santa Marta. Also, there are some taxonomic problems associated with these species (see APPENDIX, and below).

The fifth subcategory contains a single species, *Cordia macuirensis*, which is the only species in the flora to have possible endemic status. It is closely related and similar in appearance to *C. curassavica*, which is widespread in the surrounding dry lowlands and may simply be an incipient species (see APPENDIX).

The sixth element is not delimited in the same strict sense as the first five, since it represents a variety of distribution patterns. The species in this element have only the relatively restricted nature of their distri-

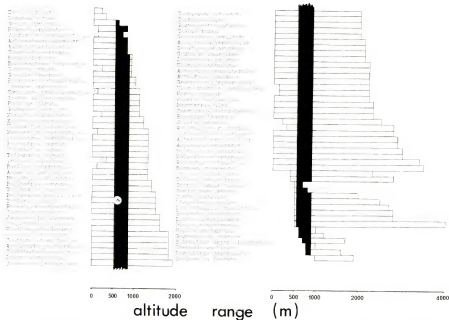


FIGURE 1. Altitudinal ranges of Macuira Cloud Forest species. Black bar represents altitudinal limits of Macuira Cloud Forest.

butions in common and have been grouped together for interpretative purposes only. Strictly, the subcategories of element 6 are elements in themselves.

ECOLOGICAL DISTRIBUTION

It is not practical to divide the flora into precise ecological elements, partly because of the wide habitat preferences of many of the species, and partly due to the variation in quality of the sources of information. The extent to which the flora is specialized to low-altitude cloud forest can be partly determined by examining the range of altitude and types of vegetation across which the species are distributed. The geographic evidence has already indicated that the level of specialization must be quite low.

In FIGURE 1 the altitudinal ranges are shown for the ninety-one species for which there are sufficient data. Most of the species occur in lowland habitats, and only sixteen are restricted to montane regions. Of these sixteen species, eight (*Cordia macuirensis*, *Croton margaritensis*, *Elleanthus arphyllostachys*, *Guzmania cylindrica*, *Hillia costanensis*, *Maxillaria sophronitis*, *Schlegelia fuscata*, and *Stemmadenia minima*) are confined to low-altitude cloud forests, and all have relatively restricted geographic distribution.

Of the large proportion of species occurring in lowland habitats, only nine do not occur at elevations higher than that of the highest peak of the Serranía de Macuira (865 m); the remainder occur at elevations both higher and lower than the limits of the Macuira Cloud Forest. Sixty-six species occur over altitudinal ranges of 1000 m or more; thirty-three of these occur over ranges of 2000 m or more, with *Rapanea guianensis* having the widest range (0–3500 m).

The range of habitats in which each species has been recorded is given in TABLE 1. The 11 habitat types included are grouped under the broad headings of Lowland, Montane, and Disturbed. The lowland habitats include littoral zones, savanna and cerrado, dry forest, moist forest (including lowland rain forest), and swamp. The montane habitats include moist (and cloud) forest and páramo. Disturbed habitats include secondary vegetation, banks of rivers and streams, exposed rocky hillsides, and ravines, without regard to altitude. In the present context, the definition of these terms must be somewhat loose because of the imprecise nature of basic information. A lowland species is here defined as one that occurs from at or near sea level to no more than 1000 m, while a montane species is one occurring only above 500 m; the overlap is necessary due to the "Massenerhebung" effect, or the lowering of montane vegetation belts on isolated mountains and ridges (Grubb, 1971). Disturbed habitats are difficult to define precisely; disturbance can be broadly regarded as the combination of mechanisms that limit plant biomass by causing its partial or total periodic destruction (Grime, 1979). Disturbance may be regular, as in the case of riverbanks subject to flooding or landslides, or may have occurred but once, as in a tract of land cleared for human use and subsequently abandoned.

In TABLE 1 the species are listed according to life form, and their occurrence in any given habitat is recorded on the basis of presence or absence.

TABLE 1. Ecological distribution of Macaira Cloud Forest species.*

	LOWLAND HABITATS				MONTANE HABITATS		DISTURBED HABITATS			
	Littoral	Savanna/Cerrado	Dry Forest	Moist Forest	Swamp	Cloud Forest/ Moist Forest	Paramo	Secondary	River banks	Exposed rocky hillsides
CANOPY TREES†										
<i>Blechnum arborescens</i>							+		+	
<i>Cyathea arborea</i>							+			+
<i>Stemmadenia minima</i>							+			
<i>Dendropanax arboreus</i>			+	+						
<i>Euphorbia cotinifolia</i>		+						+		
<i>Margaritaria nobilis</i>			+	+					+	
<i>Persea caerulea</i>						+		+		+
<i>Conostegia icosandra</i>		+	+	+				+		
<i>Miconia acinodendron</i>				+		+		+	+	
<i>Miconia laevigata</i>						+		+		+
<i>Mouriri rhizophoraefolia</i>			+			+		+		
<i>Ficus perforata</i>	+	+	+	+				+		+
<i>Rapanea guianensis</i>	+	+	+		+	+		+		
<i>Myrcia fallax</i>		+		+				+		
<i>Guapira fragrans</i>	+		+			+				

<i>Ouratea nitida</i>					+				
<i>Coccoloba coronata</i>				+			+		+
<i>Genipa spruceana</i>					+			+	
<i>Randia formosa</i>	+	+	+		+		+		

UNDERSTORY SHRUBS AND COARSE HERBS

<i>Equisetum giganteum</i>					+		+	+	
<i>Maranta divaricata</i>				+		+			
<i>Stromanthe lutea</i>						+		+	
<i>Heliconia bihai</i>				+				+	
<i>Heliconia latispatha</i>				+	+		+	+	
<i>Costus guanaiensis</i>				+	+	+	+		
<i>Costus villosissimus</i>				+				+	
<i>Renealmia occidentalis</i>						+		+	
<i>Alternanthera pubiflora</i>	+		+				+	+	
<i>Chamissoa altissima</i>			+	+	+		+	+	
<i>Acalypha diversifolia</i>	+			+		+			
<i>Actinostemon concolor</i>			+			+			+
<i>Croton margaritensis</i>						+			
<i>Malvaviscus arboreus</i>	+		+	+	+	+	+		
<i>Clidemia hirta</i>							+	+	
<i>Chiococca alba</i>	+	+	+				+	+	
<i>Psychotria alba</i>				+	+	+			
<i>Psychotria barbiflora</i>				+			+		
<i>Psychotria nervosa</i>	+					+			
<i>Spermacoce suffrutescens</i>		+			+		+	+	+
<i>Cestrum alternifolium</i>	+	+	+			+	+	+	

GROUND LAYER

<i>Adiantum latifolium</i>		+	+	+			+	+	+
<i>Adiantum petiolatum</i>		+	+	+				+	+

TABLE 1 (continued).

	LOWLAND HABITATS				MONTANE HABITATS		DISTURBED HABITATS		
	Littoral	Savanna/Cerrado	Dry Forest	Moist Forest	Swamp	Paramo	Cloud Forest/ Moist Forest	Secondary	River banks Exposed rocky hillsides Ravines
<i>Asplenium cristatum</i>					+		+		
<i>Asplenium myriophyllum</i>							+		
<i>Blechnum occidentale</i>			+	+			+		
<i>Polybotrya cervina</i>				+			+		+
<i>Tectaria incisa</i>									+
<i>Rhynchospora comata</i>			+	+			+		
<i>Scleria secans</i>			+		+		+		
<i>Ichnanthus pallens</i>		+		+	+		+		
<i>Xiphidium caeruleum</i>			+	+			+		
<i>Campylocentrum micranthum</i>			+	+				+	
<i>Encyelia fragrans</i>		+	+	+			+		
<i>Ruellia malacosperma</i>									+
<i>Liabum asclepiadeum</i>								+	
<i>Pilea microphylla</i>					+			+	
EPIPHYTES									
<i>Grammitis blepharolepis</i>				+					

Hymenophyllum hirsutum					+		+
Nephrolepis rivularis			+	+	+		
Microgramma piloselloides					+		
Polypodium phyllitidis			+				+
Anthurium scandens			+		+	+	+
Guzmania cylindrica					+		
Guzmania lingulata			+	+	+		+
Guzmania monostachya	+		+	+	+		
Guzmania sanguinea			+		+		
Tillandsia anceps			+	+	+		
Tillandsia bulbosa		+	+		+		
Vriesea heterandra					+		
Vriesea splendens			+	+	+		+
Campylocentrum micranthum			+	+		+	+
Elleanthus arphylllostachys					+		
Jacquinella globosa			+			+	+
Maxillaria sophronitis					+		
Pleurothallis ruscifolia			+		+		
Polystachya foliosa		+	+	+	+		+
Utricularia alpina				+	+	+	+
Peperomia glabella	+		+	+	+		
Hillia costanensis					+		

GROUND-ROOTED CLIMBERS AND SCRANBLERS

Iresine argentata			+		+		
Mandevilla bella							+
Cynanchum atrovirens	+						
Schlegelia fuscata					+		

*Derived mainly from information accompanying herbarium specimens.

†Species listed in same order and under same categories as in table 3 in Sugden (1982). Category under which each species is listed refers to its life form in Macuira Cloud Forest only (e.g., *Blechnum arborescens* is not a canopy tree, by definition, in páramo).

Species missing from the list include those for which information was not available, as well as the widespread weedy species in geographic element 1; the latter tend to occur in early secondary vegetation. The table thus includes 82 species, or 66 percent of the flora. The ecological distribution of each life form, taken from information in TABLE 1, is depicted in FIGURE 2.

The remarkable general feature of these results is the wide ecological distribution of most of the Macuira Cloud Forest species; there are only eighteen that do not occur in more than one of the three major habitat groups. These include the eight species restricted to low-altitude cloud forest. Of the remaining ten, *Clidemia hirta*, *Ruellia malacosperma*, *Liabum asclepiadeum*, and *Mandevilla bella* are apparently restricted to disturbed habitats, *Dendropanax arboreus* to lowland dry and moist forest, *Ouratea nitida* to lowland swamps, *Grammitis blepharolepis* to lowland moist forest, *Cynanchum atrovirens* to dry scrub and lowland savanna, and *Microgramma piloselloides* and *Vriesea heterandra* to moist montane forest. However, *Microgramma piloselloides* occurs as low as 100 m, as shown in FIGURE 1, so these data should be viewed with some caution.

That so many species should occur across such a wide range of habitat shows that the flora is largely composed of "generalist" rather than "specialist" species. Moreover, the fact that 56 of the 82 species listed in TABLE 1 occur in disturbed habitats suggests that the flora has a strong colonizing or pioneering element. The histograms in FIGURE 2 demonstrate the high proportion of species from disturbed habitats in each life form (with the exception of the epiphytes, where the proportion from undisturbed habitats is higher).

TAXONOMY

Alongside the trends of wide geographic distribution and ecological amplitude, there appears to be a tendency in the flora toward species with substantial infraspecific variation. There are at least 34 variable species in the flora (see APPENDIX), most of which are widely distributed. There are examples of variation at the subspecific (*Encyclia fragrans*, *Psychotria nervosa*) and the varietal levels (*Guzmania lingulata*, *Vriesea splendens*), and of continuous variation (*Anthurium scandens*, *Dendropanax arboreus*, *Ficus perforata*), although these different kinds of variation must in part reflect the individual preferences of taxonomists. The evidence is not sufficient to determine whether ecotypic variation occurs, but such patterns might emerge given more detailed field studies and more extensive collections; certainly, some of the variation has a geographic basis (see APPENDIX). Nevertheless, there are at least 15 species, some with wide distribution, that exhibit little or no infraspecific variation; these include *Aphelandra pulcherrima*, *Costus villosissimus*, *Epidendrum stenopetalum*, *Equisetum giganteum*, *Guzmania monostachya*, *Heliconia latispatha*, *Hillia costanensis*, *Mouriri rhizophoraefolia*, *Ouratea nitida*, *Peperomia glabella*, *Ruellia macrophylla*, *Talinum paniculatum*, *Tillandsia anceps*, *T. bulbosa*, and *Vriesea heterandra*.

Among the species with narrower ecological and geographic distribution, there are several with dubious taxonomic status (see APPENDIX); these may

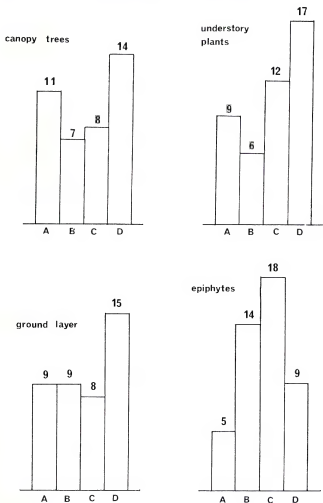


FIGURE 2. Histograms of ecological distribution of Macuira Cloud Forest species, drawn from data in Table 1. Letters indicate habitat: A, dry; B, moist lowland; C, moist montane; D, disturbed.

be no more than infraspecific forms of more widely distributed taxa. There are others, also with narrow distribution, that are members of geographically replacing species complexes or superspecies *sensu* Mayr (1963) and F. White (1979), and these may have evolved recently from common ancestral stock (see APPENDIX).

The taxonomic status of the 38 species not discussed in this section or in the APPENDIX has not been examined, either because there was no information available, or because (in the case of species with wide extra-neotropical distribution) information was not sought. This does not, however, affect the general conclusion that the flora has a large component of variable species—a component that may become larger when more data become available. An expansion of this component would also reduce the proportion of narrowly distributed species, thus reinforcing the evidence that the Macuira Cloud Forest flora is composed largely of opportunist species with wide ecological and geographic distribution.

DISCUSSION

COMPARISON WITH OTHER CLOUD FORESTS

Before consideration of the origin of the Macuira Cloud Forest, it is necessary to consider briefly the extent to which its flora is unique, both in species composition and in the characteristics (low species diversity, lack of specialization, low endemism, and high dispersibility) described above and in Sugden (in press). Comparative discussion will be restricted mainly to those neotropical forests that most closely resemble the Macuira Cloud Forest in terms of physiognomy, area, climate, and isolation by arid lowlands. The two forests that appear to fulfill these criteria (see Sugden, 1982) are in coastal Venezuela, one on the summit of Cerro Santa Ana, Peninsula de Paraguaná, Edo. Falcón, and one on Cerro San Juan, Isla Margarita, Edo. Nueva Esparta. Floristic accounts for these two mountains have been produced respectively by Tamayo (1941) and Johnston (1909), although Tamayo's list is incomplete due to the short duration of his visit to Cerro Santa Ana.

Specific and generic diversity are similar on the Serranía de Macuira and Cerro San Juan. The somewhat higher number of species on the latter (166, vs. 126 on the Serranía de Macuira) is almost entirely the result of a larger complement of pteridophytes (55 species, vs. 19 on the Serranía de Macuira)—an interesting feature for which there is no ready explanation. The numbers of species of other vascular plants are almost equal (111 on Cerro San Juan, 106 on the Serranía de Macuira), and the relative proportions of monocotyledons and dicotyledons are also similar in the two localities. As on the Serranía de Macuira, the ratio of species to genera is low on Cerro San Juan; this also applies to Cerro Santa Ana. Those genera that are represented by two or more species are generally ferns and monocotyledons; among the dicotyledons only *Miconia* and *Psychotria* have more than one species on each mountain.

There is relatively little overlap in species composition between the three cloud forests. Of the 56 species of vascular plants recorded by Tamayo (1941) on Cerro Santa Ana, and the 155 species in Johnston's (1909) list for Cerro San Juan, only 18 percent and 11 percent, respectively, are shared with the Macuira Cloud Forest. Only three species (*Guzmania lingulata*, *Vriesea splendens*, and *Utricularia alpina*) are known from all three mountains. Thus, there is no distinct association of species that can be considered characteristic of these cloud forests. At the generic level there is more overlap, with Cerro Santa Ana and Cerro San Juan each sharing ca. 50 percent of their genera with the Macuira Cloud Forest. Genera that occur on all three mountains are *Elaphoglossum*, *Microgramma*, *Polypodium*, *Blechnum*, *Hymenophyllum*, *Lycopodium*, *Scleria*, *Guzmania*, *Tillandsia*, *Epidendrum*, *Piper*, *Clusia*, *Myrcia*, *Miconia*, *Utricularia*, *Hillia*, and *Passiflora*; with the exception of *Hillia*, all are large genera with wide neotropical distributions. It would probably be wrong to conclude that there is a distinct core of genera characteristic of these cloud forests since most of them can be found in most moist neotropical forests.

There are few instances of closely related species replacing one another on the three mountains. Between the Serranía de Macuira and Cerro San Juan, vicariousness of this kind is confined mainly to herbaceous and epiphytic genera (e.g., *Lycopodium*, *Rhynchospora*, *Scleria*, *Anthurium*, *Tillandsia*, *Heliconia*, *Maranta*, *Stromanthe*, and *Epidendrum*) rather than the dominant woody genera. The presence on Cerro San Juan of families not represented in the Macuira Cloud Forest (Palmae, Commelinaceae, Liliaceae, Dioscoreaceae, Iridaceae, Proteaceae, Aristolochiaceae, Oxalidaceae, Rutaceae, Marcgraviaceae, Violaceae, Flacourtiaceae, Begoniaceae, Thymelaeaceae, Combretaceae, Ericaceae, Gentianaceae, Gesneriaceae, and Campanulaceae) supports the conclusion that the similarity of these cloud forests has a weak floristic basis.

In spite of these compositional differences, the three floras have several important characteristics in common, as well as their similar species diversity and physiognomy. Endemism is low in all three cases. No endemic species appear to have been recorded from Cerro Santa Ana. Although Johnston's (1909) original list for Cerro San Juan contained eight endemics (5 percent of the flora), four belong to large genera with many variable species (*Passiflora*, *Piper*, and *Pleurothallis*), one has been reduced to a subspecies of a widespread variable species (*Chiococca alba*; see APPENDIX), and one (*Croton margaritensis*) has since been found on the Serranía de Macuira. Johnston confidently expected that many of the 42 new species described from his entire collection from Isla Margarita would be found in other regions then not yet visited by collectors.

The levels of endemism in various other less isolated and more extensive neotropical cloud forests are apparently higher than those in the Serranía de Macuira or Cerro San Juan. Steyermark (1975) found that 6 percent of the flora of the cloud forest on the Sierra de San Luis, Edo. Falcón, Venezuela, was endemic to the mountain, while an additional 29 percent had been recorded previously only from the Cordillera de la Costa to the east. Although

the San Luis cloud forests are isolated by arid lowlands, they are more extensive and have a greater diversity of habitats than the Macuira Cloud Forest. Lewis (1971) estimated that about 25 percent of the vascular plant species in Panamanian and Colombian cloud forests are endemic to either particular localities or vegetation types, indicating a greater degree of specialization to the habitat than is shown by the Macuira or San Juan floras. This high figure may, however, be due in part to weak taxonomy in many groups and to the tendency to expect that isolated, unexplored mountains are bound to support new species. Hodge (1954) showed that the elfin forests in Dominica support more endemics and species of restricted distribution than do other vegetation formations on the island. On the other hand, Howard (1973) observed that elfin forests in the Antilles support few endemics, most species being widespread in comparable habitats—in spite of the high proportion (32 percent) of species from the Elfin Forest on Pico del Oeste, Luquillo Mountains (Howard, 1968) that are endemic to Puerto Rico. Clearly, it is unwise to generalize in these matters since there is so much variation between localities and because the term "endemism" is often loosely applied in the literature.

Cursory inspection of the floristic lists from Cerro Santa Ana and Cerro San Juan indicates that the dispersibility of the cloud forest species is generally good, as in the Serranía de Macuira (Sugden, in press b). In both localities there is a high proportion (40–50 percent) of wind-dispersed epiphytes and herbs; the majority of the trees and shrubs have fruits and seeds that suggest endozoic dispersal by birds.

Thus, while the Macuira Cloud Forest is physiognomically similar to some other low-altitude isolated cloud forests, and although its flora bears some gross resemblances to the floras of these forests, it consists of a unique assemblage of species that do not form a distinct association or community in any other situation. This is as true of the dominant or common species as it is of the entire flora.

A final cautionary note should be added to the effect that the above comparisons (especially those concerning the floristics of Cerro Santa Ana) have relied partly on incomplete data. It will probably be necessary to refine and update these comparisons in the light of the new information being gathered in the current Venezuelan floristic projects in Edo. Falcón and Isla Margarita.

ORIGIN OF THE MACUIRA CLOUD FOREST: A HYPOTHESIS

HISTORICAL ORIGIN. The lack of endemic species in the Cloud Forest clearly demonstrates that the flora is not even a partial relict comprising species representing ancient groups that have become extinct or drastically reduced in their distribution elsewhere. The only possible exception to this is the cycad *Zamia muricata*, but the taxonomic relationships of this species have not received adequate treatment and its evolutionary status is unknown. The lack of endemics also demonstrates that isolation has not been effective, either spatially or temporally, in allowing the evolution of species unique to the Serranía de Macuira (with the possible exception of *Cordia macuirensis*).

The Cloud Forest also does not appear to be an ecological refuge in the sense of the Pleistocene Amazonian refugia originally proposed by Haffer (1969), in which widespread species characteristic of lowland moist forest were constricted into isolated pockets during drier climatic periods. The lack of endemics, together with the wide ecological amplitude and high dispersibility of most of the Cloud Forest species, argues against the notion that they were once widespread in the Guajira lowlands and have been forced to the summits of the Serranía de Macuira by increasing aridity.

An additional important negative point is that the prominent colonizing component of the flora is not the result of recent disturbance of the Cloud Forest. Human interference on the upper slopes of the Serranía de Macuira is, and always has been, very limited. There are several features of the Cloud Forest that tend to confirm this view. The most striking are the floristic and physiognomic uniformity both within and between the three principal "islands" of Cloud Forest on the Serranía, and the very small number of species that could owe their presence to dispersal by man or livestock (Sugden, in press b).

Since the Cloud Forest is not an evolutionary relict or an ecological refuge, an alternative hypothesis concerning its origin is necessary. The prevalence of widespread species characteristic of disturbed habitats suggests that at some time the conditions on the summits of the Serranía changed in some manner favorable for colonization by successional species of this kind. This change would of necessity have been from a dry to a wet climate rather than from a very wet to a less wet climate; the latter would have resulted in an ecological refuge, which has already been shown to be unlikely. It would also have been a change from a seasonal climate, such as prevails over the Guajira lowlands at present, to a less seasonal climate with a more even distribution of annual precipitation. This could have occurred as a result of an increase in the frequency, regularity, and duration of periods of cloud cover and a lowering of the average cloud base level.

A situation may therefore be envisaged in which the dry forest types presently occurring immediately below the Cloud Forest (Sugden, 1982) extended to the highest summits of the Serranía de Macuira, as they do now in the neighboring Serranía de Jarara. As the frequency and duration of cloud cover increased, reaching the critical point at which Cloud Forest can be maintained, propagules of Cloud Forest species carried by air currents and by birds were able to germinate successfully and to establish populations on the summits of the hills. These populations gradually expanded as the critical level of cloud cover extended down the hills to its present altitude. At the same time, the dry forest species—unable due to their seasonal growth patterns to compete in the wetter and darker conditions prevailing in the advancing Cloud Forest—were forced down the slopes.

As the Cloud Forest spread down the slopes from the summits of the Serranía, its area increased and its topographical habitats diversified (see Sugden, 1982, for a summary of present habitat diversity in the Cloud Forest), permitting the establishment of more species—particularly the epiphytes and coarse herbs that are the likely beneficiaries of an increase in habitat diversity

(Sugden, in press a). The development of streams and small swamps in the gullies provided a habitat suitable for large monocotyledons such as *Heliconia*, *Costus*, *Renealmia*, *Maranta*, and *Dieffenbachia*. The more prolonged and heavy cloud cover toward the summits (Sugden, 1982, table 1) permitted the establishment of populations of epiphytic species with a high moisture requirement (e.g., *Vriesea splendens* (Sugden, in press a)). Other epiphytes, such as *Tillandsia anceps* and *Guzmania monostachya*, which are tolerant of the drier conditions prevailing toward the lower limit of the Cloud Forest (Sugden, in press a), maintained their densest populations nearer to the retreating edge of the dry forest. Because moisture supply is not such a critical factor in the distribution of trees and shrubs (Grubb & Tanner, 1976), the dominant woody species maintained their presence throughout the Cloud Forest as it expanded.

If events of this kind occurred, then the remaining questions concern when the sequence was initiated and from where the flora was derived. While there is no firm evidence that the Macuira Cloud Forest has not been present for a very long time (i.e., since before the Pleistocene), this is unlikely for several reasons. The flora itself has no features that indicate great age. Furthermore, there is evidence for some recent climatic changes that would have affected the regime of cloud cover on the Serranía de Macuira. Although there are no data concerning the climatic history of Guajira itself, there have been events (e.g., the drier, more seasonal period ca. 8000–4000 years B.P., and the rise in sea level that has continued since the end of the last glacial epoch 12,500 years B.P. (see Sugden, in press b, for details and references)) in neighboring regions that could have accompanied a reduction in cloud cover to a level below that required to sustain the Cloud Forest. Such a reduction could have resulted in a more seasonal climate, a higher cloud base level, less prolonged daily periods of cloud cover, or a combination of any of these. In short, the existence of the Cloud Forest is precarious, and it is unlikely that the requisite climatic conditions have been constant for many millenia, let alone geologic eras. It is not unreasonable to conclude that the sequence of events proposed above began only a few thousand years ago.

This hypothesis does not preclude the existence of a moist summit forest at earlier times. Such a forest, as a vegetation type rather than a floristic assemblage, may have undergone a cycle of colonization and extinction in the Serranía de Macuira in response to climatic fluctuations during the Quaternary and before, although the present flora provides no such evidence. It also does not preclude the possibility that colonization and local extinction are occurring at present. There are a number of species, including *Blechnum arborescens*, *Cyathea arborea*, *Equisetum giganteum*, *Grammitis blepharolepis*, *Microgramma piloselloides*, *Dichaea* sp., *Elleanthus arpophyllostachys*, *Encyclia fragrans*, *Jacquinella globosa*, *Erigeron bonariensis*, and *Psychotria barbiflora*, that were encountered only once or twice, either as single individuals or in clumps, and there may be more rare species that were never encountered during this study. Such rarity suggests that these species are scarcely established in the Cloud Forest, although it is impossible to say whether they are remnants of a larger population on the verge of local ex-

tion or the newly colonized forebears of a future larger population.

A similar hypothesis has been proposed for the origin of the moist upland flora of the Galapagos archipelago, which was mostly derived through long-distance dispersal from the mainland of South America (Johnson & Raven, 1973; Porter, 1976). The upper slopes of the higher islands in the Galapagos receive substantially more rainfall, and sometimes more cloud cover, than the lower slopes. The percentage of the flora that is endemic to the archipelago is lower in the moist uplands than in the arid and transition zones. On the basis of this and evidence from core samples of Galapagos lake sediments that indicate a much drier climate 30,000–10,000 years B.P., Johnson and Raven (1973) suggest that most of the species of the upland flora have arrived from the mainland during the last 10,000 years. The majority of these species are adapted for endozoic dispersal by birds (Johnson & Raven, 1973; Porter, 1976).

GEOGRAPHIC AFFINITIES. The evidence concerning the geographic derivation of the Cloud Forest flora is perhaps less equivocal. Because the flora does not closely resemble the floras of other cloud forests on the Caribbean coast of South America or the Antilles, it clearly does not fit any wider chorological pattern. Also, the various distributions of the relatively restricted species (element 6) show that the present complement of species in the flora cannot be the result of derivation from any single source. Rather, there are definite relationships with regions to the west, the southwest and south, and the east, as evinced by the species in element 6 with the Serranía de Macuira as one of their geographic limits of distribution. This indicates the existence of long-distance dispersal routes from all the neighboring parts of the South American mainland, as well as from Panama.

That some species may have been derived from the Antilles is also possible. *Cyathea arborea*, apart from one dubious record from Caracas, is known only from the Antilles (Tryon, 1979) and Isla Margarita (Steyermark & Ortega, 1981). Its propagules may have arrived in the Serranía de Macuira borne on the trade winds blowing from the Lesser Antilles. There are no other wind-dispersed species for which such a derivation would have to be invoked, but the possibility cannot be ruled out. Also, some of the migratory birds from the Antilles and beyond may make their first landfall in the region of the Serranía de Macuira (Sugden, in press b); again, however, there are no bird-dispersed species in the Cloud Forest flora that demand such an origin.

There are several indications that the greater proportion of the flora may have been derived from northern and northwestern Venezuela. The largest subcategory in geographic element 6 (species with restricted distributions) comprises species that have their westernmost outpost in the Macuira Cloud Forest; this perhaps constitutes evidence for more migration from northern Venezuela than from other mainland regions. Steyermark (1975) reached a similar conclusion regarding the derivation of the flora of the Sierra de San Luis, Edo. Falcón, Venezuela. The large element of Venezuelan endemics in the San Luis flora was mainly derived from the Cordillera de la Costa,

which was in existence before the uplift of the Sierra de San Luis. About 30 percent of the flora had not previously been recorded outside the Cordillera de la Costa. This appears to be good evidence for the existence of a migration route from east to west. A smaller proportion of the San Luis flora (ca. 12%) was apparently derived from the Andes to the south. If the Cordillera de la Costa retained its moist climate throughout the Pleistocene and was, as Prance (1974, 1977) has suggested, a refuge for moist forest species, then it is indeed likely to have been an important source of species colonizing younger moist forests to the west. The strong easterly component of the prevailing winds in Guajira and northern Venezuela is probably an important factor contributing to the affinities between the floras of the two regions. This would affect not only those plants with wind-dispersed propagules, since migratory and vagrant birds tend to travel with the wind rather than against it. Indeed, both wind- and bird-dispersed species in the Macuira Cloud Forest demonstrate the Venezuelan connection.

Further evidence for a stronger link with northern Venezuela than with other regions is provided by some of the animal groups that have been investigated in the Serranía de Macuira. Many of the butterflies of the Cloud Forest are probably of Venezuelan derivation (J. L. B. Mallet, pers. comm.). Examination of the distribution of birds recorded by Marinkelle (1970) in the Serranía reveals, out of a total of 38 narrowly restricted taxa, 19 species and subspecies restricted mainly to northern Venezuela and the Serranía de Macuira. These data must be viewed with caution, however, partly because the collections were made over short periods and are probably incomplete, and partly because the taxonomic criteria and the factors affecting the distribution of these organisms are different from those affecting plants.

The species of restricted distribution that have arrived in the Serranía de Macuira from the south and west are fewer than those that are apparently derived from Venezuela. Successful dispersal events in this direction might be expected to be restricted to the brief rainy season, when the winds blow mainly from the south.

Since the bulk of the flora is widely distributed, it cannot be used to interpret the geographic derivation of the component species. There is no reason to suppose, however, that the patterns of dispersal and migration of the widespread species are governed by factors different from those affecting species of more narrow distribution. Given the possible existence of an important migration route from northern Venezuela, mediated by the prevailing winds, it is likely that most of the widely distributed species in the Macuira Cloud Forest flora have a Venezuelan derivation.

To summarize, it has been postulated that the Cloud Forest was formed *de novo* following a recent climatic change, and that the flora has been derived from various parts of the South American mainland (especially northern Venezuela) and possibly the Antilles. This hypothesis is based on the assumptions that there is a critical amount of cloud cover below which the Cloud Forest cannot be sustained, and that long-distance dispersal can be held accountable for the presence of virtually all the species in the flora. Habitat diversity increased as the Cloud Forest expanded, with favorable

consequences for the epiphytic and herbaceous communities but with little effect on the distribution of the woody species within the Cloud Forest. It is suggested that the homogeneity of the woody flora is the result of a wider tolerance of soil moisture levels.

THE CLOUD FOREST, ISLAND BIOLOGY, AND SUCCESSION: CONCLUSIONS

The hypothesis for the origin of the Cloud Forest flora is based on inference and speculation concerning historical events, and although plausible, it is clearly untestable. Also, it does not by itself account for several of the more interesting features of the Macuira Cloud Forest, in particular, the relatively low number of species, the uniqueness of the assemblage of species, and the presence of a large pioneering contingent in an apparently mature forest. These issues may profitably be considered in light of some of the current ideas concerning insular biogeography and vegetation succession; in so doing, one can arrive at some predictions and possibilities that could be investigated by further fieldwork.

The Serranía de Macuira, in spite of its modern lowland links to other mountain ranges, is analogous to oceanic islands in several ways. Oceanic islands and archipelagoes are characterized by their permanent isolation, dating from their genesis, from continental regions. The Serranía de Macuira has never had a high-altitude connection to either the Andes or the Sierra Nevada de Santa Marta, and the geologic evidence (Macdonald, 1964; Lockwood, 1965) indicates that faulting and erosion separated it from the neighboring Serranía de Jarara during the Oligocene. Indeed, it was a true island during the Pliocene, when a major marine transgression inundated the lowlands of Guajira. Also, there is no element in the Cloud Forest flora that requires a lowland connection to explain its presence. The risks of drawing parallels between oceanic islands and the upper slopes and summits of continental mountains have been discussed by F. White (1971) and by Mabberley (1979); due to climatic fluctuations, montane vegetation belts can contract and expand, sometimes forming extensive connections with those of other mountains, and floristic isolation may be reduced or broken down altogether. The insularity of the Macuira Cloud Forest, however, appears to be permanent and genuine (Sugden, in press b).

The hypothesis for the origin of the flora entailed an initial disturbance—that is, a climatic change that permitted the establishment of the Cloud Forest—followed by a gradual retreat of the drier formations down the slopes of the Serranía. P. S. White (1979), drawing partly on the ideas of Grime (1977, 1979), has stressed that assemblages of species in disturbed habitats tend to be transient and locally unique—i.e., they are not repeated in space. Insular species assemblages sometimes show a similar lack of organization into well-defined communities (Linhart, 1980). Moreover, species of disturbed habitats tend to be tolerant of wide ecological extremes, which is exactly the case with the bulk of the Macuira Cloud Forest flora. However, if disturbance ceases and there are no species of later successional stages to

take the place of the pioneers (Mabberley, 1979), then the succession is curtailed and the pioneers form the "climax" (P. S. White, 1979). In the case of the Macuira Cloud Forest, isolation may have reduced the frequency of successful dispersal events so as to prevent the establishment both of species of later successional stages and of other pioneering species with less mobile propagules.

It may be suggested that the uniqueness of the assemblage of species in the Macuira Cloud Forest (and of the equally individual assemblages on the summits of Cerro Santa Ana and Cerro San Juan) is simply the result of colonization by a random subset of taxa with good dispersibility and wide ecological tolerance. Random colonization of this kind is regarded by some as an important determinant of island species composition (Simberloff, 1978; Connor & Simberloff, 1978, 1979). The size and composition of this subset must initially have been constrained by the ability of the propagules to germinate and eventually to establish a population of reproducing adults in the conditions prevailing in the Cloud Forest. The establishment of such a population might be expected to be favored by an ability to produce large quantities of seed (and/or vegetatively propagated individuals) and by unspecialized pollination systems that reduce competition for pollinators. Early successional species often have less-specialized pollination mechanisms than species of later successional stages (Parrish & Bazzaz, 1979); similarly, island species may have pollination mechanisms that are unspecialized relative to those of mainland species (Linhart & Feinsinger, 1980). Groups with efficient dispersal may be unable to establish populations in new areas if their pollinators are absent (Carlquist, 1967). It is interesting in this context that most of the Cloud Forest species with large, showy (specialized?) flowers (*Stemmadenia minima*, *Mandevilla bella*, *Hillia costanensis*) have restricted distributions (element 6), while most of the widely distributed species have small, apparently unspecialized flowers.

Reproductive biology would probably not be the sole determinant of the composition of the community. There is no reason to assume that propagules of a wide variety of species did not continue to arrive in the Serranía de Macuira by long-distance dispersal following the appearance of the Cloud Forest, and do not continue to do so now. If conditions remain the same, later arrivals may have less chance of establishment because of the reduction in available regeneration niches caused by earlier arrivals. The availability of regeneration niches is a significant factor affecting species richness (Grubb, 1977), and the frequency of disturbances affects the chances of establishment of pioneer species (Grime, 1979; P. S. White, 1979; Bazzaz & Pickett, 1980). The frequency of gaps in the Cloud Forest is low, possibly due to the slow growth rates imposed by nutrient stress and a concomitant low rate of disturbance. It may be significant that some of the extremely rare species in the flora were found in gaps rather than under a closed canopy. *Cyathea arborea* and *Equisetum giganteum* were each encountered once, on open, sunlit streambanks, and *Erigeron bonariensis* was found on a small, open patch of ground at the summit of Cerro Huarech (see Sugden, 1982, map 3) that had been cleared for a helicopter landing site some years pre-

viously and had subsequently been abandoned. Large-scale disturbances (such as hurricanes or earthquakes) that could afford opportunities for colonization by new species have not been recorded in the region.

There is a persistent pool of seedlings and young plants of the dominant tree species in the Cloud Forest. In a restricted survey of 98 m² on a sheltered ridge at 650 m, there were 218, 100, and 73 seedlings less than 20 cm tall of *Guapira fragrans*, *Rapanea guianensis*, and *Myrcianthes fragrans*, respectively. It is not known whether these seedlings remain in a "dormant" post-germinative state awaiting a light gap caused by a fallen tree, as do many species of later successional stages in lowland rain forest (Whitmore, 1978; Grime, 1979), or whether they grow continuously. In either case, however, they would have a great numerical advantage over seedlings germinated from newly arrived propagules. Low species diversity in the Macuira Cloud Forest may thus be due in part to competitive exclusion of later arrivals, regardless of the ecological amplitude and competitive ability of the latter. It might also be expected that species with wide ecological tolerance would tend to exclude species with narrower niches (see, for example, Lack, 1976).

Random colonization, unspecialized pollination systems, high seed-set, and competition for regeneration niches may thus be considered as possible determinants of the unique species assemblage and low species number in the Macuira Cloud Forest. There are other factors that should be entertained as well. First, the generations of the present Cloud Forest species may have undergone selection subsequent to their initial colonization; they may have lost some of their pioneering qualities and gained some attributes that are better suited to the Cloud Forest habitat. Second, the uniqueness of the assemblages of species in the Macuira, Santa Ana, and San Juan summit forests may be due in part to variation in the communities of herbivores and seed predators. Finally, the habitat itself may have characteristics, such as nutrient stress, that tend to cause impoverishment, as in the montane rain forests of Jamaica (Tanner, 1977, 1980).

Each of the possibilities considered above, except that of inherent impoverishment due to the combination of edaphic and climatic factors, is a function of isolation. This leads to the question of what is the most useful approach to the study of insular floras, in particular those that—like the Serranía de Macuira—are probably of relatively recent origin. With the advent of the equilibrium theory of island biogeography (MacArthur & Wilson, 1967), students of insular biotas became broadly split into two camps, with zoologists (especially ornithologists) adhering to the new mathematical models (see Simberloff, 1974) and botanists following the more traditional evolutionary and taxonomic paths (the recent symposium volume, *Plants and Islands* (Bramwell, 1979), contained only three passing mentions of the equilibrium theory). The equilibrium theory has been criticized in a general way by Sauer (1969), and its applications have recently been brought seriously into question by Gilbert (1980); both considered that the theory failed to take into account the biological complexity of insular ecosystems. This failure, especially with respect to studies based largely on species lists, was also pointed out by Connor and Simberloff (1978), who showed that the best

single predictor of species number was the number of collecting trips made to any particular island (in the Galapagos archipelago). Nevertheless, the more traditional botanical approach can also be faulted for its tendency to rely heavily on species lists and point samples made on single expeditions. The logical consequence of these criticisms is that more emphasis should be placed on longer-term studies of the ecology of island communities, alongside the continuing effort to improve taxonomic and distributional data concerning island species.

The approach of the present study has been biological, and the results, although largely derived from a species list, have provided some clues to the kinds of characteristics that might be expected of species constituting a flora of relatively recent origin. The insignificant level of endemism in the Macuira Cloud Forest flora has led to an appreciation of the importance of widespread variable species in insular situations—species that often receive inadequate attention in studies of insular floras with higher proportions of endemic species. These characteristics could not have been predicted by the equilibrium theory. I have not discussed whether the flora is at equilibrium, in the sense of MacArthur and Wilson (1967); given the nature of the sample and the impossibility of determining rates of colonization and local extinction, this would be a meaningless exercise. For the same reasons, and also because of the paucity of comparative data, the possible effects of area and distance from sources of propagules have not been considered; in any case, this would obscure some of the more important biological issues (see Gilbert, 1980).

Future work should be directed toward a greater understanding of these isolated summit forest communities on the Caribbean coasts of Colombia and Venezuela. The next step would be to investigate the possible determinants, outlined above, of the unique species assemblages and low species number in these forests. With the exception of random colonization, which is almost impossible to test empirically, the contribution of each factor (for example, pollination mechanisms, seed production, and availability of regeneration niches) could be assessed by observation and experiment in the field. Lastly, it should be emphasized that any such studies are enhanced by a firm taxonomic and chorological basis; the present study, which in a sense is a test of the adequacy of the taxonomic and distributional data concerning a small, random set of neotropical species, demonstrates the urgent need for further collections (accompanied by better notes) and improved taxonomic knowledge of the neotropical flora.

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APPENDIX. Notes on the taxonomy of Macuira Cloud Forest species.

The following notes are brief summaries of the information that is available concerning the taxonomy of the species in the Macuira Cloud Forest flora that show

intraspecific variation, belong to a complex of two or more closely related species, or have dubious status as distinct species. Although the species are listed below under these three separate headings for convenience, it should be noted that some of them fit more than one of the categories. Fifty-nine of the 126 species in the flora are listed. Those not listed include species that show little or no intraspecific variation and have no close relationships (listed on p. 42), species that are distributed outside the neotropics (geographic element 1), and species for which no information was found.

1. VARIABLE SPECIES

- Acalypha diversifolia* Jacq. Pl. Rar. Horti Schoenbr. 2: 63. t. 244. 1779. Variable in leaf size, shape, and pubescence. Three varieties distinguished (Pax & Hoffman, in Engler, Pflanzenz. IV. 147(16): 107. 1924), according to amount and type of pubescence on leaves, petioles, and shoots.
- Actinostemon concolor* Mueller-Arg. in DC. Prodr. 15(2): 1102. 1866. Seventeen varieties recognized (Mueller-Arg., *op. cit.*), differing in leaf shape. Sixteen varieties confined to southeastern Brazil, and one (var. *caribaeus*) to Lesser Antilles and Venezuela.
- Anthurium scandens* (Aublet) Engler in Martius, Fl. Brasil. 3(2): 78. 1878. Variable species with one close relative (*A. trinerve* Miq.), together forming distinct group with overlapping distributions. Variation in *A. scandens* continuous; species best regarded as having no subdivisions (S. Mayo, pers. comm.).
- Baccharis trinervis* Pers. Synopsis Pl. 2: 423. 1807. Great variation in leaf size and texture, and degree of pubescence on leaves and stems. Extremes of variation assigned to two varieties (Baker in Martius, Fl. Brasil. 6: 73. 1844), var. *rheoides* having smaller, densely pubescent leaves. Ranges of varieties overlap completely (Cuatrecasas, Revista Acad. Colomb. 13: 49-55. 1967).
- Campylocentrum micranthum* (Lindley) Rolfe, Orchid Rev. 11: 245. 1903. Variable in leaf size.
- Cestrum alternifolium* (Jacq.) O. E. Schulz in Urban, Symb. Antill. 6: 270. 1910. Easily confused with *C. latifolium* Lam., which has more conical than cylindrical corolla and occurs in West Indies and tropical South America (Francey, Candollea 6: 211. 1934). Closely related to *C. bogotense* Willd., of southern Andes of Colombia. Schulz described two varieties, differing slightly in floral dimensions: var. *pendulinum* (from Colombia eastward) and var. *mitanthum* (from Venezuela and Isla Margarita westward). Range of typical variety not stated.
- Chiococca alba* (L.) Hitchc. Ann. Rep. Missouri Bot. Garden 4: 94. 1893. Variable in leaf size, inflorescence size, and habit. Varieties and subspecies distinguished (Steyermark, Mem. New York Bot. Garden 23: 380. 1971) in terms of gradation from elongated, many-flowered inflorescences with well-developed peduncles through reduction series to few-flowered inflorescences, shorter peduncles, and smaller leaves. Typical subspecies represents many-flowered extreme and occurs throughout range of species.
- Clidemia hirta* (L.) D. Don, Mem. Wernerian Soc. 4: 309. 1823. Variable in pubescence and in pattern of leaf margins. Macuira material resembles var. *elegans* (Aublet) Griseb., which has more crenulate margins and longer pubescence than typical variety.
- Conostegia icosandra* (Sw.) Urban, Repert. Sp. Nov. 17: 404. 1921. Variable in pubescence. Northern Venezuelan (and Macuira) specimens more glabrous than material from other regions (Wurdack in Lasser, Fl. Venezuela 8: 523. 1973).
- Costus guanaiensis* Rusby, Bull. Torrey Bot. Club 29: 694. 1902. Variable in form of pubescence on leaves and sheaths. Four varieties recognized (Maas, Fl. Neotrop. 8: 51. 1972), of which three, including typical variety, have wide, overlapping distributions.

- Dendropanax arboreus* (L.) Decne. & Planchon, *Revue Hort.* IV. 3: 107. 1854. Considerable plasticity of form, especially leaf shape and stature of mature individuals, according to habitat.
- Desmodium axillare* (Sw.) DC. *Prodr.* 2: 333. 1825. Three intergrading varieties recognized (Schubert, *Jour. Arnold Arb.* 44: 287. 1963), differing in leaf size and corolla color, with distributions overlapping in Antilles.
- Encyclia fragrans* (Sw.) Lemée, *Fl. Guyane Fr.* 1: 148. 1855. Divided into two geographically replacing subspecies (Dressler, *Phytologia* 21: 440. 1971); typical subspecies in Greater Antilles, southeastern Central America, and western Panama; subsp. *aemula* (Lindley) Dressler in Lesser Antilles, tropical South America, and eastern Panama. Also member of complex of 16 species, most with restricted or disjunct distributions within range of *E. fragrans* (Dressler, *op. cit.*).
- Euphorbia cotinifolia* L. *Sp. Pl.* 1: 453. 1753. Variable in leaf shape, size, and color. Closely related to *E. caracasana*, which occurs throughout northern Andes and is considered (Webster & Burch, *Ann. Missouri Bot. Garden* 54: 333. 1967) possible infraspecific form of *E. cotinifolia*. Leaves of Macuira material similar to those of specimens from Santa Marta, Colombia.
- Ficus perforata* L. *Pl. Surinam*. 17. 1775. Exceedingly variable species (de Wolf, *Ann. Missouri Bot. Garden* 47: 154. 1960). Very similar to Antillean species *F. jacquinifolia* A. Rich., *F. sintenisii* Warb., and *F. perforata* L.
- Guapira fragrans* (Dum.-Cours.) Little, *Phytologia* 17: 368. 1968. Variable in leaf shape and size; variation shows no geographic pattern, and entire range of leaf size and shape sometimes seen on one individual.
- Guzmania lingulata* (L.) Mez in DC. *Monogr. Phanerog.* 9: 899. 1896. Five varieties maintained (L. B. Smith, *Fl. Neotrop.* 14: 1349. 1977), differing in plant size, flower number per inflorescence, and involucre bract orientation and color. Typical variety, which Macuira material resembles, occurs throughout range of species; other varieties have narrower distributions.
- Guzmania sanguinea* (André) André ex Mez in DC. *Monogr. Phanerog.* 9: 901. 1896. Exhibits varietal differences in shape of floral bracts (L. B. Smith, *Fl. Neotrop.* 14: 1334. 1977).
- Heliconia bihai* L. *Mant. Pl.* 2: 211. 1771. Variable, polymorphic species (L. Andersson, pers. comm.).
- Malvaviscus arboreus* Cav. *Monad. Cl. Diss.* 3: t. 48. 1787. Variable in overall size (treelet 2–10 m tall), petal shape.
- Miconia acinodendron* (L.) Sweet, *Hortus Brit.* 1: 159. 1826. Variable in leaf pubescence. Plants from cloud forest in Yaracuy, Venezuela (Wurdack in Lasser, *Fl. Venezuela* 8: 429. 1973) and Serranía de Macuira have near-glabrous leaves and may differ infraspecifically from material from other regions (Wurdack, *loc. cit.*).
- Miconia laevigata* (L.) DC. *Prodr.* 3: 188. 1828. Varies infraspecifically in many characters; subspecific evaluation may be required (Wurdack in Lasser, *Fl. Venezuela* 8: 382. 1973).
- Myrcia fallax* (Rich.) DC. *Prodr.* 3: 244. 1828. Highly variable in many characters.
- Myrcianthes fragrans* (Sw.) McVaugh, *Fieldiana Bot.* 29: 486. 1963. Very variable in petiole characters, leaf blade width, and flower number per dichasium (McVaugh, *loc. cit.*).
- Pilea microphylla* (L.) Liebm. *Danske Vidensk. Selsk. Skrifter* 5(2): 296. 1851. Variable in size, habit, and leaf size; closely allied to three other species with more restricted range (Killip, *Contr. U. S. Natl. Herb.* 26: 477. 1939).
- Pleurothallis ruscifolia* R. Br. in Aiton, *Hortus Kew.* ed. 2. 5: 211. 1813. Floral segments continuously variable (Foldvik in Lasser, *Fl. Venezuela* 15(2): 392. 1970).
- Polystachya foliosa* (Lindley) Reichenb. f. in Walp. *Ann. Bot. Syst.* 6: 640. 1864. Variable in size, and closely related to *P. flavescent* J. J. Sm. (widespread tropical species).

- Psychotria alba* Ruiz & Pavon, Fl. Peruv. 2: 58. 1799. Generally confused and misidentified in herbaria (Steyermark, Mem. New York Bot. Garden 23: 228. 1972) due to close resemblance to *P. horizontalis* Sw. (variable species widespread in neotropics) and to *P. carthaginensis* Jacq. (also widespread but absent from West Indies). Inclusion of *P. alba* with *P. carthaginensis* recommended by Smith and Downs (Jour. Washington Acad. 48: 284. 1958).
- Psychotria barbiflora* A. DC. Prodr. 4: 509. 1830. Variable in length and shape of bracts, and closely related to *P. hoffmanseggiana* (Steyermark, Mem. New York Bot. Garden 23: 602. 1972).
- Psychotria nervosa* Sw. Prodr. 43. 1788. Very variable in leaf and corolla pubescence. Two subspecies maintained (Steyermark, Mem. New York Bot. Garden 23: 479. 1972), with almost completely overlapping distributions. Typical subspecies represents glabrous extreme; subsp. *rufescens*, which Macuirea material resembles, has densely pilose or villous corolla and is commoner subspecies in Colombia and Venezuela.
- Randia formosa* (Jacq.) Schum. in Martius, Fl. Brasil. 6: 342. 1889. Variable, especially in length of corolla and calyx tubes. Three varieties maintained (Steyermark, Mem. New York Bot. Garden 23: 327. 1972) with fairly distinct distributions.
- Renealmia occidentalis* (Sw.) Sweet, Hortus Brit. 2: 493. 1830. Two varieties recognized (Maas, Fl. Neotrop. 18: 103. 1977), differing in peduncle length, fruit size, and flower number per inflorescence. Closely related to *R. floribunda* K. Schum., which occurs in humid parts of Amazon basin, Guianas, and Trinidad.
- Vriesea splendens* (Brongn.) Lem. Fl. Serres 6: 162. 1851. Four varieties maintained (L. B. Smith, Fl. Neotrop. 14: 1217. 1977) according to leaf variegation. Macuirea material resembles var. *formosa*, which occurs throughout range of species.
- Xiphidium caeruleum* Aublet, Pl. Guian. 1: 33. 1775. Variable in many characters.

2. SPECIES OF DUBIOUS TAXONOMIC STATUS

- Cordia macuirensis* Dugand & I. M. Johnston, Caldasia 7: 107. 1955. Endemic to Serranía de Macuirea, but very closely related to *C. curassavica* (Jacq.) Roemer & Schultes, which is widespread in neotropical dry lowlands and common on sandy slopes on northwestern sides of Serranía de Macuirea. Differs from *C. curassavica* in its smaller, glabrous leaves, pulverulent to glabrous calyx, and higher ratio of corolla length to calyx length. *Cordia curassavica*, however, shows phenotypic variation, with small-leaved xerophytic form and large-leaved mesophytic form; *C. macuirensis* may be incipient species. In Serranía de Macuirea, maintenance of reproductive isolation between these two species must depend on constancy of habitat preferences of insect pollinators, since flowering periods overlap and *C. curassavica* is self incompatible (Opler, Baker, & Frankie, 1975).
- Croton margaritensis* J. R. Johnston, Proc. Am. Acad. 40: 690. 1905. Very closely related to *C. populifolius* P. Miller (Johnston, loc. cit.), which is common in northern lowland Venezuela and Colombia; differs from latter in having shorter bracts and stipules and more lanceolate leaves, and in lacking petals in pistillate flowers. More critical analysis of these species required, in view of apparent disjunct distribution of *C. margaritensis* (in Serranía de Macuirea and Isla Margarita) and its close relationships with more widely distributed *C. populifolius*.
- Elleanthus arpophyllostachys* Reichenb. f. in Walp. Ann. Bot. Syst. 6: 479. 1862. Closely related to *E. columnaris* (Lindley) Reichenb. f., which is slightly more robust and occurs in Colombia and Venezuela, 2000–2800 m (Foldats in Lasser, Fl. Venezuela 15(1): 209. 1969). May be varieties of same species (Foldats, op. cit.), varying phenotypically according to altitude.
- Epidendrum agathosmicum* Reichenb. f. Linnaea 22: 841. 1849. Identification of Macuirea material tentative due to paucity of flowering material. Similar and closely

- related to *E. polyanthum* Lindley, which occurs in Mexico, Central America, Venezuela, and Brazil (Foldats in Lasser, Fl. Venezuela **15**(3): 169, 1970).
- Genipa spruceana* Steyerin. Mem. New York Bot. Garden **23**: 353, 1972. Separated from *G. americana* L. (widespread neotropical species) on basis of calyx tube with mainly glabrous interior and thin, noncallose margin, degree of pubescence on inner surface of corolla, and thinner, glabrous, lustrous leaves (Steyermark, loc. cit.). Serranía de Macuira well outside northern Amazonian range of *G. spruceana*, but within range of *G. americana*. Characters distinguishing species minor; *G. spruceana* and *G. americana* might be better considered as single variable species.
- Guettarda divaricata* (Humb. & Bonpl.) Standley, Publ. Field Mus. Bot. **7**: 403, 1931. Closely related to (possibly not distinct from) *G. parviflora* Vahl, which occurs in West Indies, Guianas, and Venezuela (Standley, op. cit.). Also closely related to *G. odorata* (Jacq.) Lam. of West Indies, *G. elliptica* Sw. of Greater Antilles, Florida, and Mexico, and *G. rusbyi* Standley of Colombia (Steyermark, Mem. New York Bot. Garden **23**: 361, 1972).
- Maranta divaricata* Roscoe, Monandr. Pl. t. 27, 1828. Variable in leaf color (Schumann in Engler, Pflanzenz. IV. **48**: 126, 1902) and closely related to widespread neotropical *M. arundinacea*. Doubtful whether former is more than poor variety of latter (Standley & Steyermark, Fieldiana Bot. **24**: 218, 1952).
- Philodendron erubescens* C. Koch & Augustin, Index Sem. Hort. Bot. Reg. Berol. Collect. App. 6, 1854. Described from cultivar; field collections so scarce that natural distribution unclear. Appears closely related to *P. krugii* Engler, which occurs in Trinidad. Macuira material sterile.
- Polypodium maritimum* Hieron. Bot. Jahrb. **34**: 527, 1904. Very similar to *P. loricatum* L. (widespread, variable species).
- Schlegelia fuscata* A. Gentry, Ann. Missouri Bot. Garden **60**: 925, 1973. Possibly local form of *S. parviflora* (Oersted) Monachino, which occurs in moist lowlands of Central and South America (Gentry, loc. cit.) and is very variable in several characters. Former differs most conspicuously from latter in having more or less racemose inflorescence and extremely coriaceous leaves.
- Solanum dulcameroides* Dunal in Poiret, Encycl. Suppl. **3**: 751, 1813. Closely allied to *S. seaforthianum* André (pan-Caribbean species) (W. G. D'Arcy, pers. comm.); relationships between these species and their allies poorly understood.
- Zamia muricata* Willd. Sp. Pl. **4**: 847, 1805. Macuira material tentatively identified, in absence of good collections and adequate monographic treatment of *Zamia* in tropical America.

3. SPECIES BELONGING TO GROUPS OR COMPLEXES OF TWO OR MORE CLOSELY RELATED SPECIES

- Anthurium crassinervium* (Jacq.) Schott, Wiener Zeitschr. Kunst Lit. Theater Mode **1829**: 828, 1829. Member of complex of ca. 15 species that as group have pan-Caribbean distribution (S. Mayo, pers. comm.). Differences between them slight, perhaps suggesting recent and continuing divergence due to geographic isolation. Habitat-related diversity of form is common in complex.
- Blechnum arborescens* (Klotzsch & Karsten) Hieron. Hedwigia **47**: 239, 1908. Related to *B. schiedianum* (Presl) Hieron., which occurs in Andes of Ecuador and southern Colombia. Differs mainly in degree of purplish coloring of rachis and leathery pinnae. Also similar to *B. lineatum* (Sw.) (montane Antillean species).
- Chamissoa altissima* H.B.K. Nova Gen. Sp. Pl. **2**: 197, 1817. Closely related to *C. macrocarpa* H.B.K., which is restricted to Amazon basin (J. A. Duke, Ann. Missouri Bot. Garden **48**: 21, 1961).
- Cynanchum atrovirens* (Rusby) Sugden. Closely related to *C. parviflorum* (R. Br.) Alain, which occurs in Lesser Antilles, Venezuela, and Colombia. Most distinctive

- feature separating these species is abundance of short (0.5 mm) hairs covering entire interior corolla of *C. atrovirens* (Dugand, *Caldasia* 9: 444, 1966).
- Grammitis blepharolepis* (C. Chr.) Morton, Contr. U. S. Natl. Herb. 38: 98, 1967. Closely related to *G. daguensis* (Hieron.) Morton (lowland Cauca and Valle, Colombia) and *G. trichomanoides* (Sw.) Ching (West Indies) (Morton, *op. cit.*).
- Guzmania cylindrica* L. B. Sm. *Phytologia* 5: 282, 1955. First described from specimen from Serranía de Maculra. Closely related to *G. mucronata* Mez, which is restricted to low-altitude cloud forest in northern Venezuela (L. B. Smith, *op. cit.*).
- Jacquinella globosa* (Jacq.) Schlechter, Repert. Sp. Nov. 7: 124, 1920. Closely allied to *J. colombiana* Schlechter, from Cauca, Colombia, but differing in labellum shape.
- Machaerium humboldtianum* Vogel, *Linnaea* 11: 194, 1837. Member of complex of at least six species with various neotropical distributions (V. E. Rudd, pers. comm.).
- Persea caerulea* (Ruiz & Pavon) Mez, *Jahrb. Bot. Gart. Berlin* 5: 171, 1889. One of seven closely related species. *Persea caerulea* shows clinal variation in leaf shape (Kopp, Mem. New York Bot. Garden 14: 34, 1966).
- Scutellaria verecunda* Epl. Feddes Repert. 85: 173, 1936. One of group of five closely allied species, all except *S. verecunda* having wide overlapping distributions. Possible that these species are varieties or subspecies of single variable species (Epling, Univ. Calif. Publ. Bot. 20: 1-146, 1942).
- Stemmadenia minima* A. Gentry, Ann. Missouri Bot. Garden 64: 322, 1977. Closely related to *S. allenii* Woodson, which occurs west of Panama Canal Zone and Costa Rica, and to *S. lagunae* Woodson, known only from Bocas del Toro, Panama.
- Utricularia alpina* Jacq. Enum. Pl. Carib. 11, 1760. One of five closely allied tropical American species (Taylor, Ann. Missouri Bot. Garden 63: 569, 1976).

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THE WEST INDIAN TAXA IN SOLANDER'S
"FLORULA INDIAE OCCIDENTALIS"

R. A. HOWARD AND E. S. HOWARD

DANIEL SOLANDER was the first of three famous botanists to serve as librarian and curator for the collections of Sir Joseph Banks. Born in Sweden and a pupil of Linnaeus, Solander was sent to England in 1760. As "a friend and a guest," he accompanied Banks on Cook's first voyage (1768-1771) to the Pacific aboard the *Endeavour* and the following year went with Banks to Iceland (Smith, 1911, p. 16). On the expeditions Solander contributed to the collecting, wrote descriptions of the plants, and aided in the preparation of drawings. Upon returning to London, Solander was employed by Banks to continue work on the specimens and to care for his library. According to Smith (1911, pp. 62, 63),

Banks had taken the large house in Soho Square . . . in the autumn of 1777. Everyone was welcome who, by improvements in the Arts or by further unravelling the secrets of Nature, had any scheme for the benefit of his fellow men. . . . Foreigners and strangers were welcome; and although suitable introductions were rigidly exacted, these helped to swell the crowd of inquiring visitors. The house was a vast museum; in which books, pictures, rarities from all parts of the world, and innumerable botanical specimens, delighted the varied company. . . . Over all these things, Dr. Solander reigned as Librarian and Curator.

In his role as curator, Solander compiled florulas of the various areas of the world well represented in the Banks herbarium. Most of these remain unpublished. The most famous was "Illustrations of Australian Plants, collected in 1770 during Captain Cook's voyage round the world in the *Endeavour*." The manuscript is credited to Banks and Solander, and only now are plans underway to publish it. A manuscript entitled "Flora of South Africa," also attributed to Solander, is in the hand of Sigismund Bacstrom, an assistant in the Banks library (Britten, 1905). Oliver (1951) told of the preparation of text and illustrations for a "Primitiae Florae Novae Zelandiae" by Solander and commented: "Had the manuscript been published, we would now be using Solander's names for over 340 kinds of our native plants, instead of names proposed by other botanists at later dates. Many of these botanists, however, adopted names suggested by Solander."

Less well known is Solander's "Florula Indiae Occidentalis, Being a systematic list of the plants of the West Indies, Central America and Guiana with records of the localities where the plants have been found and of the persons who collected them, and notes on the species." The present paper will consider the West Indian specimens cited in the *Florula*.

The manuscript is undated, and although it was started by Solander (curator from 1772 to 1782), additions were made after his death by his successor, Jonas Dryander. The binomial names are arranged in the Linnaean system. Many are followed by the abbreviation "mss" and a brief diagnosis in Latin, suggesting they are new species. The area of origin is given, and the collector is designated by an abbreviation consisting of one or more letters; not all of the abbreviations have been identified. During Solander's curatorship the Banks herbarium may have contained specimens from the West Indies collected by Browne, Catesby, Greg, Houston, Jacquin, Ryan, Shakespear, and William Wright. Collections of Alexander Anderson, Masson, and Ponthieu were probably added during Dryander's administration. In 1939 Harold Box placed a note in the manuscript stating, "Solander cites Masson's plants from the West Indian islands. According to the British Museum Catalogue these were received in 1778, therefore the date of the present work may be considered as circa 1780." The manuscript does refer to Masson's plants from the West Indies, but the particular catalog entry of the British Museum refers to Masson's collections from the Azores, the Canary Islands, and Madeira. Dryander's additions to the *Florula* are clearly recognizable and were made after 1782. The manuscript was an active catalog until at least 1788, since there are frequent references to Swartz's *Prodromus* (1788) but none to the first volume of his *Flora Indiae Occidentalis* (1797).

The contents of the Banks herbarium have been described by Britten (1905) and Maiden (1909). The West Indian collections in it were studied by Olof Swartz in 1786 in the preparation of his *Nova Genera & Species Plantarum seu Prodromus* and were cited there as well as in the *Flora Indiae Occidentalis* (1797-1804). William Stearn (1980, p. 5) writes that Swartz was in Jamaica and that he sailed in 1786

to London, where Sir Joseph Banks and his Swedish librarian Jonas Dryander welcomed him. Banks' house at Soho Square, with its rich library and collections, was then the scientific centre of London and, as G. R. Crome remarks, "almost the nucleus of a learned society, frequented by scientists, British and foreign." Banks possessed many West Indian specimens. . . . His former librarian Daniel Solander had already classified this material according to the Linnean system and had listed it in a manuscript "Florula Indiae occidentalis." It thus provided Swartz with a valuable reference collection for the naming of his material. Aided by Dryander, he set this in order and drafted the prodromus of a large work on West Indian botany, incorporating descriptions of plants in the Banksian herbarium not represented among his own gatherings. These Banks permitted him to publish. In return Swartz gave Banks numerous specimens of plants which the latter did not already possess. Hence the majority of the species published in Swartz's prodromus can be typified by specimens in the Banksian herbarium now incorporated in the general herbarium of the Department of Botany, British Museum, Natural History, London.

There is no direct evidence of the use Swartz made of the Solander manuscript. His handwriting was not recognized in the *Florula*, but it was on some of the specimens cited. The entries in the *Florula* do bear the names that Swartz either adopted or published in his *Prodromus*, and references to the

Prodromus are frequent. It is possible that some clerk added the references to the listing after its publication. Rydberg (1907, p. 14) noted that "Solander has contributed the descriptions of many new plants from America as well as elsewhere. Six of the new genera published in Swartz's West Indian flora are really from Solander's hand, as Swartz found the descriptions as well as the names in Solander's manuscript in the Banksian herbarium." In fact, the *Florula* contains a total of sixty-five binomials for West Indian plants with the abbreviation "mss" and a complete or partial Latin diagnosis prepared by Solander or Dryander. Fourteen of these also appear in Swartz's *Prodromus*, where they are cited with an asterisk indicating that Swartz did not have material in addition to that of the Banks herbarium. Forty of the manuscript names were used without change by Swartz, and for an additional eight manuscript names Swartz changed either the generic or the specific name in his *Prodromus*. Another eight manuscript names can not be associated with taxa recognized by Swartz. Only by chance would these be found in the herbarium today.

There is a problem, then, of determining the type of Swartz species and the location of a holotype. In his *Prodromus* Swartz rarely cited collectors, but he did record areas of collection. Many new genera and species are marked with an asterisk ("an asterisk against a diagnosis indicates that this was based on a specimen in Banks' possession not collected by Swartz himself" —Stearn, 1961, p. cvii). In his later *Flora Indiae Occidentalis*, Swartz cited locations and the collectors, but not his own collections, and he did not use the asterisk to help determine locations of type material. The holotypes of *Cephaelis axillaris* Sw. (= *Psychotria aubletiana* Steyermark), *Melastoma ramiflora* Sw. (= *Henriettea ramiflora* (Sw.) DC.), and *Paullinia vespertillio* Sw. were all specifically stated by Swartz to be in the Banks herbarium. The holotypes of all three species are Masson collections. They are among many others mentioned in the *Flora* for which additional data may be obtained from the *Florula*. In the *Prodromus* Swartz may have cited one or two specific islands, while for the same entry in the *Flora* he might have indicated the collectors as well as the islands. In such cases it is possible to determine which specimen or specimens Swartz consulted for the *Prodromus* and which ones might have been added to his resources later, while he was compiling the *Flora*. The lectotypes for such Swartz species should be selected from the choices in the *Prodromus* and can be corroborated by referring to Solander's *Florula*.

Still unresolved is the question of the possible role of Swartz's own collections that he did not cite in typifying the species he described. Although it has been stated that Swartz gave to Banks specimens that Banks did not possess, it seems that Banks (or perhaps Dryander) shared his collections with Swartz, for the same collection may today be present both in the British Museum and in the herbarium at Stockholm. We know, for example, that Masson collected on islands that Swartz did not visit, but that both men collected on Jamaica. Swartz might have cited the Masson collection but not his own; the latter is still preserved in the British Museum and the Stockholm

herbaria. Thus, a lectotype must be chosen after collections have been compared. When no collector was cited by Swartz, a Swartz specimen in the herbarium at Stockholm is a better choice; however, when Masson or another collector was cited by Swartz, the better quality specimen is usually that of the Banks herbarium in the British Museum.

The following notes concern the collectors represented in the Solander *Florula* whose specimens were in the Banks collection.

ANDERSON

In describing the Banks herbarium, James Britten (1905, p. 124) listed among the collections "Alexander Anderson (d. 1815), plants from Demerara in 1791 and later from the St. Vincent Garden, of which he was curator." Unpublished documents written by Anderson are in the library of the Linnean Society, and some of his letters are in the archives at Kew; these are presently being studied. From these sources we have determined that the place and date of Anderson's birth are unknown, but that he was collecting plants in the areas of New York and Philadelphia in 1775 and 1776 and shortly thereafter sailed for South America to avoid the war in North America. He was captured by the French and later exchanged as a prisoner of war in the West Indies. There he served the British forces as a hospital assistant in Dominica, St. Lucia, and Grenada before being appointed the second director of the botanical garden in St. Vincent in 1785. He collected in Trinidad and Tobago and made a trip to the interior of Guiana via the Essequibo River in 1791. He corresponded with Banks, William Forsythe, and the staff at Kew. Swartz cited Anderson specimens in the first two volumes of his *Flora* (1797, 1800), and these by cross-reference apply to taxa described in the *Prodromus*. The following taxa are typified by Anderson specimens in the Banks herbarium:

Grammadenia parasitica (Sw.) Griseb. BASIONYM: *Ardisia parasitica* Sw. Prodr. 48 (with an asterisk), Montserrat. In the *Flora* (1: 474) Swartz cited an Anderson collection from Dominica (BM), now designated the lectotype. The species is not known today from Montserrat.

Quararibea turbinata (Sw.) Poir. BASIONYM: *Myrodia turbinata* Sw. Prodr. 102. 1788 (with an asterisk), Montserrat, St. Lucia, and St. Kitts. In the *Flora* (2: 1227) Swartz noted collections of Ryan (Montserrat), Masson (St. Kitts), and Anderson (St. Lucia). The Anderson specimen from St. Lucia (BM) has been marked "type specimen."

Styrax glaber Sw. Prodr. 74. 1788 (with an asterisk), St. Vincent. In the *Flora* (2: 848) a collection by Anderson (BM) is cited, and this is the holotype (Howard, 1974; Nicolson & Steyskal, 1976).

Ormosia monosperma (Sw.) Urban. BASIONYM: *Sophora monosperma* Sw. Prodr. 66 (with an asterisk). "Browne jam. 298" and *India occidentalis* are cited by Swartz. In the *Flora* (2: 722) Swartz cited "Jamaica (Browne) in *India occidentalis* (Anderson)." Rudd (1968, p. 356) noted that Browne

stated, "I have seen this tree pretty often in Montserrat, where it grows naturally." She apparently was unable to find a specimen collected by Browne and chose *Anderson s.n.* (BM) as the lectotype. Another specimen by Anderson without number (G) bears the data, "India occidentalis, St. Vincent." Still another specimen by Anderson at Geneva proved to be "a mirror image of table 20 which illustrated Jackson's original description of *Ormosia dasycarpa* Jacks" (Rudd, *loc. cit.*).

Anderson's collections are also found in other herbaria. The type specimen of *Freziera hirsuta* Smith from St. Vincent is in the Lamarck herbarium (P), and the type of *Eugenia dussii* Krug & Urban from St. Lucia is at Kew.

One unusual note appears in the Florula following the manuscript name "*Telopia nitida* mss" for a plant from Grenada. It states the species "does not belong to this genus if the fruit really belongs to it which is pasted with the specimen from Anderson, but this fruit was not sticking to the plant, only laying in the same paper, so that it is very uncertain if it belongs to it." The specimen was not located; however, it probably is not *Telopea* R. Br. (Proteaceae) since the genus is not in Anderson's notes on plants of the St. Vincent Botanical Garden. It may be *Telopea* Solander ex Baillon, now a synonym of *Aleurites* J. R. & G. Forster (Euphorbiaceae), which was cultivated in the West Indies in Anderson's time, having been brought by Captain Bligh in 1793 along with the breadfruit.

GREG

Urban (1902) said of this man only that he collected before 1786 in Dominica, Barbados, and Tobago, and that his collections are in Banks's herbarium. "*Eugenia gregii*" is listed in Solander's Florula as a manuscript name with the annotation "*Myrtus gregii* Sw. Prodr. 78." Swartz used an asterisk with the species and stated, "India occidentalis, Antigua." In the *Flora* (2: 896) Swartz noted the synonym "*Gregia* Gaert. fruct. 33" and credited J. Greg with a specimen from Dominica. The type (BM), from Dominica, is dated 1777. The combination in the genus *Eugenia* was made by Poiret in Lamarck (Encycl. Suppl. 3: 126. 1813) as "*E. greggii* from Saint Dominique."

The genus *Greggia* is attributed to Solander in Gaertner (1788, p. 168, t. 33). The species *Greggia aromatica* Gaertner is supplied with a common name, Bastard Gloves (spalm cloves), "Angl. barbadens.," which some workers have interpreted to represent the occurrence of the taxon in Barbados. Miller (Gard. Dict. *Myrtus gregii* (#25) 1807) stated that it is a native of Antigua, Barbados, and Dominica. The plant was introduced to cultivation in 1776 from Dominica (Aiton, 1789). No collections have been seen from either Antigua or Barbados.

Smith (in Rees, 1811) stated, "*Greggia*, in botany, so named by the late Dr. Solander, in compliment to Mr. John Greg, a gentleman long resident in Dominica, the correspondent of Ellis, Garden, and other naturalists of his day."

JACQUIN

Britten (1905, p. 123) reported that "Jacquin's herbarium, consisting largely of plants cultivated by him in the Vienna and Schönbrunn Gardens and containing some of his West Indian plants, was purchased by Banks and is incorporated with his collections. . . ." The purchase was made in May, 1777, and "on 5 March 1778 Jacquin wrote that he was glad to hear of the safe arrival of the herbarium" (Stafleu, 1967, p. iii).

Jacquin's collections are listed in Solander's *Florula*. The entries attribute sixty-one taxa to Cartagena, twenty-three to Martinique, thirteen to Cuba, eight to Hispaniola, six to Jamaica, and one to Tobago. Twenty-four give no location, and three are listed as "ex Herb. Mygind." Only one is attributed to "Hort. Vindob." Of the few that have been located in the general herbarium, most are fragments or only a single leaf.

There has been speculation concerning what Jacquin plants the Banks herbarium might have contained, and Solander's records in the *Florula* offer the most comprehensive list (Howard, 1973). The names in the following list have been given modern equivalents as far as possible, and specimens that have been reported in the literature are cited as (BM). A deliberate search for others may be useful.

Acanthaceae

- Justicia carthaginensis*** Jacq., Cartagena
Justicia hexangularis L. (ined.), Cuba

Anacardiaceae

- Comocladia dentata*** Jacq., Cuba

Apocynaceae

- Echites agglutinata* Jacq., no loc., = ***Prestonia agglutinata*** (Jacq.) Woodson
Echites repens Jacq., "Jamaica," = ***Mesechites repens*** (Jacq.) Miers
Echites spicata Jacq., no loc., = ***Forsteronia spicata*** (Jacq.) Meyer
Echites trifida Jacq., no loc., = ***Mesechites trifida*** (Jacq.) Mueller-Arg.
Rauvolfia tomentosa Jacq., Cartagena, = ***Rauvolfia tetraphylla*** L.

Aristolochiaceae

- Aristolochia anguicida*** Jacq., Cartagena
Aristolochia bilobata L., no loc.
Aristolochia caudata Jacq., Haiti
Aristolochia maxima Jacq., Cartagena, = ***Aristolochia pentandra*** Jacq.
Aristolochia peltata L., no loc.
Aristolochia pentandra Jacq., Cuba

Asclepiadaceae

- Cynanchum clausum* Jacq., Cartagena, = ***Sarcostemma clausum*** (Jacq.) Roemer & Schultes
Cynanchum maritimum Jacq., Cartagena, = ***Matelea maritima*** (Jacq.) Woodson

Bataceae

Batis maritima L., Santo Domingo

Bignoniaceae

Bignonia dichotoma Jacq., Cartagena, = **Arrabidea obliqua** (H.B.K.) Bur.

Bignonia echinata Jacq., Cartagena, = **Pithecoctenium echinatum** (Jacq.) K. Schum.

Bignonia orbiculata Jacq., Cartagena, = **Anemopaegma orbiculatum** (Jacq.) DC.

Boraginaceae

Ehretia exsucca L., Cartagena, = **Bourreria exsucca** Jacq.

Varronia alba L., no loc., = **Cordia alba** (Jacq.) Roemer & Schultes

Capparaceae

Capparis frondosa L., Cartagena, = **Capparis baduella** L.

Capparis hastata Jacq., Cartagena

Capparis jamaicensis Jacq., Jamaica, = **Capparis cynophallophora** L. (BM)

Capparis linearis Jacq., Cartagena

Capparis nemorosa Jacq., Cartagena, = **Belencita nemorosa** (Jacq.) Dugand

Capparis tenuisiliqua Jacq., Cartagena

Cleome procumbens Jacq., Santo Domingo

Cleome serrata Jacq., Cartagena

Celastraceae

Myginda uragoga Jacq., Cartagena

Combretaceae

Combretum laxum Jacq., Hispaniola (BM)

Combretum secundum Jacq., Cartagena, = **Combretum fruticosum** (Loefl.) Stuntz (BM)

Compositae

Cacalia ruderalis Jacq., Martinique, = **Porophyllum ruderales** (Jacq.) Cass.

Pectis punctata Jacq., Cartagena, = **Pectis linifolia** L.

Convolvulaceae

Convolvulus martinicensis Jacq., Martinique, = **Aniseia martinicensis** (Jacq.) Choisy

Convolvulus pentaphyllus L., Martinique, = **Merremia aegyptia** (L.) Urban

Cuscuta americana L., Cartagena

Ipomoea carnea Jacq., Cartagena

Cucurbitaceae

Anguria trilobata L., Cartagena, = **Psiguria trilobata** (L.) Howard

Elaterium carthagenense Jacq., Cartagena, = **Rytidostylis carthagenensis** (Jacq.) Kuntze

Sicyos edulis Jacq., Cuba, = **Sechium edule** (Jacq.) Sw.

Euphorbiaceae

Croton balsamiferus Jacq., Martinique

Croton niveus Jacq., Cartagena

Euphorbia graminea Jacq., Cartagena

Euphorbia obliterated Jacq., Cartagena

Hippomane mancinella L., Martinique

Tragia hexandra Jacq., Cuba, = **Platygyne hexandra** (Jacq.) Mueller-Arg.

Flacourtiaceae

Laetia apetala L., Cartagena, = **Laetia americana** L.

Laetia completa Jacq., Cartagena, = **Hecatostemon completus** (Jacq.) Sleumer (BM)

Samyda nitida L., Cartagena, = **Casearia nitida** (L.) Jacq.

Samyda parviflora L., Martinique, = **Casearia sylvestris** Sw.

Gesneriaceae

Columnnea scandens L., Martinique (Hort. Vindob.)

Leguminosae

Clitoria virginiana L., Cartagena, = **Centrosema virginianum** (L.) Benth.

Copaifera officinalis L., Cartagena

Cytisus cajan L., Jamaica and Martinique, = **Cajanus cajan** (L.) Millsp.

Diphysa carthagenensis Jacq., Cartagena

Dolichos luteolus Jacq., Cartagena, = **Vigna luteola** (Jacq.) Benth.

Dolichos minimus L., Cartagena, = **Rhynchosia minima** (L.) DC.

Dolichos pruriens L., Cartagena, = **Mucuna pruriens** (L.) DC.

Dolichos urens L., Cartagena, = **Mucuna sloanei** Fawcett & Rendle

Galega littoralis L., Cartagena, = **Tephrosia cinerea** (L.) Pers.

Glycine striata Jacq., Cartagena, = **Galactia striata** (Jacq.) Urban

Mimosa mangensis Jacq., Cartagena, = **Pithecellobium mangense** (Jacq.) Macbr.

Mimosa retusa Jacq., Cartagena, = **Acacia retusa** (Jacq.) Howard

Nissolia arborea Jacq., Cartagena, = **Machaerium arboreum** (Jacq.) Vogel

Phaseolus jacquinii mss., no loc.

Piscidia carthagenensis Jacq., Cartagena (BM)

Psoralea enneaphylla L., Cartagena, = **Dalea domingensis** P. DC.

Lentibulariaceae

Utricularia foliosa L., Cartagena

Lythraceae

Glinoria americana Jacq., Cuba

Malpighiaceae

Hiraea reclinata Jacq., Cartagena

Malvaceae

Malachra angulata mss., Martinique

Sida abutiloides Jacq., no loc., = **Abutilon abutiloides** (Jacq.) Garcke

Sida multiflora Jacq., Cartagena, = **Sida paniculata** L.

Sida triquetra L., no loc., = **Abutilon trisulcatum** (Jacq.) Urban

Melastomataceae

Melastoma discolor L., Martinique, = **Tetrazygia discolor** (L.) DC. (BM)

Meliaceae

Trichilia glabra L., Cuba

Myrtaceae

Eugenia acris mss., no loc.

Pedaliaceae

Craniolaria annua L., Cartagena

Polygalaceae

Polygala trichosperma L. "Gr."(?)

Securidaca erecta L., Martinique, = **Securidaca diversifolia** (L.) Blake

Securidaca scandens Jacq., Cartagena, = **Dalbergia monetaria** L. f.

Polygonaceae

Coccoloba barbadensis Jacq., no loc.

Coccoloba emarginata Jacq., no loc., = **Neomillspaughia emarginata** (Gross) Blake

Coccoloba leoganensis Jacq., no loc. (BM)

Coccoloba nivea Jacq., "Jamaica," = **Coccoloba venosa** L.

Coccoloba pubescens L., no loc.

Rhamnaceae

Gouania tomentosa Jacq., no loc., = **Gouania polygama** (Jacq.) Urban

Rhamnus colubrinus Jacq., Cartagena = **Colubrina arborescens** (Miller) Sarg.

Rhamnus cubensis Jacq., Cuba, = **Colubrina cubensis** (Jacq.) Brongn.

Rubiaceae

Gardenia armata mss., Martinique, = **Randia armata** (Sw.) DC.

Portlandia hexandra Jacq., Cartagena, = **Coutarea hexandra** (Jacq.) Schum.

Rondeletia odorata Jacq., Cuba

Rondeletia trifoliata mss., Jamaica, = **Rondeletia stipularis** (L.) Druce (BM)

Rutaceae

Amyris sylvatica Jacq., Cartagena

Sapindaceae

Paullinia barbadensis Jacq., no loc. (ex Herb. Mygind.) (BM)

Paullinia canboea L. (ined.), no loc.

Paullinia carthaginensis Jacq., Tobago, = **Serjania curassavica** (L.) Radlk. (BM)

Paullinia carthaginensis Jacq., Tobago, = **Serjania curassavica** (L.) **ersifolia** (Jacq.) Radlk. (BM)

Paullinia nodosa Jacq., no loc. (ex Herb. Mygind.), = **Serjania nodosa** (Jacq.) Radlk. (BM)

Paullinia pinnata L., Cartagena

Sapotaceae

Chrysophyllum microphyllum Jacq., Cuba, = **Chrysophyllum oliviforme** L.

Scrophulariaceae

Russelia sarmentosa Jacq., Cuba

Scutellaria havanensis Jacq., Cuba

Solanaceae

Cestrum vespertinum L., Martinique, = **Cestrum alternifolium** (Jacq.) Schulz

Sterculiaceae

Helicteres apetala Jacq., no loc., = **Sterculia apetala** (Jacq.) Kunth

Helicteres bahamensis L. (ined.), no loc.

Helicteres barbadensis L., no loc., = **Helicteres barbadensis** Jacq.

Helicteres carthagenensis Jacq., Cartagena

Triumfetta rhombea mss., Cartagena, = **Triumfetta rhomboidea** Jacq.

Triumfetta semitriloba Jacq., Cartagena

Umbelliferae

Astronium graveolens Jacq., Cartagena

Urticaceae

Catuma ramiflorus L., no loc., = **Boehmeria ramiflora** Jacq.

Parietaria microphylla L., Martinique, = **Pilea microphylla** (L.) Liebm.

Verbenaceae

Avicennia tomentosa L., Cartagena, = **Avicennia germinans** (L.) L.

Lippia hemisphaerica Jacq., Cartagena, = **Lippia americana** L.

Citharexylum cinereum L., no loc., = **Citharexylum fruticosum** L.

Citharexylum quadrangulare Jacq., no loc.

Petitia domingensis Jacq., Hispaniola

Zygophyllaceae

Zygophyllum arboreum Jacq., Cartagena, = **Bulnesia arborea** (Jacq.) Engler

Agavaceae

Agave cubensis Jacq., Cuba, = **Furcraea hexapetala** (Jacq.) Urban

Araceae

- Arum hederaceum* L., Cartagena, = ***Philodendron hederaceum*** (Jacq.) Schott

Commelinaceae

- Callisia repens*** L., Martinique

Orchidaceae

- Epidendrum altissimum* Jacq., Martinique, = ***Oncidium altissimum*** (Jacq.) Sw. (BM)

- Epidendrum anceps* Jacq., Martinique, = ***Epidendrum secundum*** Jacq. (BM)

- Epidendrum ciliare*** L., Martinique

- Epidendrum coccineum* Jacq., Cartagena, = ***Maxillaria coccinea*** (Jacq.) L. Williams

- Epidendrum globosum* Jacq., Martinique, = ***Jacquinella globosa*** (Jacq.) Salisb.

- Epidendrum rigidum*** Jacq., Martinique (BM)

- Epidendrum secundum*** Jacq., Martinique

- Epidendrum tetrapetalum* Jacq., Jamaica, = ***Oncidium tetrapetalum*** (Jacq.) Willd.

- Epidendrum trigoniflorum* Jacq., Martinique, = ***Stelis scabrida*** Lindley (BM)

- Satyrium plantagineum* L., Martinique, = ***Spiranthes lanceolata*** (Aublet) León

Palmae

- Bactris minor*** Jacq., no loc.

Smilacaceae

- Smilax hastata*** Jacq., Santo Domingo

- Smilax havanensis*** Jacq., Cuba

MASSON

Francis Masson is best known for his several collecting trips to South Africa, since these led to the introduction of many Cape Province plants into cultivation in England. Masson's contributions to the knowledge of West Indian plants can be appreciated through the records in Solander's *Florula*. Solander met Masson on at least one occasion, for Maiden (1909, p. 90) noted on August 28, 1775, that "Dr. Solander was last Saturday at Kew where he saw Mr. Masson, who is lately come back from the Cape of Good Hope, with a great cargo of new plants, all in perfect health." The following year Masson was commissioned by Banks to make a trip to the Azores, Madeira, and the Canary Islands en route to the West Indies and the Spanish Main. Little is known of this trip beyond what was learned from the records and accounts supplied by Banks and published by Britten (1884). Masson left England May 19, 1776, and was in the Azores that year, in the Canary Islands in 1777, and in Madeira in 1778. Solander, who worked with Aiton

in the preparation of *Hortus Kewensis*, credited Masson with introducing *Cassia multiglandulosa* into cultivation from Teneriffe in 1779 (Aiton, 1789). In 1781 Masson sent *Cassia diphylla* from the West Indies (Aiton, 1789). Herbarium specimens acquired from this first portion of the voyage were sent to Banks and to Linnaeus filius, and it is this shipment to Banks that Box referred to as having been received at the British Museum in 1778. In the *Supplementum Plantarum* Linnaeus filius described from Masson collections twenty-three new species from Teneriffe, eight from Madeira, and one from the Azores.

Masson arrived in the West Indies in 1779. Britten (1884, p. 116) wrote,

When Mr. Masson arriv'd in the West Indian Islands, the war, then somewhat advanced, made it necessary for him entirely to drop his plan of visiting the Spanish Main, to which it was in vain for him to apply for a passport. The Islands themselves he found in so unsettled a state that it was with the utmost difficulty he found means to send home what he collected, parts of which were frequently lost by capture or waiting for Convoy.

Masson arrived in Grenada in August, 1779, at which time the French attacked the colony and Masson "was called upon to bear arms in its defence, which he did and was taken prisoner fighting in the trenches" (*ibid.*). Masson was thought to have been in Antigua in November, 1779, and back in St. Lucia during the hurricane of October 14, 1780. "He lost there all the collections at that time in his possession, and great part of his clothes and papers" (*ibid.*). Masson's route in the Antilles was described by Britten (1894) as from Madeira to Barbados, Grenada, St. Eustatius, Antigua, St. Kitts, and then to St. Lucia, Nevis (November, 1780), and Jamaica (March, 1781). He returned to England in 1782. Since Solander died in May, 1782, it seems probable that Masson's West Indian collections were handled by Solander's successor, Jonas Dryander. The *Florula* attributes to Masson a total of 601 species, of which 48 bear manuscript names as new taxa. The collections listed were 270 from Jamaica, 147 from St. Kitts, 39 from St. Lucia, 36 from Grenada, 33 from St. Eustatius, 29 from Nevis, 24 from "Carib.," and 1 each from Barbados, Dominica, Guadeloupe, and Haiti.

The following taxa have been based on Masson collections, or where a lectotype has not been designated, a Masson specimen is in consideration.

Araliaceae

Didymopanax attenuatum (Sw.) March. BASIONYM: *Panax attenuata* Sw. Prodr. 54. 1788 (with an asterisk), "India occidentalis." In the *Flora* (I: 562) Swartz stated, "Habitat in monte la Souffriere Guadeloupe insulae Indiae occidentalis, nec non in ins. St. Christophori." In spite of Swartz's comment, the only material of that period in the Banks herbarium is a Masson specimen from St. Kitts (BM), which should be considered the lectotype. A new combination for the species in *Schefflera* is given on an annotation label of D. G. Frodin dated 1970 but has not been published.

Caprifoliaceae

Viburnum villosum Sw. Prodr. 54. 1788 (without an asterisk); Fl. Ind.

Occ. 1: 564. A Masson specimen from Jamaica (BM) has been marked "type specimen."

Compositae

Gnaphalium albescens Sw. Prodr. 112. 1788 (without an asterisk), Jamaica; Fl. Ind. Occ. 3: 1334. 1804. No material of this taxon was found in Stockholm, and the Masson specimen (BM) is probably the holotype. Although Volume 3 of Swartz's *Flora Indiae Occidentalis* is dated 1806, Garay (1974) has shown that the probable date of publication is 1804.

Spilanthes uliginosa Sw. Prodr. 110. 1788 (without an asterisk), Jamaica; Fl. Ind. Occ. 3: 1291. 1804. There are four Swartz specimens at Stockholm to be considered for lectotypification. A Masson collection (BM) was listed in the Solander Florula with "*Verbesina decumbens* mss.," a name not used by Swartz.

Elaeocarpaceae

Sloanea massonii Sw. Prodr. 82. 1788 (without an asterisk), "Insulae caribaeae, Christoph. etc.;" Fl. Ind. Occ. 2: 938. 1800, "Ins. St. Christophi (Masson)." This name appears in the Solander Florula with the notation that the material differs from *Sloanea* of Plumier, and the lectotype is a Masson specimen (BM).

Gentianaceae

Lisianthus exsertus Sw. Prodr. 40. 1788 (without an asterisk), Jamaica; Fl. Ind. Occ. 1: 346. 1797. A Swartz specimen (s) has been designated as the lectotype. A Masson specimen (BM) bears the manuscript name of Solander's Florula, "*Lisianthus arboreum*," an epithet not adopted by Swartz.

Guttiferae

Marila racemosa Sw. Prodr. 84. 1788 (with an asterisk and as a new genus), "India occidentalis, Montserrat, Christophor." In the *Flora* (2: 965) Swartz used the name *Bonnetia racemosa* (Sw.) Sw. and cited a Ponthieu specimen without specific location, a Masson specimen from St. Kitts, and a Ryan specimen from Montserrat. The name "*Marila racemosa* mss." appears in Solander's Florula. The Masson collection (BM) has been marked "type specimen" and is a better specimen than the one in Stockholm, which indicates that Banks shared his material with Swartz.

Leguminosae

Inga laurina (Sw.) Willd. BASIONYM: *Mimosa laurina* Sw. Prodr. 85. 1788 (without an asterisk); Fl. Ind. Occ. 2: 978. 1800, "St. Christopher (Masson)." Although Masson material from St. Kitts is in Stockholm and London, "holotype" is marked on the sheet at the British Museum.

Melastomataceae

Clidemia strigillosa (Sw.) DC. BASIONYM: *Melastoma strigillosa* Sw. Prodr. 71. 1788 (without an asterisk), "India occidentalis." The location of Jamaica is given in the *Flora* (2: 793) but not the collector. A Masson specimen (BM) is regarded as the holotype.

Clidemia umbrosa (Sw.) Cogn. BASIONYM: *Melastoma umbrosa* Sw. Prodr. 72. 1788 (without an asterisk), "St. Christopher." Although several locations and collectors are cited by Swartz (Fl. Ind. Occ. 2: 817), the single location of St. Kitts in the *Prodromus* can be associated with the Masson specimen (BM), which should be considered as the holotype.

Henriettea ramiflora (Sw.) DC. BASIONYM: *Melastoma ramiflora* Sw. Prodr. 69. 1788 (without an asterisk), Jamaica. In the *Flora* (2: 775) Swartz stated, "Habitat in Jamaica in Paroeciae St. Thomae in valle locis paludosis. (Masson) Mus. Banks." (BM).

Miconia elata (Sw.) DC. BASIONYM: *Melastoma elata* Sw. Prodr. 70. 1788 (without an asterisk); Fl. Ind. Occ. 2: 781. 1798. No collectors are cited in either work, and the location is given as Jamaica. There is no appropriate material at Stockholm, and a collection by Masson (BM) is listed under the name *Melastoma elata* in the *Florula*.

Ossea microphylla (Sw.) Triana. BASIONYM: *Melastoma microphylla* Sw. Prodr. 72. 1788 (with an asterisk). A Masson specimen (BM) is cited by Swartz (Fl. Ind. Occ. 2: 813), and the name is listed as "mss." in Solander's *Florula*.

Oleaceae

Chionanthus compacta Sw. Prodr. 13. 1788 (with an asterisk), "Insulae caribae." In the *Flora* (1: 22) Swartz cited specimens of von Rohr from St. Croix and of Masson from Nevis. Masson's (BM) should be considered the lectotype.

Phytolaccaceae

Microtea debilis Sw. Prodr. 53. 1788 (with an asterisk and as a new genus), "St. Christopher." In the *Flora* (1: 543) Swartz stated, "Habitat in India occidentali, Insulisque Caribaeis: Grenada (de Ponthieu), St. Eustathii (Masson), Guadaloupe (v. Rohr)." The entry as a mss. name in Solander's *Florula* cited the location with the abbreviation for Caribaeis. The Masson specimen (BM) should be considered the lectotype.

Rubiaceae

Psychotria aubletiana Steyerl. BASIONYM: *Cephaelis axillaris* Sw. Prodr. 45. 1788 (with an asterisk), "St. Christopher," not *Psychotria axillaris* Willd., 1798. In the *Flora* (1: 441) Swartz stated, "Provenit in Insula St. Christophori. Herb. Banks. (Masson)." Steyerl (1972, p. 694), when transferring *Cephaelis axillaris* Sw. to *Psychotria*, proposed the new name *Psychotria aubletiana*. He attributed the type to Swartz incorrectly, for the Masson specimen (BM) is the holotype.

Chomelia fasciculata (Sw.) Sw. BASIONYM: *Ixora fasciculata* Sw. Prodr. 30. 1788 (with an asterisk), "Jamaica." In the *Flora* (1: 238) Swartz cited a Masson specimen from "Granada." The entry "*Ixora fasciculata*" appears as a "mss." name in Solander's catalogue as a collection of Masson from Grenada. The holotype is in the British Museum.

Psychotria grandis Sw. Prodr. 43. 1788 (without an asterisk), "Jamaica, Domingo." In the *Flora* (1: 417) Jamaica is the only location given. Al-

though there is a Swartz specimen in Stockholm, a Masson collection (BM) has been marked "type specimen." An entry with this binomial appears in Solander's Florula for a Masson collection from Jamaica.

Rondeletia hirta Sw. Prodr. 41. 1788 (with an asterisk), "Jamaica." No collector is cited by Swartz in the *Flora* (1: 373). The entry "*Rondeletia hirta* mss." appears in Solander's Florula for a Masson specimen from Jamaica. The Masson specimen (BM) is the holotype.

Sabicea hirta Sw. Prodr. 46. 1788 (without an asterisk), "Jamaica." In the *Flora* (1: 450) Swartz accepted the genus *Schwenkfelda*, listing *Sabicea* as a synonym, and made the combination *Schwenkfelda hirta* (Sw.) Sw. without citing a collector. In Solander's Florula the entry "*Sabicea hirta* mss." appears with a diagnosis for a Masson collection from Jamaica. This should be considered the holotype (BM).

Sapindaceae

Paullinia vespertilio Sw. Prodr. 64. 1788 (with an asterisk), "India occidentalis." In the *Flora* (2: 695) Swartz stated, "Habitat in Insula St. Christophori Indiae occidentalis. (Masson) E Museo Banksiano." Although a Masson collection from St. Kitts is in Stockholm, the holotype is clearly the specimen at the British Museum.

Theaceae

Freziera undulata (Sw.) Willd. BASIONYM: *Eroteum undulatum* Sw. Prodr. 85. 1788 (with an asterisk), "India occidentalis; Christopher, Montserrat, Guadeloupe etc." In the *Flora* (2: 974) Swartz made the combination *Freziera undulata* (Sw.) Sw., but this is antedated by Willdenow (Sp. Pl. 2: 1179. 1799). Swartz cited several specimens: *Masson*, from St. Kitts; *Ryan*, from Montserrat; *Ponthieu* and *Fahlberg*, from Guadeloupe; and *Anderson*, from St. Vincent. Kobuski (1941, p. 464) cited a Masson specimen in the Gray Herbarium as a "probable isotype," but the origin of this specimen cannot be determined. A Masson specimen (BM) is marked "type specimen," while similar sheets (s) are marked "holotypus" and "isotypus." Since Swartz indicated by the asterisk that he did not have material himself, the specimen in the British Museum is the true holotype. The entry "*Eroteum undulatum*" appears as a "mss." name in Solander's Florula, suggesting where Swartz obtained the name.

Verbenaceae

Vitex divaricata Sw. Prodr. 93. 1788 (with an asterisk), "St. Crux, Christopher." In the *Flora* (2: 1078) Swartz altered the distribution to St. Luciae (Masson) and St. Crucis (Ryan). The binomial appears as a "mss." name in Solander's Florula for a Masson specimen from St. Lucia. Such a specimen (BM) should be considered the lectotype.

Violaceae

Viola stipularis Sw. Prodr. 117. 1788 (with an asterisk), "India occidentalis, Guadeloupe." In the *Flora* (3: 1956) Swartz wrote, "Lecta in monte excelso (Misery dicto) Insulae St. Christophori (Mus. Banks)." The entry

in Solander's *Florula* is for a collection of Masson from Mt. Misery, St. Kitts. Such a specimen (BM) is the holotype.

Orchidaceae

Malaxis massonii (Ridley) Kuntze. BASIONYM: *Microstylis massonii* Ridley, Jour. Linn. Soc. Bot. **24**: 323. 1888. Ridley cited three collections in the original description: *Masson*, from St. Kitts; *Imray*, from Dominica; and *Crueger*, from Trinidad. Garay and Sweet (1974, p. 118) designated the Masson collection (BM) as the lectotype and noted, "Specimens referable to this species often have been reported in the literature under *Malaxis spicata* Sw., a species limited in distribution to the Greater Antilles." In Solander's *Florula* a Masson specimen called "*Malaxis spicata*" is indicated from St. Kitts; although Swartz probably saw this specimen the only location he gave for *M. spicata* in the *Prodromus* (p. 119) and the *Flora* (**3**: 1441) is Jamaica.

The value of Francis Masson's collections from the West Indies has never been fully appreciated. This is partly due to the fact that Britten stated that Masson's collections were destroyed in a hurricane in St. Lucia.

PONTHIEU

According to Urban (1902), Ponthieu collected in Jamaica, Antigua, Barbuda, Montserrat, Guadeloupe, Grenada, and Tobago in 1786. His collections are reported to be in the Banks (BM), Delessert (G), and Swartz (S) herbaria. A number of references in Swartz's *Flora* indicate that Ponthieu also collected in Dominica. The following species have been typified by material in the Banks herbarium:

Charianthus alpinus (Sw.) Howard. BASIONYM: *Melastoma alpina* Sw. Prodr. 71. 1788 (without an asterisk); Fl. Ind. Occ. **2**: 800. 1798 (*Ponthieu*, Mus. Banks cited). Lectotype designated by Howard (1972, p. 402): *Ponthieu s.n.*, Guadeloupe (BM).

Guettarda rugosa Sw. Prodr. 59. 1788 (with an asterisk), India occidentalis; Fl. Ind. Occ. **1**: 632. 1797, Antigua, Dominica (*Ponthieu*, Mus. Banks). A lectotype might be chosen, but the taxon is a synonym of *G. scabra* (L.) Lam.

Rudgea citrifolia (Sw.) Schum. BASIONYM: *Psychotria citrifolia* Sw. Prodr. 43. 1788 (with an asterisk); Fl. Ind. Occ. **1**: 398. 1797. Swartz did not cite a collector and gave only the general location of "India occidentalis" in both references. A Ponthieu collection (BM) is indicated as "Insulae Caribaeae" and is considered the lectotype. A second sheet "Ex montibus Dominicae. De Ponthieu" is in the British Museum herbarium.

Tibouchina ornata (Sw.) Baillon. BASIONYM: *Melastoma ornata* Sw. Prodr. 69. 1788 (with an asterisk); *Osbeckia ornata* (Sw.) Sw. Fl. Ind. Occ. **2**: 647. 1800. Lectotype designated by Howard (1972, p. 399): *Ponthieu s.n.*, Guadeloupe (BM).

Swartz cited the following species with an asterisk in his *Prodromus* and in the *Flora* indicated only collections of Ponthieu, thus suggesting that the type might be in the Banks herbarium:

Calolisianthus frigidus (Sw.) Gilg. BASIONYM: *Lisianthus frigidus* Sw. Prodr. 40. 1788; Fl. Ind. Occ. 1: 352. 1797. Dominica.

Lobelia stricta Sw. Prodr. 117. 1788; Fl. Ind. Occ. 3: 1952. 1804, Guadeloupe.

Phyllanthus mimosoides Sw. Prodr. 27. 1788, Antigua. In the *Flora* (2: 1101) Swartz cited Caribaeis, Antigua, and Dominica. Webster (1958) attributed the lectotype (G) to Antigua. This species is common on Dominica and has not been re-collected on Antigua. No likely location for this wet-forest species exists on Antigua today, and the location of Dominica is probably correct.

Scutellaria purpurascens Sw. Prodr. 89. 1788; Fl. Ind. Occ. 2: 1013. 1800, Guadeloupe.

There are several species for which Swartz cited more than one collection in his treatment in the *Flora*. The designation of a lectotype remains to be made.

Ilex sideroxyloides (Sw.) Griseb. BASIONYM: *Prinos sideroxyloides* Sw. Prodr. 58. 1788 (with an asterisk), Montserrat. A Ponthieu collection from Montserrat and a Fahlberg collection from St. Kitts are cited in the *Flora* (1: 624). The Ponthieu collection, when located, should be chosen the lectotype.

Lantana radula Sw. Prodr. 92. 1788 (without an asterisk), India occidentalis. Although Swartz had a specimen, in the *Flora* (2: 1057) he cited an Anderson collection from St. Vincent and a Ponthieu collection from Dominica.

Pisonia subcordata Sw. Prodr. 60. 1788 (with an asterisk), India occidentalis, Antigua. In the *Flora* (2: 641) Swartz cited Antigua (Ponthieu), and St. Kitts and St. Barts (Fahlberg). The Ponthieu collection, when located, should be the lectotype.

Ternstroemia elliptica Sw. Prodr. 81. 1788 (with an asterisk), "India occidentalis, Guadeloupe, Vincentii." In the *Flora* (2: 929) collections by Ryan from Montserrat, Ponthieu from Guadeloupe, and Anderson from St. Vincent are cited. The lectotype would be chosen from the Ponthieu or Anderson collections.

RYAN

Little is known of Dr. John Ryan, who collected on Montserrat, St. John, and St. Jan at the end of the eighteenth century. Although his collections were sent to Vahl in Copenhagen, a few are in the Solander catalog and the

Banks herbarium. Swartz used an asterisk in describing two species, indicating that specimens should be in the Banks collection.

Gesneria ventricosa Sw. Prodr. 90. 1788 (with an asterisk); Fl. Ind. Occ. 2: 1028. 1800. Swartz indicated "Jamaica, Montserrat, Dominica" in the *Prodromus* and Jamaica, Montserrat (*Ryan*), Martinique (*Fahlberg*), and Dominica (*Ponthieu*) in the *Flora*. Skog (1976) has designated the *Ryan* collection (BM) as the lectotype.

Tetrazygia angustifolia (Sw.) DC. BASIONYM: *Melastoma angustifolia* Sw. Prodr. 71. 1788 (without an asterisk), "India occidentalis." In the *Flora* (2: 796) the species is attributed to Jamaica, Insulis Caribaeis (*Ponthieu*), and St. John (*Ryan*). No lectotype has been chosen.

Tetrazygia eleagnoides (Sw.) DC. BASIONYM: *Melastoma Aelegnoides* Sw. Prodr. 72. 1788 (with an asterisk), "India occidentalis." In the *Flora* (2: 815) the only collection cited is *Ryan* from St. John, but this specimen has not been cited by subsequent workers on the Melastomataceae.

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ANATOMY OF THE PALM RHAPIS EXCELSA, VIII. VESSEL NETWORK AND VESSEL-LENGTH DISTRIBUTION IN THE STEM

MARTIN H. ZIMMERMANN, KENT F. McCUE, AND JOHN S. SPERRY

THE CONCEPT of the vessel, a conducting unit consisting of a series of vessel elements lined up end to end, has been known for well over a century (e.g., Hartig, 1878). The fact that vessels are of limited length is of considerable functional importance. If a vessel is damaged (for example, by an insect), air is drawn into its lumen as water withdraws into neighboring tissue, because xylem water is normally under less than atmospheric pressure. The damaged vessel is thus permanently lost as a functioning unit. Numerous small vessels therefore represent a conservative and safe water-conducting system, while wide and long vessels are much more vulnerable, although a great deal more efficient (Zimmermann, 1978).

Vessels are far too long to be seen in their entirety in single microtome sections. Macerations may reveal individual elements that can be interpreted as vessel ends (see Bierhorst & Zamora, 1965; Handley, 1936), but terminal elements are thus seen only in isolation. Length and arrangement of vessels within the xylem is of interest to anyone studying the hydraulic construction of a plant. It was not really known how and where vessels end until the method of three-dimensional cinematographic analysis first described in the initial paper of this series (Zimmermann & Tomlinson, 1965) had been developed. Cinematographic analysis proved to be a powerful tool that enabled us to sort out the most complex vascular systems with relative ease. In previous papers of this series as well as in many other publications, we described the course of entire vascular bundles. Vascular bundles are, of course, the pathways of both xylem and phloem transport. The direction and pathway of phloem transport has been studied by following thousands of autoradiographs through the *Rhapis* stem (Zimmermann, 1973). In this paper, attention is focused on the xylem, with descriptions of the precise layout of vessels within vascular bundles and of the functional significance of their arrangement.

MATERIALS AND METHODS

Individual vessels were followed in some of the motion picture films that we had made earlier for the analysis of the vascular system of *Rhapis* (see

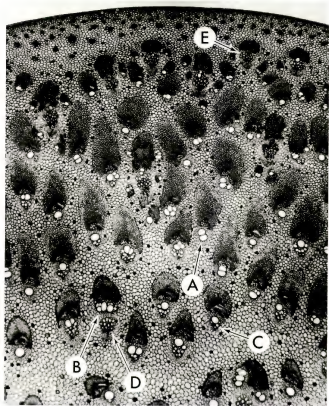


FIGURE 1. Transverse section of stem of *Rhaps excelsa*, $\times 35$. Axial bundles more than 10 cm below leaf contact have no protoxylem. Two metaxylem vessels overlapping (A). Leaf traces containing small amount of protoxylem (C), much protoxylem (D) and metaxylem (B), and only protoxylem (E).

Zimmermann & Tomlinson, 1965). Most of these films are made up of individual frames that show 50- μm -thick transverse sections spaced at 250- μm intervals. Magnification in these films is high enough that individual vessels are seen clearly. In some cases it is easy to distinguish vessels from vessel elements. In an axial bundle a metaxylem-vessel end may overlap the end

of the continuing vessel by 2 cm—the length of about 40 elements. Transverse sections show the vessel pair (e.g., at A in FIGURE 1). To be certain that one is dealing with vessels and not merely with element ends—especially in areas such as leaf-trace departures, where vessels are crowded (e.g., at B in FIGURE 1)—the film must be run back and forth in order to ascertain vessel continuity.

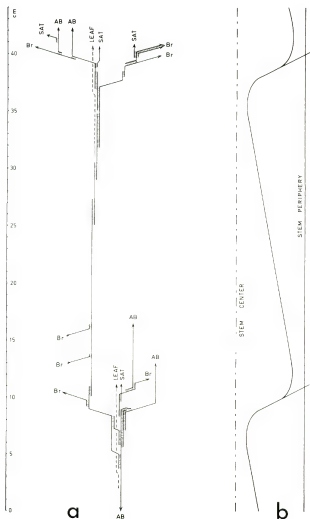
Vessel-length distribution measurements were made with the latex-paint infusion technique (Zimmermann & Jeje, 1981). Fresh stems of plants grown at the Harvard Forest greenhouse and outdoors at the Fairchild Tropical Garden were cut at the base (just above the root system), trimmed cleanly with a razor blade or microtome, and vacuum infiltrated with water to remove any air that might have been drawn into the vessels by cutting the stem. The plant was then allowed to transpire in a horizontal position, taking up a dilute suspension of latex paint particles, until wilted (1–2 weeks). This procedure fills all vessels that are cut open at the basal end with paint particles. When no more liquid was taken up by the plant, the stem was cut into 5-cm-long segments. The ends were trimmed with the microtome, the paint-containing vessels were counted, and the vessel-length distribution was calculated.

RESULTS AND DISCUSSION

THE VESSEL NETWORK

Representation of three-dimensional vascular systems in two-dimensional illustrations is always difficult. Some simplification is usually necessary in order to bring out a specific feature. In the past we have shown the path of vascular bundles in monocotyledonous stems projected onto a radial plane (radial coordinate projection), as in FIGURE 2, b. These plots were usually foreshortened five to ten times to enhance radial displacement. In order to show vessel contacts, we have projected the vascular system here radially onto a tangential plane (FIGURE 2, a). In this case radial displacement in the stem is ignored. The diagrams show the axial extent of vessels and vessel overlaps—the feature of specific interest here. Horizontal distances in the drawing are shown greatly expanded and without scale. In visualizing dimensions, one has to keep in mind that the width of the entire leaf-trace complex shown in FIGURE 2, a, is, at the most, 1 mm. In other words, if the horizontal scale were the same as the vertical one, the whole leaf-trace complex would not occupy much more space than the thickness of the vertical line illustrating a vessel!

FIGURE 2, a, shows the vessels in a major vascular bundle over an entire leaf-contact distance. Solid lines indicate metaxylem (mx) vessels. Hatching between two parallel-running vessels indicates that the two are connected by intervessel pitting. Protoxylem (px) vessels and tracheids are shown as dashed lines. A single dashed line indicates presence of px, regardless of whether it is a small group of px elements at the lower end of a leaf trace (such as in FIGURE 1 at C) or a larger group near the leaf-trace departure



(such as in FIGURE 1 at D). All wide mx vessels remain within the central cylinder of the stem; it is the narrow px only that connects the vascular system of the stem with the leaf base (FIGURE 1 at E) (Zimmermann & Tomlinson, 1965).

The situation shown in FIGURE 2, a is summarized in another way in FIGURE 3. As we follow an axial bundle up the stem, we make the following observations (FIGURE 2, a). In its lowest portions, near the stem periphery, the bundle has a single mx vessel. The bundle gradually approaches the stem center. At some point (at 2 cm on the scale, FIGURE 2, a), we observe the appearance of px (position 3 in FIGURE 3). We are now about 10 cm below the leaf contact. Additional mx vessels appear, and the bundle becomes wider (position 4 in FIGURE 3). Usually, but not always, new mx vessels appear next to an existing mx vessel. However, a px vessel may "grow" to become an mx vessel as we follow the vascular bundle upward.

At ca. 9 cm on the scale (FIGURE 2, a), the leaf trace begins to break up, as shown in position 5 of FIGURE 3. The branches are bridges, connecting to neighboring axial bundles (outward-pointing arrows in FIGURE 2, a), axial bundles continuing their way up and repeating the cycle, or satellites connecting to the inflorescence. The leaf trace proper, containing px only, enters the leaf base (as also shown in FIGURE 1, at E).

The leaf trace shown in FIGURE 2, a, at 10 cm has three axial bundles, two bridges, and one satellite bundle. The film follows the axial bundle on the left on the diagram. The vessel of the axial bundle ends, and a new one begins with an overlap of only about 1 cm. Two bridges are then "received" from neighboring leaf traces (position 1 in FIGURE 3). Before the bundle increases in size to become a leaf trace again, the vessel ends twice more and is replaced by a new one. The longest vessel in the diagram extends from levels 10 to 27 cm, a length of 17 cm. The leaf-contact distance of this bundle is about 30 cm. The upper leaf-trace complex breaks up into three bridges, three satellites, and two axial bundles.

Extended continuity along individual bundles, like that shown in FIGURE 2, a, is difficult to obtain on film since it requires a continuous series of about 2000 high-quality transverse sections. We have only one such 40-cm-long section series. In order to look at vessels of some other stems, we plotted the vessel network in a number of shorter series, some of which are given in FIGURE 4. FIGURE 4, a-d, shows the lower parts of four axial bundles, each of them "receiving" bridges from departing leaf traces.

FIGURE 2. a, vessels of vascular bundle (plotted from film) over complete leaf-contact distance of 40 cm, projected radially onto tangential plane. Metaxylem vessels, solid lines; parallel-running vessels with vessel-to-vessel pitting between them, connected by hatching; dashed line indicates that bundle contains protoxylem (regardless of amount). AB = axial bundle, Br = bridge, SAT = satellite bundle (to inflorescence). Arrows indicating bridges always shown pointing away from leaf trace. Diagram greatly expanded laterally (leaf-trace complex ca. 1 mm wide). b, same bundle, radial coordinate projection.

FIGURE 4, e, shows a leaf trace complex that branches into three continuing axial bundles and no bridges. The axial bundle branch shown on the right "receives" three bridges from neighboring departing leaf traces. FIGURE 4, f, shows another leaf-trace complex, which breaks up into three bridges and one axial bundle. Two bridges are "received" by that axial bundle. In this

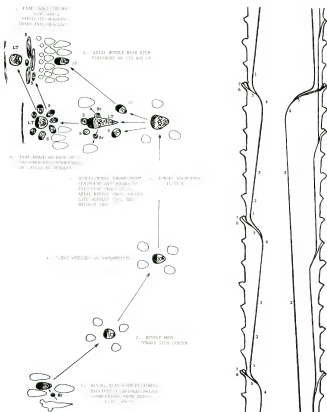


FIGURE 3. Course of vascular bundles in stem of *Rhaps*. In diagram on right, stem axis foreshortened four times in relation to stem diameter. (Slightly modified from Zimmermann & Tomlinson, 1965.)

particular series (FIGURE 4, e, f) it was possible to determine the position of the nodes; they are given as horizontal lines next to the scale. The axial bundles shown in FIGURE 4, a-d, could easily be the continuation of the axial bundles at the upper ends of FIGURE 4, e, f. In summary, the results represented in FIGURE 2 and 4 are very similar.

FIGURE 5 is a three-dimensional representation of a leaf-trace departure.

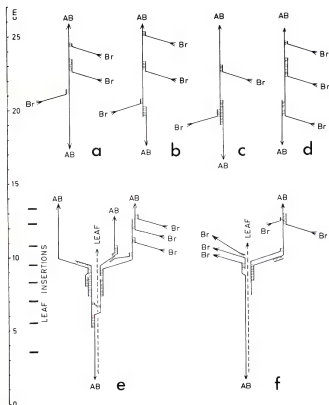


FIGURE 4. Plots of vessel distributions in shorter portions of vascular bundles: a-d, lower portions of axial bundles; e, f, leaf-trace complexes. Description as in Figure 2.

The axial scale is five times foreshortened; the actual axial extent of the section is 2.5 cm. Protoxylem is again shown as a single dashed line. At the lower end the leaf trace has three mx vessels. Where vessels run in close contact, we can assume vessel-to-vessel pit areas between them. The leaf trace gives off three bridges on the right to the neighboring axial bundles marked AB 1-3. The lower part of AB 3 was outside the field of view. An axial bundle branches off on the left (AB 4), and a small bridge connects to it (higher up). The leaf trace, containing px only, is seen leaving the central cylinder, accompanied by two satellites (S), at the upper surface of the block.

VESSEL-LENGTH DISTRIBUTION

FIGURE 2, a, shows eight vessels throughout their entire length; seven more are shown in FIGURE 3, f. If we classify these vessels according to their length, we find that nine (60%) are 0-5 cm long, five (33%) are 5-10 cm long, and one (7%) is 15-20 cm long. These percentages are vessel lengths within a given stem volume—namely, the volume covered by the plots. It must be emphasized that this is a very small statistical sample.

There are methods by which one can calculate the distribution of vessel lengths in a stem by recording distances to which paint particles are perfused. Paint particles, when sufficiently small, can pass scalariform perforation plates, but they cannot cross vessel-to-vessel pit membranes. The method, first described by Skene and Balodis (1968) and later modified by Zimmermann and Jeje (1981), assumes random distribution of vessels within the stem and yields percentages of vessels (per transverse-sectional area) of different length classes. Readers interested in the methods are referred to the above papers.

The method of Skene and Balodis works only if vessels are randomly distributed within the stem. Upon casual consideration, this does not seem to be the case: there may be more short bridge vessels in the nodal than in the internodal area. However, careful examination of FIGURE 4, e, f, reveals that each leaf-trace complex is spread out over a considerable axial distance; thus, the internal anatomy of the stem is not sharply segregated into nodal and internodal regions.

A total of six vessel-length distribution measurements were made with the paint-infusion technique, some with plants grown at the Harvard Forest greenhouse and some with taller plants grown outdoors at the Fairchild Tropical Garden. FIGURE 6 (left) shows the results calculated from the pooled counts of all six specimens. This includes 4264 metaxylem vessels to which paint was applied. We also calculated each of the experiments separately. FIGURE 6 (right) shows an example of a small specimen with a stem diameter of 8 mm. It is interesting to note that the percentage of the shortest vessels (75%) is about the same in this small specimen as it is in the larger, more vigorous ones (stem diameter 1.5-2 cm), but the distribution of the longer vessels is different: only the longer vessels are longer in the larger specimens.

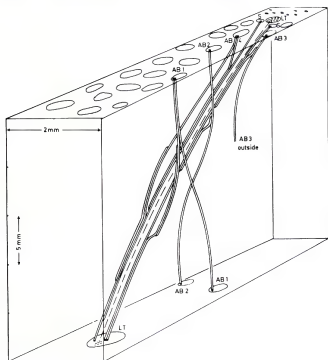


FIGURE 5. Reconstruction of three-dimensional arrangement of vessels associated with leaf-trace complex. Note that axial scale is five times foreshortened in comparison with horizontal scales.

This probably means that leaf-contact distances of major bundles are longer.

An interesting phenomenon that is not shown in FIGURE 6 is the fact that some vessels of the shortest length class are extremely short. This became evident when we recut the paint application surface with the microtome. The paint-containing vessels decreased very quickly to half or less when a few microtome sections were removed from the transverse surface of the stem. From this it is quite obvious that the shortest length-class contains the bridge vessels, and the longer length-classes contain axial-bundle vessels that vary in length depending upon leaf-contact distance.

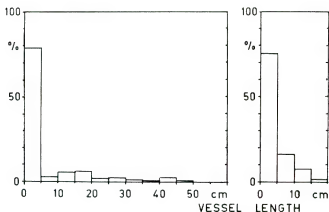
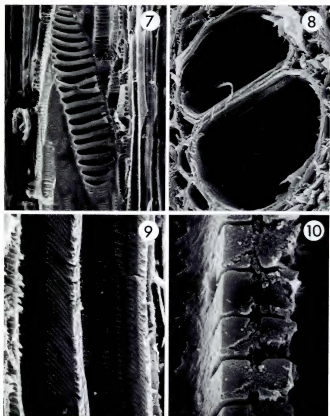


FIGURE 6. Metaxylem-vessel lengths in stem of *Rhapis*. Left diagram calculated from pooled results of six stems (total of 4264 metaxylem vessels). Right diagram figured from small greenhouse specimen with a stem diameter of 8 mm, which showed 323 metaxylem vessels on single transverse section.

DIMENSIONS IN RELATION TO WATER MOVEMENT

We looked at vessel-to-vessel contact areas with the scanning electron microscope in order to make certain measurements. An understanding of such areas is a prerequisite for the understanding of water movement in the palm stem.

A scalariform perforation plate is shown in FIGURE 7. The perforations between the bars are approximately $8 \times 40 \mu\text{m}$. Such openings permit relatively unimpeded flow of water and, also important, permit the passage of an air-water interface. If air is admitted to the xylem via an injury, water recedes to the ends of the vessel, whereby the air-water interface passes through all perforation plates. An air-water interface passes through a wet pore if the pore diameter and the pressure gradient across the pore reach a certain magnitude. This is governed by the capillarity equation (Zimmermann, 1978). Individual vessels end by tapering out gradually, overlapping with one or more other vessels. The common walls of parallel-running vessels of the overlap region consist of bordered pit-pairs, which expose a large pit membrane area (the primary wall pair). The secondary wall arches over the pit cavities (FIGURES 8-10), thus reinforcing the pit membrane area against stress. The micropores in the pit membranes of vessels have never been measured, but we know that pores in other primary walls are ca. 25 nm in diameter (see Strucker & Peveling, 1961)—far too small to permit



FIGURES 7-10. Scanning electron micrographs of xylem as seen on cut stem surfaces: 7, scalariform perforation plate between vessel elements, $\times 240$; 8, transversely cut stem surface, $\times 700$, showing vessel pair and vessel-to-vessel pit area; 9, longitudinal section through vessel pair separated by scalariform vessel-to-vessel pits, $\times 540$; 10, vessel-to-vessel pits, longitudinal section (cutting across wall), $\times 3380$.

passage of an air-water interface. In other words, an air embolus remains confined to an individual vessel. Water, on the other hand, can readily pass through the bordered pits from vessel to vessel because the exposed pit membrane area is very large.

Let us look at some dimensions. If we take the vessel in FIGURE 8 to be circular with a diameter of 60 μm , the transverse-sectional area of the vessel lumen is $2.8 \times 10^{-3} \text{ mm}^2$. The width of the scalariform pit area is ca. 35 μm , as seen in FIGURES 8 and 9. The length of the vessel overlap may be 2 cm (FIGURES 2, 4) of which ca. 40 percent is membrane area and 60 percent is secondary-wall contact (FIGURE 10). From this we can calculate the total area of pit membrane through which water moves from one vessel to the next. It is ca. 0.28 mm^2 —about 100 times larger than the transverse-sectional area of the vessel. Considering that water has to move through the very small micropores of the pit membranes and that vessel-overlap distances are often much shorter, the resistance to flow from vessel to vessel must still be appreciable.

By comparing experimental flow rate through a piece of xylem with the calculated flow rate through ideal capillaries of the same diameters as the vessels, one can get an estimate of the resistance to flow across perforation plates and through vessel-to-vessel pits. Such measurements have been made with both coniferous and dicotyledonous wood. For dicotyledons the resistance to flow from one vessel to the next is about equal to the resistance to flow along the vessel (see the citations in Zimmermann & Brown, 1971). Such calculations are not very accurate and must be considered as estimates only. A small error in the measurement of the vessel diameter gives a large error in the flow-rate calculation because of the fourth-power relationship of the flow equation (Zimmermann, 1978). For example, a 10 percent overestimate of vessel diameter causes a flow-rate overestimate of 50 percent because $1.1^4 \approx 1.5$. For the same reason we can say that vessels that are only 50 percent efficient when compared with ideal capillaries are equal in performance to capillaries with 85 percent of the vessel diameter (i.e., $0.85^4 \approx 0.5$).

ACKNOWLEDGMENTS

We wish to thank the staff of the Fairchild Tropical Garden, who made plant material available and helped us in various ways. We thank Dr. P. B. Tomlinson, who collaborated in the earlier parts of this series of papers and read this manuscript. Last but not least, we thank Monica Mattmuller, who has helped us all the way through the project.

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A REMARKABLE NEW DIMORPHIC EUPHORBIA
(EUPHORBACEAE) FROM SOUTHERN MEXICO¹

MICHAEL J. HUFT

IN VIEW OF the large number of undetermined *Euphorbia* collections in most major herbaria, it is perhaps not surprising that a few common species remain undescribed. While preparing a monographic treatment of *Euphorbia* section TITHYMALOPSIS (Klotzsch & Garcke) Boissier, I recognized one such species allied to *E. sphaerorrhiza* Benthham, a well-known species of the pine and oak forests of western Mexico.

Section TITHYMALOPSIS comprises 16 species of perennial herbs in the eastern and south-central United States, Mexico, and Guatemala that are characterized by an umbellate or dichasial inflorescence, five cyathial glands, undivided petaloid appendages, styles that are united at the base and divided for one third to one half of their length, and ovate, ecarunculate seeds that are irregularly tuberculate, shallowly pitted, or smooth (Huft, 1979). The five Mexican taxa are further distinguished by a globose root and variously pubescent inflorescences, cyathia, and capsules.

***Euphorbia ixtlana* Huft, sp. nov.**

FIGURE 1.

Herba perennis, erecta. Radix globosa. Caules glabri vel villosi. Folia alternata vel opposita, raro ternata, inferiora fugacia, squamiformis, superiora supra glabra, subtus pilosa vel villosa; laminae dimorphae, formae duae in eadem plantae raro coaetaneae, aliquot ovatae vel ovata-lanceolatae, margine dentato, hyalino, revoluti, ceterum lineares vel anguste lanceolatae, margine integro, revoluti. Stipulae glanduliformes, minutae. Inflorescentiae terminales, umbellatae, radiis (2-)3(-5), dichasialibus vel raro trichasialibus vel laterales, dichasiales, in nodis 1-3 infra umbellam ortae. Cyathia campanulata, extus dense villosa; glandulae 5; appendices supra albae, glabrae, delatae vel lanceolatae, subtus brunneae, margine albo villosi. Capsula viridis, in sicco brunnescent, pilosa vel glabra.

Erect perennial herb 18-45 cm high. Root globose, occasionally proliferating, (7-)10-18 mm high, (7.5-)11-17 mm thick, giving rise on upper end to short, erect rhizome 7-10(-30) mm long, from which arises a solitary (rarely 2) stem(s), this (0.8-)1(-1.6) mm in diameter at base, glabrous to villous, the hairs uniseriate, multicellular, somewhat flattened. Branching below inflorescence somewhat sparse; nodes below umbel (3 or) 4 to 6 (or

¹Based on part of a doctoral thesis submitted to the H. H. Rackham School of Graduate Studies, The University of Michigan.

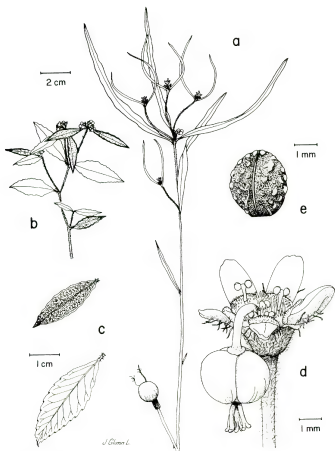


FIGURE 1. *Euphorbia ixtlana*: a, habit of linear-leaved form (Lundell 12289); b, inflorescence of ovate-leaved form (Lundell 12288); c, lower and upper surfaces of ovate leaf (Lundell 12288); d, cyathium with mature capsule (Cruden 1102); e, seed (Lundell 12288).

7); internodes (2.5-)3.5-6.5(-9) cm long. Leaves alternate or opposite (rarely ternate), progressively reduced from umbel downward; lower stem leaves fugacious, ascending or appressed, the lowest scalelike, 0.8-1.5 by ca. 1 mm; upper stem leaves and bracts glabrous above, moderately to densely pilose to villous below, petiolate; petiole 1-4 mm long, villous; blade dimorphic, the two forms occurring at same time in population but rarely on same plant—one form ovate to ovate-lanceolate, 15-36(-42) by 10-16 mm, 1.2-3 times as long as wide, the apex acute, the base cuneate, the margin dentate, hyaline, revolute, with teeth irregularly spaced, 6 to 12 per cm, acute and ascending but often appearing rounded due to revolute margin; the other form linear to lanceolate, 3-10 cm by 2-3 mm, 10-40 times as long as wide, the apex acute, the base narrowly cuneate, the margin entire, revolute. Stipules glanduliform, minute, ca. 0.3 by ca. 0.2 mm, often obscured by indument. Bracts similar to upper stem leaves, gradually reduced upward. Inflorescence a terminal umbel; rays (2 or) 3 (to 5), dichasial (rarely trichasial), forking 2 to 5 times; first internode (1.5-)4-6(-10) cm long, second usually much shorter, 2-5(-25) mm long; lateral inflorescences, if present, at 1 to 3 nodes below umbel, dichasial. Cyathia green, campanulate, 1.5-2 mm high, (1.5-)2-3 mm in diameter below glands, 4-5.5(-6) mm across appendages, densely villous outside with indument extending onto adaxial surface of appendages, glabrous within; peduncles (1-)2.5-5 mm long, glabrous or with few hairs; lobes deltate, fimbriate, 0.5-0.8 by ca. 0.7 mm, glabrous to villous; glands 5, green, drying brown, 0.8-1.2 mm long parallel to rim of cyathium, 0.4-0.7 mm wide, the margin slightly erose, hyaline; appendages white above, brown with white margins below, deltate to lanceolate, the base rounded, exceeding gland by (0.5-)0.7-1.7 mm, 1-1.3 mm wide at gland. Staminate flowers 20 to 25; bracteoles numerous, plumose. Gynophore strongly reflexed at maturity, glabrous, (2-)3.5-6 mm long. Capsule green, drying brown, 2.5-3 mm high, (3.5-)4-5 mm in diameter, pilose or glabrous, with persistent styles 1-1.2 mm long. Seeds black or dark brown, ovate, (2.2-)2.5-2.8 by 1.7-2 mm, ecarunculate, tuberculate, the tubercles widely and irregularly spaced, low, dull orange.

TYPE: Mexico, Oaxaca, on mountainside in pineland, above Tejocote, July 25, 1943, *C. L. Lundell 12288* (holotype, MICH; isotype, LL).

SPECIMENS EXAMINED. **Mexico.** DISTRITO FEDERAL: Desierto de los Leones, *Hernández X 651* (LL (2 sheets)). GUERRERO: DISTR. Mina, Yesceros, 2000 m alt., oak and pine forest, *Hinton 14399, 14402* (LL, UC, US). OAXACA: N of Oaxaca on Hwy. 190, 1 mi S of km 495, *Breckon & Breckon 790* (DAV), 805 (DAV, GH); road between Ixtlán and Valle Nacional, *Breckon & Christman 631* (DAV); La Carbonera, *Conzatti 4010, 4010½* (US); Cerro de San Felipe, alt. 3000 m, *Conzatti & Gonzalez 255* (F), 255a (F, GH); Cumbre de la Carbonera, alt. 2640 m, *Conzatti & Gonzalez 257* (F, GH); de Papalo a la Cumbre de Cheve, Cuicatlán, alt. 2000 m, *Conzatti & Gonzalez 775, 775a* (F, GH); ca. 3 km SE of Ixtlán de Juárez, Vivero Rancho Teja, alt. 2300-2400 m, relatively dry pine and oak woods with lots of litter, *Cruden 1102* (GH, MICH, TEX, UC), 1104 (UC); 13.5 mi SW of Sola de Vega along road to Puerto Escondido, *G. & J. Davidse 9660* (MO); ca. 40 mi N of Oaxaca, near Herradura de Oro, S of No-

chistlán, Dressler 1793, 1794 (GH); 12 km N of Ixtlán de Juárez on road to Valle Nacional, Rte. 175, King 2072 (MICH); on mountainside in pineland, above Tejocote, Lundell 12287 (LL (2 sheets), MICH, UC), 12288 (LL, MICH), 12289 (LL (2 sheets), MICH, UC); above Vivero Rancho Teja (Hallberg Ranch), Ixtlán de Juárez, McPherson 704, 705 (MICH); vic. of La Parada, alt. 7500–8500 ft, Nelson 1013 (F, GH, US); Cerro Verde, vic. of San Luis Tlutiltanapa, Puebla, Purpus 3431 (UC); 23 km S of Ixtlán at km 35 on road from Oaxaca, alt. ca. 1500 m, hillside covered with *Quercus* scrub with understory of shrub Ericaceae, Roe & Roe 2007 (MO); San Juan del Estado, alt. 7000 ft, Smith et al. 26 (F, GH), 26a (F); ca. 9 mi N of Teixtlahuaca along Hwy. 131, Stevens 1335 (MICH); Hallberg's finca near Ixtlán, NE of Oaxaca, Webster 11597 (MICH); ca. 15–16 mi by road NE of Teotitlán del Camino, approx. 18°10'N, 97°00'W, alt. 7100 ft, common in oak woods, Webster et al. 17290 (MO). PUEBLA: above Coxcatlán between Apala and top of Cerro Chichiltepec, igneous and sedimentary rock outcrops with dark soils, primarily oak-pine forest, alt. ca. 2000–2500 m, Smith et al. 3821 (F, US).

Euphorbia ixtlana is named after the town of Ixtlán de Juárez, Oaxaca, near which several of the collections were made. It is widespread in northern Oaxaca and adjacent areas of Puebla and Guerrero, and it occurs at medium elevations in pine and oak forests, where its associates also include *Arbutus*, *Clethra*, and *Sambucus* (label data from Breckon & Christman 631 and Stevens 1335), as well as *Cuphea*, *Eryngium*, *Geranium*, *Monotropa*, and *Salvia* (Cruden 1102).

The new species strikingly resembles *Euphorbia sphaerorrhiza* in aspect but may be distinguished by its glabrous or pilose (vs. retuscabrous) stems, spreading (vs. appressed) hairs on the cyathium, petaloid appendages that are brown on the lower surface (probably green in living plants) except for a narrow white margin (vs. completely white, or occasionally green and reduced), and irregularly tuberculate (vs. smooth) seeds. The coloration of the lower surface of the appendages is also characteristic of another close relative, *E. hintonii* L. C. Wheeler, known only from a restricted area in the western part of the state of Mexico, but that species differs in having much shorter (1–3 dm) stature, usually slightly cordate leaf bases in the inflorescence, shorter and broader leaves, and globose capsules.

A most spectacular feature of *Euphorbia ixtlana* is the extreme dimorphism of the leaves and bracts. One form is linear with entire margins, while the other is ovate with dentate margins. The margins of both forms are revolute; thus the teeth of the dentate form, which are acute, often appear rounded. The two leaf forms rarely appear together on the same plant (an exception is Conzatti & Gonzalez 255a) but are apparently both present at the same time within a single population. This is evident because, although the two forms are nearly always placed on separate herbarium sheets, both were often gathered by the same collector on the same day and at the same locality and were given adjacent, or nearly adjacent, collection numbers. Other than the shape and margin of the leaves, there are no differences between the two forms. According to the label of Webster et al. 17290, the linear- and broad-leaved forms are randomly mixed.

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I wish to thank Dr. Rogers McVaugh for checking the Latin description, Dr. James R. Estes for reading the manuscript, and the curators of the following herbaria for the loan of specimens and other courtesies: the University of California, Davis (DAV), the Field Museum (F), the Gray Herbarium, Harvard University (GH), the University of Texas, Austin (LL, TEX), the University of Michigan (MICH), the Missouri Botanical Garden (MO), the University of California, Berkeley (UC), and the U. S. National Herbarium (US). The illustration was drawn by Janice Glimm Lacy.

LITERATURE CITED

- HUFT, M. J. 1979. A monograph of *Euphorbia* section *Tithymalopsis*. 276 pp. Unpubl. Ph.D. Thesis, University of Michigan.

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A TAXONOMIC REVISION OF *PIERIS* (ERICACEAE)

WALTER S. JUDD

THE GENUS *Pieris* comprises seven allopatric and rather distinctive species occurring in both eastern Asia and eastern North America and is closely related to several genera in the Andromedeae (Ericaceae) (see Stevens, 1971; Judd, 1979). Many of the species are commonly cultivated as ornamentals. I have attempted here to compare the taxa, to interpret their evolutionary relationships, to determine consistent generic and specific concepts, and to develop practical keys for identification.

There are really only two major taxonomic problems involving the genus or taxa within it. The first is to define the limits of the group—that is, to determine the distinctive characters of *Pieris* that separate it from related genera and to determine whether certain species such as *P. nana*, *P. floribunda*, or *P. phillyreifolia* should be segregated as distinct genera (see Nuttall, 1843; Small, 1914, 1933; Makino, 1961; Ohwi, 1965). This problem is discussed in part in Judd (1979). The second is to determine which species can be recognized within the wide range of variation that is found in the eastern Asian plants with subapical placentae and elongated testa cells (i.e., the *Pieris japonica*–*P. formosa* complex).

GENERIC AND INFRAGENERIC RELATIONSHIPS

The genus *Pieris* (Ericaceae subfam. Vaccinioideae tribe Andromedeae—see Stevens, 1970, 1971; Judd, 1979) is closely related to *Agarista* D. Don (including *Agauria* (DC.) Hooker f.), *Craibiodendron* W. W. Sm., and *Lyonia* Nutt. However, it can easily be differentiated from these genera by a combination of several characteristics. These include: 1) usually unifacial leaf midrib and petiole bundle; 2) coriaceous, serrate to entire, often pseudoverticillate or whorled leaves; 3) inflorescence exposed for some time before flowering, with meiosis occurring in the fall; 4) two more or less alternate

bracteoles; 5) urceolate to elongate-urceolate corollas lacking stomata on the abaxial surface; and 6) usually more or less straight filaments with 7) a pair of stout, minutely papillose spurs at the anther-filament junction; and 8) disintegration tissue on the back of the anther not extending into the spurs. The loculicidal capsules lack the thickened sutures of *Lyonia*, and the seeds do not have the prominent unilateral wing so characteristic of *Craibiodendron*. The multicellular, biseriate-stalked, glandular-headed hairs have only small heads and are thus unlike the swollen-headed glandular hairs or peltate scales of *Lyonia*. All species have an obviously heterogeneous pith except *P. nana* (homogeneous) and *P. cubensis* (heterogeneous, but poorly developed). A more detailed discussion of the evolutionary relationships of the above-mentioned genera is given in Judd (1979).

Pieris nana is very distinctive, differing from the other species of the genus in its low habit, its small, entire, usually whorled leaves, its roughened-papillose filaments, and its anthers with only poorly developed disintegration tissue. Because of these differences, this species has often been placed in the segregate genus *Arctericia*; however, it is here retained within *Pieris* since it resembles the rest of *Pieris* in the many characteristics listed above (see Judd, 1979).

The phylogenetic relationships among the species of *Pieris* have been investigated using the method of Wagner (1961, 1962, 1969, 1980; see also Eldredge & Cracraft, 1980). Sixteen characters were used and assigned generalized (primitive, ancestral, or plesiomorphous) or specialized (advanced, derived, or apomorphic) states. TABLE 1 lists these characters. For each of the characters, each taxon was scored 0 if primitive and 1 if advanced. When two or more states of a given character were considered derived, each was given a lower-case alphabetic superscript (e.g., 1^a, 1^b, 1^c). All taxa are listed in TABLE 2, with the character state values for each. The total divergence index of each taxon was determined by adding the individual character state values of each character together. Then mutual groupings of derived characters were determined (by hand), and the taxa were arranged in sequence according to these groupings. In this process the number of character state reversals was minimized. The taxa were plotted on a concentric graph (FIGURE 1), with the branching points determined by the mutual grouping of derived characters, and the distance by the divergence of each taxon.

The Wagner method, like other cladistic methods, requires numerous assumptions concerning which is the derived and which the ancestral state of each character. The problems and sources of error associated with each step in the procedure are discussed in Judd (1979). The derived state(s) of characters A-F, I-K, and M-P were determined by out-group comparison (using the *Lyonia* group of the Andromedeae as the outgroup—see Stevens, 1970, 1971; Judd, 1979) supported by in-group comparison for character states A, C^a, D, J, K, M, and N. In-group comparison was used in determining the advanced state of G, H, and L. These decisions were made after careful study of the genus and related groups.

FIGURE 1 clearly shows the cladistic distinctness of *Pieris nana* and also indicates that the remaining six species fall into two subgroups. Because of

TABLE 1. Characters used in phylogenetic study* of the species of *Pieris*.

CODE LETTER	CHARACTER	GENERALIZED STATE	SPECIALIZED STATE
A	Habit	Trees or low shrubs	a. \pm Prostrate shrubs (< 10 cm) b. Lianas, climbing within bark
B	Pith	Homogeneous	Heterogeneous
C	Leaf arrangement	Alternate	a. Whorls of 3 b. Pseudovericillate
D	Leaf length	> 1.5 cm	< 1.5 cm
E	Leaf margin	Entire	At least few teeth present
F	3 rd veins of leaf	Not prominent (leaves \pm brochidodromous)	Prominent (leaves \pm reticulodromous)
G	Petiole vascular bundle	Unifacial	Bifacial
H	Multicellular hairs	Biseriate-stalked, glandular	Multiseriate-stalked, nonglandular
I	Inflorescence position	Always axillary	Sometimes terminal
J	Flower arrangement	Alternate	Whorls of 3
K	Corolla	Weakly ribbed to unribbed	Strongly ribbed
L	Filament shape	\pm Straight	Geniculate
M	Filament pubescence	Unicellular hairs	a. Smooth b. Roughened-papillose
N	Disintegration tissue	Well developed	Poorly developed to lacking
O	Placentae	Subapical	Central to nearly basal
P	Seed-coat cells	Elongated	\pm Isodiametric

*Wagner method.

the cladistic (and patristic) divergence of *P. nana*, this species is here placed in the monotypic subgenus ARCTERICA; the remaining species are placed within subg. PIERIS, which has been divided into two sections, sect. PIERIS (including *P. japonica*, *P. formosa*, and *P. floribunda*) and sect. PHILLYREOIDES (including *P. phillyreifolia*, *P. cubensis*, and *P. swinhoei*).

The apomorphic character states distinctive of each of these groups are listed below. These characters include some that are unique to the group, indicated by a double asterisk (**), and some that are also found in other groups, indicated by a single asterisk (*). *Pieris nana* (subg. ARCTERICA) is characterized by: A^a (low, prostrate habit)**; C^a (leaves in whorls of

TABLE 2. Character divergence values for each taxon used to construct Wagner Tree.

CHARACTER	TAXA						
	<i>Pieris japonica</i>	<i>Pieris formosa</i>	<i>Pieris floribunda</i>	<i>Pieris phillyreifolia</i>	<i>Pieris cubensis</i>	<i>Pieris swinhoei</i>	<i>Pieris nana</i>
A	0	0	0	1b	0	0	1a
B	1	1	1	1	1/sl.	1	0
C	1b	1b	0	1b	0	1b	1a
D	0	0	0	0	0	0	1
E	1	1	1	1	1	1	0
F	0	1	1	0	0	0	0
G	0	0	0	0	1	0	0
H	0	0	1	0	0	0	0
I	1	1	1	0	0	1	1
J	0	0	0	0	0	0	1
K	0	0	1	0	0	0	0
L	0	0	0	1	0	0	0
M	0	0	0	1a	0	0	1b
N	0	0	0	0	0	0	1
O	0	0	0	1	1	1	1
P	0	0	0	1	1	1	0
TOTAL	4	5	6	8	5	6	8
GEOGRAPHIC LOCATION	EA	EA	NA	NA	WI	EA	EA

Explanation of abbreviations: sl. = only slightly developed, EA = eastern Asia, NA = North America, WI = West Indies.

three)**, D (small leaves)**, I (sometimes terminal inflorescences)*, J (flowers in whorls of three)**, M* (roughened-papillose filaments)**, N (disintegration tissue poorly developed)**, and O (placenta \pm central)*. Subgenus *PIERIS* is characterized by: B (heterogeneous pith, but only poorly developed in *P. cubensis*)** and E (serrate leaves)**. In addition, the group is distinguished by the plesiomorphous characters of an erect, arborescent habit (plants to at least 0.5 m tall), large leaves, and anthers with well-developed disintegration tissue. Section *PIERIS* is characterized by: B (heterogeneous pith)* and I (inflorescences sometimes terminal)*. This group tends to have paniculate inflorescences and has capsules with subapical placentae and strongly elongated seed-coat cells. Finally, sect. *PHILLYREIDES* is characterized by: B (heterogeneous pith)*, O (central to nearly basal placentae)*, and P (seeds with \pm isodiametric testa cells)**. The inflorescences of this group tend to be axillary racemes. The two sections are best differentiated

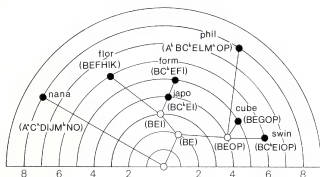


FIGURE 1. Wagner tree for the species of *Pieris*: extant taxa (black circles); hypothetical ancestors showing only derived character states shared by taxa positioned distally in tree (open circles). Derived character states for each taxon listed within parentheses; taxon names abbreviated by first four letters of specific epithet.

on the characters of placenta position and testa-cell shape.

Neither *Pieris phillyreifolia* nor *P. floribunda* has been recognized here as comprising a distinct genus, although each is a very distinct species. *Pieris phillyreifolia* is unique in its climbing habit and in its geniculate and smooth filaments; *P. floribunda*, in its large, multicellular, long-celled hairs and its strongly ribbed corolla. However, these differences are not of a magnitude comparable to those between other genera in the Andromedeae (Judd, 1979). More importantly, the above cladistic study has revealed that *P. phillyreifolia*, in spite of its striking climbing habit, is phylogenetically very close to *P. cubensis*, and that *P. floribunda*, despite its distinctive multicellular hairs, is clearly related to *P. japonica*. The possibility of a close relationship between *P. phillyreifolia*, *P. cubensis*, and *P. swinhoei* was first indicated by Stevens (1969).

DISTRIBUTION AND ECOLOGY

Pieris is likely an ancient genus since it shows an Arcto-Tertiary disjunction pattern between eastern Asia and eastern North America (see discussion in Judd, 1981). The genus is composed of seven species, one of which (*P. nana*) has been placed in the distinctive subgenus *ARCTERICA*. This species is strictly eastern Asian and occurs in the alpine vegetation of northern Japan, the Kuril Islands, and the southern Kamchatka Peninsula. The species of subg. *PIERIS* are grouped into two sections, both of which contain species occurring in eastern Asia and eastern North America. These species occur in cool to warm, temperate, broadleaved to coniferous forests on acid soils and are generally sun-loving plants. Section *PIERIS* contains the closely re-

lated *P. japonica* and *P. formosa*, whose combined distribution extends in an arc from Japan across China and west to Nepal, and the more distantly related *P. floribunda*, which occurs in the southern Appalachians of eastern North America. Section PHILLYREOIDES includes the very rare and little-collected *P. swinhoei* of southeastern China, *P. cubensis* of Cuba (Pinar del Río) and the Isle of Pines, and *P. phillyreifolia* of the southeastern United States Coastal Plain (South Carolina to Florida and west to Mississippi).

All species of the genus are allopatric (MAPS 1-5), and thus no naturally occurring hybrids are known. The process of speciation within the genus seems to have occurred via geographic isolation and subsequent morphological, physiological, and anatomic differentiation, resulting in allopatric pairs of related taxa (e.g., *P. japonica* and *P. formosa*, or *P. cubensis* and *P. phillyreifolia*—see Ehrendorfer, 1976). This process may be at work in the geographic subunits of *P. japonica* (eastern China, Taiwan, Ryukyu Islands, and Japan) since the plants of these regions differ from each other rather inconsistently in a few vegetative and inflorescence characters. It is perhaps significant that among the plants of these geographic subunits of *P. japonica*, the small population on Okinawa is the most distinctive (possibly due to the operation of genetic drift or the founder effect—see Mayr, 1969; Grant, 1971).

TAXONOMIC CRITERIA

HABIT. The species of *Pieris* vary from low, prostrate shrubs only a few centimeters tall (such as *P. nana*) to small trees of 10 m (e.g., *P. formosa* or lianas (*P. phillyreifolia*) that climb within the fibrous bark of *Taxodium*. *Pieris nana* and *P. phillyreifolia* are characteristically rhizomatous, while other species (*P. floribunda*, *P. japonica*, *P. formosa*) lack rhizomes.

As in most members of the Andromedeae, the growth of the individual shoot meristem is limited, and increase in height is by a succession of axillary, equivalent, orthotropic shoots (Lems, 1962). All species show Leeuwenburg's Model of growth (Temple, 1975; Hallé, Oldeman, & Tomlinson, 1978) or a slight variation of this architectural pattern. In *Pieris floribunda* the shoot is consistently terminated by the inflorescence; in *P. cubensis* and *P. phillyreifolia* the inflorescences are exclusively axillary, arising from buds near the shoot apex, and the shoot apex aborts. In either case growth continues by means of vegetative shoots arising from buds usually located below the floral buds or the terminal inflorescence. In *P. japonica*, *P. formosa*, *P. swinhoei*, and *P. nana* both terminal and axillary inflorescences may be produced; the axillary inflorescences always arise from buds clustered near the shoot apex. It should be added that rhizomatous species cannot be fitted into Leeuwenburg's Model unless the presence of rhizomes is discounted (i.e., unless only the orthotropic subunits of growth are considered).

With regard to growth architecture, *Pieris phillyreifolia* has diverged from the other species in that it produces orthotropic, scale-bearing shoots that climb within the fibrous bark of *Taxodium ascendens* Brongn. and that give rise at intervals to more or less plagiotropic leafy (and flowering) shoots (see

Lemon & Voegel, 1962; Hallé, Oldeman, & Tomlinson, 1978). However, this species may also form erect shrubs with a growth architecture similar to that of *P. cubensis*, and the climbing habit is likely derived from the rhizomatous-shrubby habit by several specializations involving the horizontal underground rhizome—for example, a change in the rhizomes' geotropic response.

The pith of the young stems is heterogeneous (i.e., with a mixture of large and small cells) in most species but is homogeneous in *Pieris nana* and nearly so in *P. cubensis*.

LEAVES. Leaf arrangement is often a useful taxonomic character within *Pieris*. *Pieris floribunda* and *P. cubensis* have alternate leaves, with the first-formed leaves of the shoot small, scalelike, and quickly deciduous, and those formed later much larger and persistent. *Pieris japonica*, *P. formosa*, *P. phillyreifolia*, and *P. swinhoei* have pseudoverticillate leaves, and *P. nana* usually has leaves in whorls of three.

All species have evergreen, coriaceous leaves with a prominent midvein. The secondary veins are brochidodromous in *Pieris japonica*, *P. swinhoei*, *P. phillyreifolia*, and *P. cubensis*, more or less reticulodromous in *P. floribunda* and *P. formosa*, and hyphodromous to slightly brochidodromous in *P. nana*. *Pieris swinhoei* is distinctive because of its numerous secondary veins that diverge at nearly right angles from the midvein and extend more or less straight toward the edge of the blade, where they interconnect. The leaf shape varies from widely to narrowly ovate, elliptic, or obovate, and the margin from entire to prominently serrulate or serrate. The extent of marginal serration is useful in differentiating *P. japonica* from *P. formosa*, and *P. swinhoei* from *P. cubensis*. *Pieris nana* is the only species with entire leaves. The size of the leaf blade varies from only 3–11 mm in *P. nana* to ca. 18 cm in *P. formosa*, but it also often varies greatly within a species (see especially *P. formosa*). The petiole and midvein vascular bundle is unifacial in most species (FIGURE 2). All species have included secondary veins (FIGURE 2), and the epidermal cells vary from nonlignified (e.g., *P. floribunda* or *P. japonica*) to strongly lignified (e.g., *P. phillyreifolia*). *Pieris cubensis* is distinctive in that it has fibers in the leaf mesophyll (see Stevens, 1970). There is also much variation in the thickness of the ultimate veinlets (FIGURE 2).

INDUMENTUM. The morphology of the unicellular and multicellular hairs is rather uniform within the genus. *Pieris floribunda* is easily distinguished by its large, multicellular, long-celled hairs. All species have multicellular, biserial-stalked, glandular-headed hairs, as well as unicellular ones.

The distribution of these hair types is, in general, either too uniform or too variable to be of taxonomic value. However, the capsules of *Pieris swinhoei* are densely covered with unicellular hairs, those of the related *P. phillyreifolia* are glabrous, and those of *P. cubensis* are glabrous to only very sparsely pubescent. It is of interest that the capsules of *P. nana* may be glabrous to densely pubescent; those of *P. floribunda*, *P. formosa*, and *P. japonica* are always glabrous.

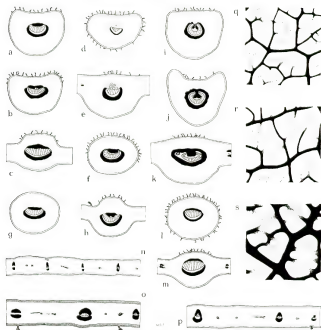


FIGURE 2. Anatomic variation within *Pieris*. a-m, vascular bundle cross sections shown semidiagrammatically; fiber sheath in black, phloem in white, xylem with vertical lines. a-c, *Pieris japonica*, $\times 25$: a, lower petiole; b, upper petiole; c, mid-vein near base of blade. d, e, *P. nana*, $\times 50$: d, mid-petiole; e, near base of blade. f, g, *P. phillyreifolia*, $\times 25$: f, mid-petiole; g, upper petiole. h, *P. swinhoei*, near base of blade, $\times 25$. i-k, *P. cubensis*, $\times 25$: i, lower petiole; j, upper petiole; k, near base of blade. l, m, *P. floribunda*, $\times 25$: l, mid-petiole; m, near base of blade. n-p, cross sections of leaf blades, $\times 50$: n, *P. floribunda*; o, *P. phillyreifolia* (note thick cuticle and lignified epidermis); p, *P. japonica*. q-s, areoles and vein endings (each square = 2.75 mm^2): q, *P. floribunda*; r, *P. japonica*; s, *P. phillyreifolia*.

INFLORESCENCE. The inflorescences in *Pieris* may be terminal or axillary, erect or pendent, and a raceme or a panicle. They are produced in the year preceding flowering—that is, meiosis occurs in the fall, and the essentially mature flowers overwinter. Consequently, most species bloom very early in the spring. The flowers are arranged spirally along the inflorescence axis in all species except *P. nana*, where they are borne in whorls of three. The inflorescence type (i.e., raceme or sparsely to densely branched panicle) and

its degree of erectness vary greatly in *P. formosa* and *P. japonica*. However, since these characteristics are not geographically or ecologically consistent and they intergrade extensively, they can not be used to support the recognition of species such as *P. polita* or *P. taiwanensis*.

FLOWERS. Floral morphology is rather uniform within the genus. The flowers are distributed from near the base to near the apex of the axis and are perfect, pendulous, and fragrant. Each one is articulated with the pedicel, which has a small bract and two lateral, more or less alternate bracteoles. The flowers are five-merous, with coriaceous, elongate-triangular, valvate calyx lobes (which probably protect the other flower parts during the winter). The calyx is usually persistent in fruit, but is often deciduous in *Pieris nana*. The sympetalous corolla is urceolate to cylindrical-urceolate, is sometimes strongly ridged (e.g., in *P. floribunda*), and varies from white to occasionally pink tinged. It is glabrous on both surfaces but is usually slightly papillose toward the mouth. The filaments of the ten stamens are more or less straight except in *P. phillyreifolia*, where they are geniculate. They are always swollen near the base and are smooth in *P. phillyreifolia*, roughened-papillose in *P. nana*, and covered with short to long, unicellular hairs in the remaining species. All species have two stout, minutely papillose spurs at the anther-filament junction. The white disintegration tissue on the back of the anthers does not extend into the spurs. The style is cylindrical and usually slightly swollen near the base. It may be deeply to only slightly sunken into the apex of the ovary.

FRUITS AND SEEDS. The fruit in all species is a loculicidal capsule with unthickened sutures and a persistent central columella on which the slightly bilobed placentae are borne. In sect. *PIERIS* the placentae are borne subapically, while in sect. *PHILLYREOIDES* and subg. *ARCTERICA* they are centrally to nearly basally attached (with respect to the apex of the capsule). The capsule varies from subglobose to ovoid or slightly urceolate.

The seeds are small, brownish, and spindle shaped to cylindrical-ovoid; they may be very slightly winged. The testa cells are of two basic types: elongated in sect. *PIERIS* and *P. nana*, and more or less isodiametric in sect. *PHILLYREOIDES*.

TAXONOMIC TREATMENT

Pieris D. Don, Edinburgh New Philos. Jour. 17: 159. 1834. TYPE SPECIES: *Pieris formosa* (Wallich) D. Don.

Portuna Nutt. Trans. Am. Philos. Soc. n.s. 8: 268. 1842. TYPE SPECIES: *Portuna floribunda* (Pursh) Nutt. (= *Pieris floribunda* (Pursh) Benth. & Hooker).

Arctericia Cov. Proc. Washington Acad. 3: 573. 1901. TYPE SPECIES: *Arctericia nana* (Maxim.) Makino (= *Pieris nana* (Maxim.) Makino).

Ampelothamnus Small, Shrubs Florida, 96. 1913. TYPE SPECIES: *Ampelothamnus phillyreifolius* (W. J. Hooker) Small (= *Pieris phillyreifolia* (W. J. Hooker) DC.).

Evergreen shrubs, trees, or woody vines, occasionally spreading by means of horizontal underground rhizomes, with terete or angled branches and usually gray, longitudinally furrowed bark. Indumentum of unicellular hairs, multicellular, biserial-stalked hairs with small glandular heads, and sometimes multicellular, multiseriate, long-celled hairs. Buds ovoid, globose, nearly hemispheric, to flattened and \pm triangular in outline, with (2 or) 3 to 6 rounded to acute or acuminate, imbricate scales. Leaves alternate, pseudovericillate, or in whorls of 3, exstipulate, simple, scalelike at base of innovation, petiolate, coriaceous, sparsely covered with multicellular, biserial-stalked, glandular-headed hairs on both surfaces (also with multicellular, long-celled hairs in *Pieris floribunda*, with unicellular hairs on midvein of adaxial surface; margin entire, obscurely to strongly toothed, or serrulate; venation brochidodromous to reticulodromous, with midvein prominent and 3rd veins reticulate. Inflorescences produced the year preceding flowering, axillary or terminal, paniculate or racemose; flowers perfect, usually fragrant, pendulous; pedicels with 1 small bract at base and 2 lateral, alternate to subopposite bracteoles near base to near apex. Calyx of 5 valvate lobes, articulated with pedicel, persistent or less commonly deciduous in fruit. Corolla urceolate to cylindrical-urceolate, sometimes strongly ridged and with conspicuous pouches between calyx lobes, with 5 short, imbricate lobes, white, usually glabrous on both adaxial and abaxial surfaces. Stamens 10 in 2 whorls, inserted at base of corolla; filaments flattened, straight or geniculate, smooth, papillose, or with long to short unicellular hairs, strongly expanded near base, with pair of stout, minutely papillose, spurlike appendages at anther-filament junction; anthers \pm ovoid, obscurely to clearly papillose, lacking apical awns, dehiscing by large, introrse-terminal, elliptic pores, usually with line of white disintegration tissue on back of each lobe but not extending into spurs; pollen tricolporate, in tetrads, without viscin strands. Stigma truncate to capitate, obscurely 5-lobed, minutely papillose; style columnar, slightly swollen near base, straight, with 5-fluted central canal, slightly to strongly impressed into apex of ovary (placentae thus appearing subapical to nearly basal with respect to apex of capsule), as long as corolla; ovary superior, 5-locular, glabrous to densely covered with unicellular hairs, the placentae axile, slightly bilobed, bearing numerous anatropous ovules; nectariferous disc an enlargement of base of ovary wall. Capsules erect, loculicidal, short-ovoid, ovoid, globose, subglobose, or slightly urceolate, with 5 unthickened sutures; placentae persistent on columella. Seeds small, brown, spindle shaped to angular-ovoid, occasionally slightly winged, end sometimes truncated, the loose, thin testa composed of single layer of elongated or \pm isodiametric (in surface view) cells; embryo small, straight, \pm allantoid, white, with 2 small cotyledons, central in cross section, nearer micropylar end to running length of seed, surrounded by fleshy endosperm.

DISTRIBUTION. A genus of seven species occurring in eastern Asia (Nepal across China and Japan to Kamchatka Peninsula and Commander Islands), eastern North America (Appalachians from Virginia and West Virginia south to northern Georgia; Coastal Plain from southern South Carolina to northern Florida and west to Mississippi), West Indies (western Cuba, Isle of Pines).

MEASUREMENTS AND TERMINOLOGY. With the exception of plant height, which was recorded in the field or taken from information included on specimen labels, all measurements included in the descriptions of specimens have been taken directly from dried herbarium material. The width of the calyx lobes was measured midway between the apex and the point where they join with adjacent lobes; the width of all other structures was measured at the widest point. All drawings of flowers, stamens, anthers, and petiole and lamina anatomy were made from material preserved in FAA, 50–70 percent alcohol, or from herbarium material previously expanded and softened by boiling in water (with a detergent solution). Drawings of capsules, seeds, and leaves were made from dried material.

Throughout the species descriptions, "pubescent" is used to refer to unicellular hairs; the distribution of multicellular hairs is described separately.

SPECIMENS EXAMINED

In the citation of herbarium specimens, abbreviations of institutions follow the sixth edition of *Index Herbariorum* (Holmgren & Keuken, 1974). Ordinarily from one to five specimens per state have been cited for species in the United States, and one specimen per major geographic locality for species of Cuba and eastern Asia. Specimens cited are arranged geographically by country and, within the larger countries, by state or province, as follows: United States (Virginia, West Virginia, Tennessee, North Carolina, Georgia, Florida, Alabama, Mississippi), Cuba (Pinar del Río, Isla de Pinos), Japan (Hokkaido, northern Honshu, central Honshu, western Honshu, Shikoku, Kyushu, Ryukyu Islands), Taiwan, Hong Kong, China (Anhwei, Chekiang, Fukien, Kwangtung, Hupeh, Kweichow, Kwangsi, Szechwan, Yunnan, Tibet), Vietnam, Burma, India (Manipur, Nagaland, Sikkim, West Bengal), Bhutan, and Nepal.

KEY TO THE SUBGENERA, SECTIONS, AND SPECIES OF PIERIS

1. Leaves entire, ca. 0.3–1.1 cm long, in whorls of 3; inflorescence a raceme with flowers similarly whorled; filaments roughened-papillose; erect to prostrate shrubs to ca. 10 cm high (subg. *ARCTERICA*). 7. *P. nana*.
1. Leaves with at least few teeth near apex, ca. (1)–2–13(–18) cm long, alternate or pseudovericillate; inflorescence a raceme or panicle with spirally arranged flowers; filaments glabrous or pubescent; erect shrubs, small trees, or lianas, much taller than above (subg. *PIERIS*).
2. Capsule with placentae appearing central to nearly basal with respect to its apex, style thus strongly sunken into apex of ovary; seeds with \pm isodiametric testa cells (sect. *PHILLYREOIDES*).
3. Filaments glabrous, strongly geniculate; capsule glabrous; corolla 6–8(–8.5) mm long; habit shrublike to scandent (climbing beneath fibrous bark of *Taxodium* and at intervals producing leafy stems). 4. *P. phillyreifolia*.
3. Filaments covered with short to long unicellular hairs, \pm straight; capsule densely pubescent to glabrous; corolla 8–13 mm long; habit shrubby, never scandent.
4. Capsule glabrous to very sparsely pubescent, 4–7 mm long; leaves \pm alternate, with only few serrations near apex, (0 or) 1 to 3 teeth per 2 cm at 1 cm below leaf apex; inflorescence an axillary raceme; vascular tissue of leaf midrib bifacial. 5. *P. cubensis*.
4. Capsule moderately to densely pubescent, 3.5–4.5 mm long; leaves

- pseudoverticillate, clearly toothed in distal half, proximal half \pm entire to obscurely toothed, 6 to 15 teeth per 2 cm at 1 cm below leaf apex; inflorescence a terminal or axillary panicle or raceme; vascular tissue of leaf midrib unifacial. 6. *P. swinhoei*.
2. Capsule with placentae appearing \pm subapical with respect to its apex, style thus only slightly sunken into apex of ovary; seeds with clearly elongated testa cells (sect. *PIERIS*).
5. Stems covered with stiff, multicellular, long-celled hairs in addition to smaller, biserial-stalked, glandular-headed ones; leaves serrulate from base to apex, each tooth associated with a long-celled hair; leaves scattered; corolla markedly urceolate, strongly 5-ridged, with conspicuous pouches between calyx lobes. 3. *P. floribunda*.
5. Stems lacking stiff, multicellular, long-celled hairs, but with biserial-stalked, glandular-headed ones; leaves nearly entire to clearly or obscurely toothed from base to apex, each tooth associated with a biserial-stalked, glandular-headed hair (at least when young); leaves \pm pseudoverticillate; corolla cylindrical-urceolate to urceolate, neither ridges nor pouches as prominent as above.
6. Leaf with proximal 1-10(-14)% of margin entire, nearly always clearly toothed from base to apex, ca. 4.6 to 13 teeth per cm (total teeth along margin of one side of leaf divided by lamina length); 3° veins usually forming prominent, clearly visible, often fine reticulum with 2° veins. 2. *P. formosa*.
6. Leaf with proximal (12-)16-85(-90)% of margin entire, essentially entire except for few apical teeth to clearly toothed except near base, ca. 0.3 to 6 teeth per cm; 3° veins less pronounced, forming \pm obscure and/or lax reticulum with 2° veins. 1. *P. japonica*.

Pieris D. Don Subgenus *Pieris*

Erect shrubs, trees, or woody vines reaching at least 0.5 m in height at maturity. Twigs usually with heterogeneous pith. Leaves alternate or pseudoverticillate, (1-)2-13(-15) cm long; margin with at least few teeth near apex and often clearly serrulate or serrate. Flowers spirally arranged in axillary or terminal racemes or panicles. Calyx lobes persistent in fruit, usually with stomata on adaxial surface; corolla 4-13 mm long; filaments 2-7.5 mm long, glabrous or covered with short to long unicellular hairs, especially near base; anthers with clearly developed line of white disintegration tissue on back. Capsule with placentae appearing central to nearly basal with respect to its apex. Testa cells strongly elongated or isodiametric (in surface view).

DISTRIBUTION. Eastern Asia (from Nepal across China to Japan), eastern North America (Appalachians from West Virginia and Virginia to northern Georgia; Coastal Plain from South Carolina to Florida and west to Mississippi), western Cuba and Isle of Pines.

NUMBER OF SPECIES: 6.

Pieris D. Don Section *Pieris*

- Portuna* Nutt. Trans. Am. Philos. Soc. n.s. 8: 268. 1842. *Andromeda* L. sect. *Portuna* (Nutt.) Gray, Man. Bot. No. U. S. ed. 2: 253. 1856. *Lyonia* Nutt. subg. *Portuna* (Nutt.) K. Koch, Dendrol. 2: 115. 1872. *Pieris* D. Don sect. *Portuna* (Nutt.) Benth. & Hooker, Gen. Pl. 2: 588. 1876. *Andromeda* L. subg. *Portuna*

(Nutt.) Gray, Synopt. Fl. N. Am. 2: 31. 1878. TYPE SPECIES: *Pieris floribunda* (Pursh) Benth. & Hooker.

Andromeda L. sect. *Pieris* (D. Don) Gray, Man. Bot. No. U. S. ed. 2. 254. 1856. *Lyonia* Nutt. sect. *Pieris* (D. Don) K. Koch, Dendrol. 2: 116. 1872. *Andromeda* L. subg. *Pieris* (D. Don) Gray, Synopt. Fl. N. Am. 2: 32. 1878. TYPE SPECIES: *Pieris formosa* (Wallich) D. Don.

Venation of lamina brochidodromous to reticulodromous. Inflorescences terminal or axillary panicles or axillary racemes. Capsule with placenta appearing subapical with respect to its apex. Seeds with strongly elongated testa cells.

DISTRIBUTION. Eastern Asia (Nepal across China to Japan), eastern North America (Appalachian Mountains from West Virginia and Virginia south to northern Georgia).

NUMBER OF SPECIES: 3.

1. *Pieris japonica* (Thunb.) D. Don ex G. Don, Gen. Syst. 3: 832. 1834.

Andromeda japonica Thunb. Fl. Jap. 181. t. 22. 1784. TYPE: Japan, "juxta Nagasaki," Thunberg (probably at UPS, not seen).

Pieris japonica (Thunb.) D. Don ex G. Don f. *pygmaea* Maxim. ex Yatabe, Ic. Fl. Jap. 2: 107. t. 30, fig. B. 1892. *Pieris japonica* (Thunb.) D. Don ex G. Don var. *pygmaea* (Maxim. ex Yatabe) Rehder in Bailey, Cycl. Am. Hort. 3: 1336. 1901. TYPE: from material in cultivation in Japan (not seen).

Pieris japonica (Thunb.) D. Don ex G. Don var. *albo-marginata* Rehder in Bailey, Cycl. Am. Hort. 3: 1336. 1901. *Andromeda japonica* Thunb. var. *albo-marginata* (Rehder) Schneider, Illus. Handb. Laubh. 2: 528. 1911. TYPE: from material in cultivation in Japan (not seen).

Pieris popowii Palibin, Bull. Herb. Boissier II. 6: 20. 1906. *Lyonia popowii* (Palibin) Chun, Sunyatsenia 4: 253. 1940. TYPE: China, Fukien prov., near Foochow, 1884, *Popoff s.n.* (holotype, LE?, not seen) (probably *P. japonica*, although Chun (1940) said that it is very close to *P. formosa*; exact placement of this name will await examination of type).

Pieris taiwanensis Hayata, Jour. Coll. Sci. Tokyo 30: 169. 1911. *Pieris japonica* (Thunb.) D. Don ex G. Don subsp. *taiwanensis* (Hayata) Hatusima, Jour. Geobot. 17: 76. 1969. *Pieris japonica* (Thunb.) D. Don ex G. Don var. *taiwanensis* (Hayata) Kitamura, Acta Phytotax. Geobot. 25: 36. 1972. TYPE: Taiwan, Taito, Daironsan, 28 Nov. 1906, T. Kawakami & U. Moru 2184 (holotype, TAI?, not seen; photos, A!, NY!).

Pieris japonica (Thunb.) D. Don ex G. Don var. *variegata* Bean, Trees Shrubs Brit. Is. 2: 168. 1914. *Pieris japonica* (Thunb.) D. Don ex G. Don f. *variegata* (Bean) Rehder, Bibliogr. Cult. Trees Shrubs, 530. 1949. TYPE: from material in cultivation in England (not seen).

Pieris polita W. W. Sm. & Jeffrey, Notes Royal Bot. Gard. Edinburgh 19: 117. 1916. *Lyonia polita* (W. W. Sm. & Jeffrey) Chun, Sunyatsenia 4: 253. 1940. TYPE: China, northwestern Fukien prov., 1914, J. de la Touche 68 (holotype, E!; isotype, K!).

Pieris koidzumiana Ohwi, Bot. Mag. Tokyo 44: 571. 1930. *Pieris japonica* (Thunb.) D. Don ex G. Don var. *koidzumiana* (Ohwi) Masamune, Sci. Rep. Kanazawa Univ. 3: 301. 1955. *Pieris japonica* (Thunb.) D. Don ex G. Don subsp. *koidzumiana* (Ohwi) Hatusima, Jour. Geobot. 17: 76. 1969. TYPE: Ryukyu Islands, Utchina, 1927, S. Sonohara s.n. (holotype, KYO, not seen).

Pieris japonica (Thunb.) D. Don ex G. Don f. *crispa* Rehder, Jour. Arnold Arb. 27: 173, 1946. TYPE: cultivated in garden of Carl S. English, Jr., Seattle, Washington, U. S. A., 31 December 1945, A. Rehder s.n. (holotype, AAH!).

Shrub to small tree to ca. 4(–10) m tall, with gray to brown, longitudinally furrowed bark. Twigs terete to slightly angled, with few glandular-headed hairs, otherwise glabrous to moderately pubescent. Buds ovoid to hemispheric, essentially glabrous or with fringe of unicellular hairs along scale margins. Scales 3 to 8, imbricate, apex acute to rounded. Expanded leaves pseudovericillate; petiole 1.5–10 mm long, vascular bundle unifacial; blade widely to narrowly obovate to occasionally elliptic, (1.5–)2.5–10(–12) by 0.8–3 cm, coriaceous, the epidermis not lignified to slightly so, the apex acute to obtuse or acuminate, the base attenuate to narrowly cuneate, the margin plane to slightly revolute (especially toward base), entire except for few apical teeth to clearly toothed except near base, (i.e., proximal (12–)16–85(–90)% of leaf entire), the venation brochidodromous, 3° veins less pronounced than in *P. formosa* and forming \pm obscure and/or lax reticulum with 2° veins, the adaxial and abaxial surfaces with very sparse glandular-headed hairs, often glabrescent, extremely sparsely to moderately pubescent on adaxial surface of midvein. Inflorescences axillary panicles or racemes, varying greatly in size and arising from 1 or more buds clustered at apex of branches, or occasionally terminal panicles, erect to pendulous. Pedicels 2–8 mm long, with few glandular-headed hairs, otherwise densely to sparsely pubescent; bracteoles from lower (25–)30 to upper (15–)25% of pedicel, linear to narrowly triangular, 0.5–2.5 mm long; bracts 1.5–6 mm long and similar to bracteoles, occasionally those of main inflorescence axis approaching leaves in shape and size. Calyx lobes triangular, acute at apex, 2–4.5 by 0.8–2 mm; adaxial surface very sparsely (near apex) to moderately pubescent; abaxial surface with few glandular-headed hairs, otherwise glabrous. Corolla urceolate to cylindrical-urceolate, weakly 5-ridged, 5–8 by 3–4.5(–5.5) mm, white to occasionally pink tinged. Filaments 2.5–4.5 mm long, straight, covered with long, unicellular hairs, especially near base. Style slightly impressed into apex of ovary. Capsule subglobose to short-ovoid, (2.5–)3–5 by (3.7–)4–7 mm, glabrous; placenta appearing subapical with respect to capsule apex. Seeds spindle shaped, 2–3 mm long, with testa composed of very elongated cells. $2n = 24$ (Callan, 1941). (FIGURE 3. For drawings based upon Japanese material, see Thunberg, 1784; Bailey, 1901; Yatabe, 1906; Bean, 1914; Graves, 1956; and Makino, 1961. For drawings based on Taiwanese material, see Hayata, 1912; Stapf, 1923; Kanehira, 1936; Liu, 1962; Li, 1963; and Anonymous, 1974. See Anonymous, 1974, for a drawing based on Chinese material.)

DISTRIBUTION AND ECOLOGY. Japan (chiefly western and southern Honshu, Kyushu, Shikoku), Ryukyu Islands (Okinawa), Taiwan, eastern China (Anhui, Chekiang, Fukien), near sea level to ca. 3300 m alt. (MAP 1; Horikawa, 1975.)

In Japan, near sea level to ca. 2100 m; common component of diverse temperate to warm-temperate areas (e.g., forests of *Chamaecyparis*

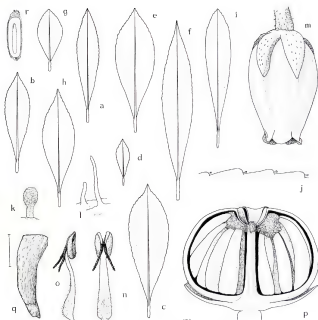
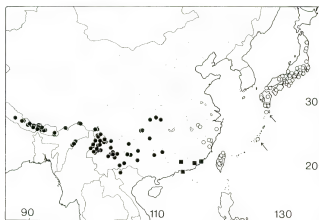


FIGURE 3. *Pieris japonica*: a-i, leaves, $\times .66$ (a-d from Japan, e-g from Taiwan, h from China, i from Okinawa); j, portion of leaf margin, $\times 8$, showing association of each serration with a multicellular, glandular-headed hair from leaf surface; k, detail of glandular-headed hair, ca. 0.1 mm long; l, unicellular hair, ca. 0.05 mm long; m, flower, $\times 4$; n, o, stamens, $\times 8.5$; p, capsule, longitudinal section, $\times 8.5$; q, seed, bar = 1 mm; r, cross section of seed, $\times 8$, showing embryo and endosperm.

obtusata, *Tsuga sieboldii*, *Abies firma*-*Illicium religiosum*, *Tsuga sieboldii*-*Rhododendron tashiroi*, *Castanopsis cuspidata*, *Cryptomeria japonica*-*Trochodendron aralioides*-*Symplocos myrtaea*, or *Fagus crenata*). For more detailed discussion of these forest types and lists of associated species, see Tatewaki and Tsujii (1956), Tatewaki (1957), Yatoh (1960), Numata (1974). In Taiwan, in forested or open grassy areas on mountain slopes, ca. 300-3300 m alt. In eastern China, ca. 200-1500 m. In Japan and China flowering chiefly March to May; in Taiwan mainly January to March.

COMMON NAMES. Asebi (Japan, Taiwan, Ryukyu Islands), ma tsui mu shu (China; Steward, 1958), ma-tsui-mu (China; Anonymous, 1974), lily-of-the-valley bush (U. S. A.).



MAP 1. Distribution of *Pieris formosa* (dots), *P. japonica* (circles), and *P. swinhoi* (squares).

REPRESENTATIVE SPECIMENS. **Japan.** NORTHERN HONSHU: Iwate pref., Miyamori, *Muroi* 4005 (A); Miyagi pref., Hanaizumi, *Muroi* 4741 (A). CENTRAL HONSHU: Aichi pref., Ooyama, Atsumi-cho, Atsumi peninsula, *Kanai & Koyama* 742686 (TNS); Chiba pref., Mt. Kiyosumi, *Ikegami* 4753 (A); Fukui pref., Kaminaka-machi, *Makino Herb.* 59424 (MAK); Gifu pref., *Shiota* 2494 (A); Gumma pref., Momoi, *Elliot* 94 (A); Hyogo pref., Kobe, *Faurie* 5424 (W), Yamamoto, *Togasi T.S.M.* 1039 (A, E); Kanagawa pref., Mt. Kamiyama, Hakone Mts., *Mizushima* 16350 (E); Kyoto pref., SE of Kyoto-city, *Konta* 5520 (E, K, UC); Mie pref., Takihara, Oh-miya-cho, Doui-gun, *Kanai* 731114 (A, E, TAI, UC), Fudo-daki, *Okayama* 13588 (TNS); Nagano pref., Nojiri, *Jack s.n.*, 6 Sept. 1905 (A, GH), Hiraoka-mura, *Takei T.N.S.* 148066 (TNS); Nara pref., Nara-city, *Muroi* 825 (A); Osaka pref., Tsibasi, *Muroi* 6676 (A); Saitama pref., Mt. Bukosan, *Makino Herb.* 81566 (MAK); Shiga pref., Kiyota, Kamogun, *Hashimoto T.S.M.* 847 (B, GH, NY, UC, W); Shizuoka pref., Fujinomiya, Mt. Fuji, *Hiroe* 12670 (UC); Mt. Higane, *Mizushima* 887 (A); Tokyo pref., Mt. Takamizu, *Suzuki* 10 (A); Wakayama pref., Mt. Odaigahara, *Hayakawa's Coll.* N1722 (UC), Futakawa, Nishimuro, *Ikegami* 1962 (A). WESTERN HONSHU: Okayama pref., Niizato village, Shingo-town, *Hiroe* 3665 (UC); Yamaguchi pref., Yoshiki-gun, Ohuchi-mura, *Nikai* 426 (TNS). SHIKOKU: Kochi pref., Sasagamine, Tosa-gun, *Makino Herb.* 81508 (MAK). KYUSHU: Hiuga pref., Mt. Sobosan, *Faurie* 3447 (UC); Kagoshima pref., Noze, Sasatama-gun, *Muroi* 3881 (A), Takushima, *Wilson* 6002 (A, US); Nagasaki pref., Nagasaki, *Oldham s.n.*, 1862 (F, GOET, M, NY, W). RYUKYU ISLANDS: Okinawa pref., Kunigami-gun, *Sonohara* 41 (E, GH, K, L, NY, US); Kungami-mura, Awa, Tanagagumui, *Amano* 7475 (NY, TAI, TNS). **Taiwan:** I-lan Hsien, Mt. Taiping, *Chuang & Kao* 2150 (NA, UC); Taipei Hsien, Tang-ming-shan, *Chuang & Lin* 4796 (A, UC); Hokuto, *Faurie* 169 (P); Hsinchu Hsien, Yen-yang Lake, *Huang* 5489 (TAI); Chiayi Hsien, Pai-ying hostel to Tung-pu, *Kueh* 1352 (TAI); Kagi prov., Arisan, *Wilson* 9777 (A, US). **China.** ANHWEI: Chimen, *Ching* 3134 (A, E, UC); Wu Yuen, *Ling* 7850 (UC).

CHEKIANG: Yun Fun, near Taichow, *Ching* 1324 (A, E, NA, P, UC). FUKIEN: Kuliang, Foochow, *Carles* 667 (E); Kuliang, *Chung* 6700 (A); Shouning, *Ching* 2254 (A, E, K, UC, US); Yenping, *Dunn* 2894 (A).

Pieris japonica is a rather variable and widely distributed species occurring in Japan, the Ryukyu Islands, Taiwan, and China. The populations occurring in each of these four areas have been considered by many botanists to be distinct species (*P. japonica*, *P. koidzumiana*, *P. taiwanensis*, and *P. polita*, respectively). However, after a careful study of this group across its entire range, it was found that the characters that supposedly distinguish these taxa are inconsistent and/or intergrade extensively (see FIGURE 4), and it is often impossible to determine from morphological criteria whether a particular individual was collected in Japan, Taiwan, the Ryukyu Islands, or China. Therefore, these taxa are considered to be conspecific. The major morphological differences between these geographically disjunct populations of *P. japonica* are indicated in FIGURE 4.

Individuals from Japan (group B) usually have obovate leaves with the proximal 15–45(–60) percent of the margin entire and from ca. 2.5 to 6 teeth/cm, and flowers in pendent to (less commonly) more or less horizontal or erect panicles or racemes. The Chinese plants (group C) are very similar to those of Japan except that they have slightly less strongly toothed leaves (i.e., proximal 30–70% of leaf margin entire and from ca. 1.5 to 4 teeth/cm). These plants were described as a species distinct from *P. japonica* because of their supposed exclusively racemose inflorescence (see Smith, 1916). However, paniculate inflorescences are common, especially in plants that appear to be growing vigorously (see *Ching* 1324 (A, UC), *Ching* 2527 (K, UC), *Chung* 6510 (A), *Chung* 6700 (A), *Ling* 7850 (UC)), and both panicles and racemes can be found on the same plant. Because of the lack of any characters unambiguously separating these populations from those of Japan, they are here considered to be conspecific. Steward (1958) also thought that these Chinese populations were *P. japonica*.

The Taiwanese plants (group D) are also very similar to those of Japan; however, they not only tend to have leaves with fewer teeth (i.e., proximal 30–70% of leaf margin entire, and ca. 1.5 to 4 teeth/cm) but also frequently have more coriaceous leaves, and flowers in often robust, erect to (less commonly) more or less horizontal or drooping panicles or racemes. The plants of Taiwan have traditionally been recognized as a distinct species on the basis of their erect paniculate inflorescences (see Hatusima, 1969). However, this character can not be consistently used because occasional Japanese plants (e.g., *Faurie* 5424 (W); *Makino* s.n., 30 March 1938 (L); *Miyamoto* s.n., 9 April 1970 (A); *Bisset* 4505 (E)) have erect panicles, and plants with more or less horizontal inflorescences (e.g., *Chuang & Lin* 4796 (A, UC)) do occur in Taiwan. Stapf (1923) has noted that "the variation [within *P. taiwanensis*] from erect racemes to such as droop after the fashion of *P. japonica* is remarkable," and he stated that "it appears to be quite independent of external conditions, both extremes occurring in the same sowing." Stapf also correctly pointed out that Japanese collections usually have "smaller thinner leaves, more finely crenulate from the base, slenderer raceme-spindles and

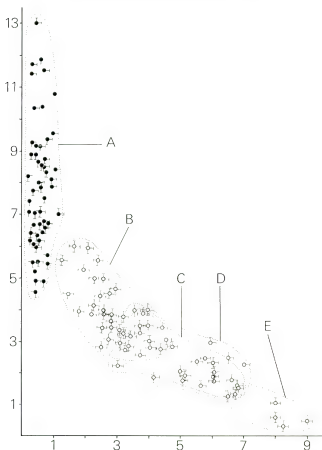


FIGURE 4. Scatter diagram showing variation in 7 characters within *Pieris japonica* and *P. formosa*. Vertical axis = number of teeth/cm (averaged across total lamina length), horizontal axis = % of leaf margin entire; solid circles = 3rd leaf veins forming \pm prominent, clearly visible, often fine reticulum with 2nd veins, open circles = 3rd veins less pronounced, forming \pm obscure and/or lax reticulum with 2nd veins; full tail up = angle of leaf base $< 50^\circ$, no tail up = angle of leaf base $\geq 50^\circ$; full tail to right = leaves obovate, no tail to right = leaves elliptic, half tail to right = \pm intermediate; full tail down = panicles with 3 or more lateral branches, half tail down

pedicels and smaller flowers" than do Taiwanese populations. However, the above-mentioned characters fail consistently to separate plants of the two geographic areas since some Taiwan specimens have slender inflorescence axes, small flowers, and only moderately coriaceous leaves and are thus identical to some Japanese or Chinese collections. The populations of Taiwan and Japan (as well as China) are thus considered to be conspecific, in agreement with the opinions of Kitamura and Murata (1972) and Hatusima (1969).

Finally, the plants of the Ryukyu Islands (group E) are quite similar to those of Japan or China, differing only in their usually slightly more coriaceous and typically narrowly obovate leaves with only (1 or) 2 to 4 (to 11) teeth near the apex (i.e., proximal 67–90% of the leaf margin entire and ca. 0.3 to 1.5 teeth/cm). The plants produce pendent to more or less horizontal panicles or racemes. These small populations found only on the island of Okinawa are more easily distinguished than those of China, Japan, or Taiwan. However, they are included here within a broadly defined *P. japonica* since there is no clear morphological gap in either leaf shape or marginal dentation between the Ryukyu plants and those of China or Taiwan. A similar conclusion was reached by Hatusima (1969) and Walker (1976).

Pieris japonica, as here defined (FIGURE 4, groups B–E), is very closely related to *P. formosa* (group A), from which it can consistently be distinguished by its more sparsely toothed leaves (i.e., proximal (12–)16–85(–90)% of leaf margin entire with ca. 0.3 to 6 teeth/cm vs. proximal 1–10(–14)% of leaf margin entire with ca. 4.6 to 13 teeth/cm in *P. formosa*). The leaves also have less pronounced tertiary veins that form an obscure and/or lax reticulum with the secondary veins vs. leaves with tertiary veins forming a prominent, clearly visible, and often fine reticulum. In addition, *P. japonica* tends to have attenuate- to cuneate-based leaves more frequently. Kitamura and Murata (1972) considered *P. formosa* to be only a subspecies of *P. japonica*, but since these two taxa can be easily separated by several criteria (see FIGURE 4), and since no intermediate plants have been found, they have been maintained here as separate species. The two species are of course reproductively isolated since they are completely allopatric, although fertile hybrids (e.g., *Pieris* 'Forest Flame'; see Meyer 10733, NA) are known in cultivation.

Plants of *Pieris japonica* were introduced early into cultivation and are beautiful and popular ornamental shrubs in many temperate regions; several cultivars have been developed (see Bailey, 1901; Yatabe, 1906; Rehder, 1940; Wagenknecht, 1961; Brown, 1973; Bailey *et al.*, 1976; and Bean, 1976).

= panicles with 1 or 2 lateral branches, no tail down = racemes; full tail to left = pendent inflorescences, no tail to left = erect inflorescences, half tail to left = ± intermediate. Group A, specimens of *P. formosa*; groups B–E, specimens of *P. japonica*: B, Japanese populations; C, Chinese populations; D, Taiwanese populations; E, Ryukyu Is. populations.

This species contains a physiologically active and toxic substance of unknown composition that has been called andromedotoxin; this compound has been known to cause livestock poisoning (Yatabe, 1906; Kingsbury, 1964).

2. **Pieris formosa** (Wallich) D. Don, Edinburgh New Philos. Jour. **17**: 159. 1834.

Andromeda formosa Wallich, Asiatic Res. **13**: 395. 1820. *Lyonia formosa* (Wallich) Hand.-Mazz. Symb. Sinicae **7**: 790. 1936. *Pieris japonica* (Thunb.) D. Don ex G. Don subsp. *formosa* (Wallich) Kitamura, Acta Phytotax. Geobot. **25**: 37. 1972. TYPE: Nepal, no definite locality, 1818, N. Wallich (holotype, not seen; presumed isotypes, A!, K(2 sheets)!).

Pieris bodinieri Lév. Bull. Acad. Géogr. Bot. **12**: 253. 1903. TYPE: China, Yunnan, "environs de Yun-nan-sen, c. dans la montagne," 9 March 1897, Fr. Ducleux 60 (lectotype, w!).

Pieris forrestii Harrow, Notes Royal Bot. Gard. Edinburgh **8**: 196. 1914. *Pieris formosa* (Wallich) D. Don var. *forrestii* (Harrow) Airy Shaw, Curtis's Bot. Mag. **157**: t. 937f. 1934. TYPE: China, Yunnan; Harrow's description based on plants growing in nurseries of Bees Limited and in Royal Botanic Garden, Edinburgh, from seed collected by George Forrest. Not seen.

Pieris huiana Fang, Contr. Biol. Lab. Sci. Soc. China Bot. **10**: 240. 1938. TYPE: China, Yunnan, near Yunnansen [Kun-ming-Hsien], E. E. Maire 1361 (lectotype, E!; fragments of lectotype, A!).

Pieris formosa (Wallich) D. Don f. *longiracemosa* Fang, Contr. Biol. Lab. Sci. Soc. China Bot. **10**: 240. 1938. TYPE: China, Yunnan, Lu-feng-hsien, 1700 m alt., 26 June 1933, H. T. Tsai 53567 (holotype, PE?, not seen; isotype, A!).

Shrub to small tree to 5(–10) m tall, with gray to brownish, longitudinally furrowed bark. Twigs terete to slightly angled, with few glandular-headed hairs, otherwise glabrous to densely pubescent. Buds ovoid to hemispheric, glabrous or with fringe of unicellular hairs along scale margins. Scales 3 to 8, imbricate, apex acute to rounded. Expanded leaves pseudoverrucillate; petiole 2–16 mm long, vascular bundle unifacial; blade widely to narrowly elliptic or obovate, (2–)2.5–10(–18) by 0.8–3.5(–5.5) cm, coriaceous, the epidermis lignified, the apex acute or obtuse to acuminate or mucronate, the base narrowly cuneate to rounded, the margin plane to slightly revolute (especially toward base), nearly always clearly toothed from base to apex (i.e., proximal 1–10(–14)% of leaf entire); the venation brochidodromous to reticulodromous, 3° veins usually forming prominent, clearly visible, often fine reticulum with 2° veins, the adaxial and abaxial surfaces with very sparse glandular-headed hairs, glabrescent, sparsely to densely pubescent on adaxial surface of midvein. Inflorescences axillary panicles or racemes, varying greatly in size and arising from 1 or more of buds clustered at apex of branches, or occasionally terminal panicles, erect to pendulous. Pedicels 2–9 mm long, with few glandular-headed hairs, otherwise usually densely pubescent; bracteoles from lower (10–)15 to upper (25–)30% of pedicel, linear to narrowly triangular or ovate, 0.8–1.8 mm long; bracts 2–5.5 mm long, ovate to obovate, occasionally those of main inflorescence axis approaching leaves in shape and size. Calyx lobes triangular, acute at apex, 2–4.5 by 1–2 mm; adaxial surface very sparsely (near apex) to densely pubescent; abaxial

surface with few glandular-headed hairs, otherwise glabrous or very sparsely pubescent near base. Corolla urceolate to cylindrical-urceolate, weakly 5-ridged, 4-9(-12) by 3.5-5.5(-8) mm, white to occasionally pink tinged. Filaments 2-4.5 mm long, straight, covered with long, unicellular hairs, especially near base. Style slightly impressed into apex of ovary. Capsule ovoid to short-ovoid, globose, or subglobose, 3-6 by (3.5-)4-7 mm, glabrous; placenta appearing subapical with respect to capsule apex. Seeds spindle shaped, 2-3 mm long, with testa composed of very elongated cells. $2n = 24$ (Wood, 1961; Mehra & Bawa, 1969). (FIGURE 5; see also Wight, 1850; Skan, 1909; Airy Shaw, 1934; Anonymous, 1974.)

DISTRIBUTION AND ECOLOGY. Southwestern China (Hupei, Kweichow, Kwangsi, west to Szechwan, Yunnan), Vietnam, along Himalayas to Nepal. (MAP 1.) Various broadleaved forests (e.g., *Symplocos pyrifolia*, *Quercus semecarpifolia*, or *Rhododendron arboreum*), *Tsuga dumosa* or *Pinus* forests, grassy and/or rocky ridges, thickets, open slopes, and ravines, or along streams, (500-)1700-3300(-3800) m alt. For more information on some of these forest types and lists of associated species, see Wang (1939) for Yunnan, Kingdon-Ward (1941), 1945) for Burma, Stainton (1972) and Ohashi (1975) for Nepal. Flowering chiefly late February to early June, varying greatly with altitude and latitude.

COMMON NAMES. Bolú (Nepal; Luce 2270 (E)); sheabogee, chemala (Nepal; Wallich, 1820); mei-li ma-tsui-mu (China; Anonymous, 1974).

REPRESENTATIVE SPECIMENS. **China.** HUPEI: Patung Hsien, Chow 1028 (A, E, NY); Hsin Tien-tze, Chun 4045 (A). KWEICHOW: Pin-fa, Cavalerie 9 (A, E); Yinkiang, Tsiang 7594 (E, NY, UC); Pichieh, Tsiang 8991 (E, NY, UC, W); Anlung, Tsiang 9369 (A, E, US); Feng Ching Shan, Ma-chao Ho, Steward et al. 759 (A). KWANGSI: Tzu-yuan Hsien, Chung 83526 (A); Ling Yun Hsien, Lao Shan, Steward & Cheo 71 (A, E, W); San Chiang Hsien, Ling Wang Shan, Steward & Cheo 983 (A, NY, W). SZECHWAN: Nan-chuan Hsien, Chin-fo Shan, Fang 597 (A); Yalung, Yen-yuen, 28°10' N, Handel-Mazzetti 2612 (W); Mou-tao-chi, vic. of Wan-hsien, Hwa 44 (A); Wushan, Wilson 442 (K, NY). YUNNAN: Tung-kwei valley, Bulley 446 (A); Tze-li, on Yangtze, Ching 20259 (A); Ganhai-tze, SW Likiang Snow Range, Ching 21724 (A); Wen-feng-tze, SW end of Likiang valley, Ching 21818 (A); N of Kunming, Feng 80 (A); Chien-chuan, Feng 241 (A); Yung-ping Hsien, Forrest 5027 (A, E); E flank of Likiang Range, 27°15' N, Forrest 5875 (E); W flank of Shweli-Salween Divide, 25°20' N, Forrest 8945 (A, E); Salwin-Kui-chang Divide, 27° N, 98°35' E, Forrest 25763 (E, K); Mengtse, Henry 11295 (A, E, NY); Yunnan-sen, Maire 1063 (UC); Ta-li, San Yong Mt., McLaren's Coll. C40 (A, E); Lake of Tali-fu, Tsangshan Range, between Tatzang and Hsia-Kuan, Rock 3100 (A, E, UC, US, W); Tali plain, Lake of Talifu, Tsangshan, Rock 3171 (A); between Talifu and Likiang to foot of Likiang Snow Range, Rock 3264 (A, US); Shweli-Salween Divide, E of Tengyueh, Rock 7647 (A, UC); between Tengyueh and Likiang-fu, Rock 8075 (A, UC); Chiu-pei Hsien, Tsai 51439 (A, E); Tung-jen Hsien, Tsai 52827 (A); Shang-pa Hsien, Tsai 56597 (A, E); Wei-se Hsien, Tsai 57878 (A, E); Cheng-kiang, Tung-lung-tang, Tsang & Wang 16320 (A); Li-kiang Hsien, Wang 70472 (A, TAI); Chungtien, Haba, Yü 14986 (A, E); Lichiang, Snow Range, Yü 15045 (A, E). **TIBET:** Chumbi, King's Coll. 556 (E); Migytun, Tsari Chu, 28°40' N, 93°38' E, Ludlow et al. 6624 (E); Trulung, Po-Tsangpo valley, Pome, Ludlow et al. 12270 (E); Showa, Po-Tsangpo valley, Ludlow et al. 12508 (E). **Vietnam:** Tonkin, Massif du Phan-si-Pan, Lao Kay, Poilane 17127 (P). **Burma:** N'Maikha-



FIGURE 5. *Pieris formosa*: a-h, leaves, $\times .66$; i, flower, $\times 4$; j, stamen, $\times 8.5$; k, anther, $\times 17$; l, m, capsule, longitudinal section, $\times 8.5$.

Salwin Divide, near Tzi-san Ho, $26^{\circ}18' N$, $98^{\circ}48' E$, *Forrest* 26518 (NY, P, US, W); Panwa Pass, *Kingdon-Ward* 394 (A, E). **INDIA**, MANIPUR: Sirohifurur, *Watt* 5960 (E). NAGALAND: Naga Hills, Japoo, Kohima, $25^{\circ}40' N$, $94^{\circ}10' E$, *Kingdon-Ward* 7719 (K). SIKKIM: Lachen, *Biswas* 6883 (A); Zenni Valley, *Smith & Cave* 2720 (B). WEST BENGAL: Darjeeling Distr., Sandakphi, *Lace* 2270 (E); Singalila Range, Mt. Tonglu, *Vos & Corbett* 39 (E). **BHUTAN**: Bela Djong, Puro, *Cooper* 3566 (E); Ha area, *Gould*

44 (E); 20 mi S of Trashigang, *Kingdon-Ward 6426* (E); Yonpu La, *Ludlow & Sherriff 1146* (E); Chumbi valley, Arno Chu R., *Ludlow et al. 16005* (A, E). **Nepal:** Chepua to Hatia, *Banerji s.n.*, 15 May 1965 (A); Namche Bazar, *Jionor 34* (E, K); Marsiandi Valley, *Lowndes 897* (A, E); Khumbu, Namche Bazar, *Poelt s.n.*, 8 Oct. 1962 (M); Arun Valley, Maghang Khola, E of Num, *Stainton 232* (A, E); S of Dhorpatan, *Stainton et al. 335* (A, E); Rambrong, Lamjung Himal., *Stainton et al. 8297* (E).

Pieris formosa is most closely related to *P. japonica*, from which it is easily distinguished by its much more prominently serrate and often wider-based leaves (FIGURE 4; see also key). In addition, the tertiary veins are more prominent, forming a clearly visible and fine reticulum with the secondary veins. The two species are completely allopatric (MAP 1).

This species is quite variable in the development of the inflorescences and in the size of the leaves and flowers (the latter especially in Yunnan). Some plants produce only short racemes, while others produce large, many-branched panicles. In some individuals the panicle has up to 15 branches. However, intermediate conditions are extremely common, and often racemes and panicles can be found on the same plant. Some plants consistently produce small leaves only 3–4 cm in length, while others have large leaves of ca. 10–15 cm; corolla length varies from 4 to 12 mm. The presence of large leaves and flowers is strongly correlated, and individuals with such large leaves and flowers have been described as *Pieris forrestii*. The continuous range of intermediate plants that connect this form with plants bearing small leaves and flowers make untenable the recognition of this morphological form at either specific or varietal rank. Even Airy Shaw (1934), who recognized the large-leaved plants as a distinct variety, stated: "Examination of the ample Chinese, Indian and cultivated material of *P. formosa* and *P. Forrestii* in the Kew Herbarium shows that the latter constitutes what may be termed the 'grandiflora' end of a long series, between the members of which no hard and fast lines can be drawn."

Plants of this species are perhaps the most beautiful of any in the genus and are commonly cultivated in temperate areas of the northern hemisphere; however, they are not as hardy as those of *Pieris japonica*. Several cultivars have been developed (see Brown, 1973; Wagenknecht, 1961; Bean, 1976).

3. *Pieris floribunda* (Pursh) Benth. & Hooker, Gen. Pl. 2: 588. 1876.

Andromeda floribunda Pursh in Sims, Curtis's Bot. Mag. 38: t. 1566. 1813. *Leucothoe floribunda* (Pursh) D. Don, Edinburgh New Philos. Jour. 17: 159. 1834. *Zenobia floribunda* (Pursh) DC. Prodr. 7: 598. 1839. *Portuna floribunda* (Pursh) Nutt. Trans. Am. Philos. Soc. II. 8: 268. 1843. *Lyonia floribunda* (Pursh) K. Koch, Dendrol. 2: 155. 1872. TYPE: United States, "the mountains of Georgia," 1811, *J. Lyons s.n.* (not seen).

Andromeda montana Buckley, Am. Jour. Sci. Arts 45: 172. 1843. Type: "Mts. Carol," *S. B. Buckley* (lectotype (here designated), G!; possible duplicates of lectotype, NY!, GA!).

Andromeda vacciniifolia K. Koch, Dendrol. 2: 116. 1872, *pro. syn.* (under *Lyonia floribunda*).

Shrub to ca. 2 m tall, with grayish to brownish, longitudinally furrowed bark. Twigs terete to occasionally very slightly angled, with few glandular-

headed hairs, conspicuously strigose due to presence of large, stiff, long-celled hairs, otherwise sparsely to densely pubescent. Buds ovoid, with few glandular-headed hairs, otherwise glabrous or nearly so. Scales 4 to 6, imbricate, apex long- to short-acuminate. Expanded leaves alternate; petiole 4–11 mm long, vascular bundle unifacial; blade elliptic to ovate, (1.5–)3–7.2 by (0.6–)1–2.8 cm, coriaceous, the epidermis nonlignified, the apex acute, the base rounded to widely cuneate, the margin plane, serrulate, each serrulation associated with a long-celled hair, the venation \pm reticulodromous, 3° veins clearly visible, the adaxial and abaxial surfaces with sparse glandular-headed hairs, glabrescent, sparsely to densely pubescent on adaxial surface of midvein. Inflorescences terminal panicles, sometimes with lowermost lateral branches of panicle arising from axils of uppermost foliage leaves, erect. Pedicels 2–4.5 mm long, with few glandular-headed hairs and often few long-celled hairs, otherwise densely pubescent; bracteoles from lower 25% to near middle of pedicel, linear to narrowly triangular, 0.9–2.3 mm long; bracts 2–9 mm long, similar to bracteoles in shape, often those of primary inflorescence axis approaching leaves in shape and size. Calyx lobes triangular, acute at apex, 2–4 by 1–1.7 mm; adaxial surface densely pubescent near apex; abaxial surface with few glandular-headed hairs, sometimes also with long-celled hairs, otherwise glabrous or sparsely pubescent. Corolla urceolate, strongly 5-ridged and with conspicuous pouches between calyx lobes at base, 4–7 by 3–5.5 mm, white. Filaments 2–3 mm long, straight, covered with unicellular hairs, especially near base. Style slightly impressed into apex of ovary. Capsule subglobose or globose to ovoid, 4–6 by 4–6 mm, glabrous; placentae appearing subapical with respect to capsule apex. Seeds spindle shaped, 2.5–3.5 mm long, usually \pm flattened, with 2 inconspicuous wings, with testa composed of very elongated cells. (FIGURE 6; see also Sims, 1813; Britton & Brown, 1913; Bean, 1914; Small, 1920, 1933; Gleason, 1952; Graves, 1956; Ingram, 1963; Radford, Ahles, & Bell, 1968; Strausbaugh & Cove, 1973.)

DISTRIBUTION AND ECOLOGY. Eastern United States from West Virginia and Virginia to northern Georgia, in Appalachian Mountains. (MAP 2.) Frequently on rocky ridges or slopes, in thickets, *Tsuga* forests, *Quercus* and/or *Pinus* forests, or mountain balds, ca. 500–1750 m alt. Flowering April to June.

COMMON NAMES. Mountain fetter-bush, fetter-bush.

REPRESENTATIVE SPECIMENS. **United States.** **WEST VIRGINIA.** Pendleton Co.: High Knob, Shenandoah Mt., Allard 9667 (GH, US). Pocahontas Co.: 1 mi W of Arborvale, Gray s.n., 3 March 1922 (A). **VIRGINIA.** Augusta Co.: Allegheny Mts., Reddish Knob, Killip 36002 (NY, US, W). Amherst Co.: trail from Rocky Row Run to Blue Ridge Pkwy., NW of Slaty Gap, Freer 2588 (GH). Bath Co.: NW slope of Beard's Mt., Zobel s.n., 6 Nov. 1966 (DUKE). Craig Co.: W of Craig's Creek, 6 mi NE of New-castle, Wherry & Adams 2683 (A, GH). Patrick Co.: Pinnacles of Dan, ca. 4.5 mi SW of Meadows of Dan, Jones 2650 (DUKE, F, NY). Pulaski Co.: Peak Mt., Small s.n., 16 July 1892 (DUKE, F, NY, US). Rockbridge Co.: Buena Vista, near Lexington, Churchill s.n., 1 Sept. 1924 (GH). Roanoke Co.: ca. 4 mi N of Hanging Rock, McAfee Knob, Wood 5887 (GH). Rockingham Co.: Shenandoah Mt., Hunnewell

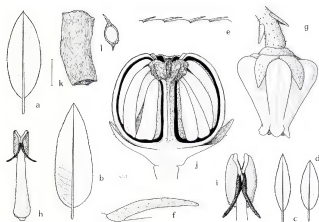
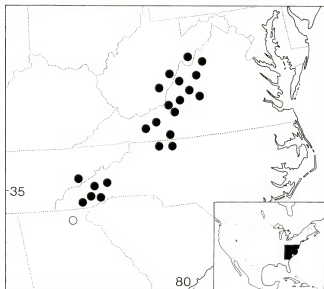


FIGURE 6. *Pieris floribunda*: a-d, leaves, $\times .66$; e, portion of leaf margin, $\times 8$, showing association of each serration with a multicellular hair; f, multicellular, long-celled hair from leaf margin, ca. 1 mm long; g, flower, $\times 4$; h, stamen, $\times 8.5$; i, anther, $\times 17$; j, capsule, longitudinal section, $\times 8.5$; k, seed, bar = 1 mm; l, cross section of seed showing "wings."

13182 (GH). TENNESSEE. Sevier Co.: on Mill Creek Trail to Mt. Le Conte, Sharp & Underwood 740 (NY). NORTH CAROLINA. Haywood Co.: Mt. Pisgah, Walton 3563 (DUKE). Surry Co.: Big Pinnacle, Pilot Mt., Williams 425 (DUKE). Transylvania Co.: N of Devil's Courthouse, Blue Ridge Pkwy., Bozeman *et al.* 9119 (E). Jackson Co.: Tennessee Bald, Jackson-Transylvania Co. line, Wherry *s.n.*, 17 July 1935 (A).

Pieris floribunda is a rather uniform species that is distinctive and is easily distinguished from all other members of the genus. It is most closely related to *P. formosa* and *P. japonica*, with which it shares the characters of elongated seed-coat cells and capsules with subapical placentae. However, it can readily be distinguished from these two species by its alternate leaves, its strigose stems (i.e., with stiff, multicellular, long-celled hairs in addition to multicellular, biseriate-stalked, glandular-headed ones), its serrulate leaves with each serrulation associated with a long-celled hair, and its more strongly ridged corolla with conspicuous pouches between the calyx lobes. Indeed, this species is so distinctive that Nuttall (1843) placed it in the monotypic genus *Portuna*.

Individuals of *Pieris floribunda* are beautiful, cold-hardy shrubs and are frequently cultivated, especially in the cooler areas of eastern North America. Several cultivars are available (see Wagenknecht, 1961). Because of the ornamental qualities of this species and *P. japonica*, several attempts have been made to hybridize them. All of these attempts have failed, resulting either in no seed production or in seed that failed to produce viable offspring



MAP 2. Distribution of *Pieris floribunda* (open circle = type collection, given as "the mountains of Georgia").

(Jaynes, 1975). However, an unusual seedling, which is very probably a hybrid between these two species, has been discovered in a group of seedlings grown from seed of plants of *P. floribunda* that had been growing in cultivation near plants of *P. japonica*. This individual has been reproduced by cuttings and is known as 'Brouwer's Beauty'. It is morphologically intermediate (even in the structure of its multicellular hairs) between the two supposed parental species and is sterile (Jaynes, 1975, and pers. obs.; see Mazzeo & Ayers 37135 (NA)).

Pieris D. Don Section **Phillyreoides** Benthams & Hooker,
Gen. Pl. 2: 588. 1876.

Ampelothamnus Small, Shrubs Florida, 96. 1913. TYPE SPECIES: *Pieris phillyreifolia* (W. J. Hooker) DC.

Venation of lamina brochidodromous. Inflorescences terminal or axillary racemes, rarely terminal panicles. Capsule with placentae appearing central to nearly basal with respect to its apex. Seeds with \pm isodiametric testa cells.

DISTRIBUTION. Southeastern China (Kwangtung and Fukien), southeastern U. S. Coastal Plain (South Carolina to Florida, west to Mississippi), western Cuba and Isle of Pines.

NUMBER OF SPECIES: 3.

4. *Pieris phillyreifolia* (W. J. Hooker) DC. Prodr. 7: 599. 1839.

Andromeda phillyreifolia W. J. Hooker, Ic. Pl. 2: t. 122. 1837. *Ampelothamnus phillyreifolius* (W. J. Hooker) Small, Shrubs Florida, 96. 1913. TYPE: United States, Florida, Apalachicola, *Drummond* 27 (holotype, E!; isotype, E!; possible isotype, an unnumbered specimen of *Drummond* collected at Apalachicola, GH!). *Andromeda croomia* Torrey ex A. Wood, Class-book Bot. 487. 1861. TYPE: United States, Florida, damp woods, Quincy, A. Wood s.n. (holotype, NY!).

Rhizomatous shrub to ca. 1 m tall, with brownish to gray, longitudinally furrowed bark, or more commonly lianas, climbing within fibrous bark of *Taxodium ascendens* (or *Chamaecyparis thyoides*) to ca. 10 m by means of flattened rhizomes bearing scalelike leaves that at intervals give rise to lateral branches bearing large photosynthetic leaves. Twigs \pm terete, with few glandular-headed hairs, otherwise sparsely to moderately pubescent. Buds ovoid, glabrous or with fringe of unicellular hairs along scale margins. Scales 3 to 6, imbricate, apex acute to acuminate. Expanded leaves \pm pseudoverticillate; petiole 1.5–6.5 mm long, vascular bundle unifacial; blade ovate, elliptic, or slightly obovate, (1–)2–6(–7) by (0.3–)0.5–2(–2.7) cm, very coriaceous, the epidermis strongly lignified, the apex acute to rounded, the base narrowly cuneate to rounded, the margin clearly revolute (especially toward base), obscurely to clearly toothed and always with several obvious serrations near leaf apex, the venation brochidodromous, 3^o veins obscure to slightly raised and reticulate, the adaxial and abaxial surfaces with sparse glandular-headed hairs, glabrescent, sparsely pubescent on adaxial surface of midvein. Inflorescences axillary racemes from 1 or several of buds near apex of branches, \pm horizontal. Pedicels 2–7.5 mm long, with few glandular-headed hairs, otherwise usually densely pubescent; bracteoles from upper 15% to near middle of pedicel, linear to narrowly triangular, 0.7–2 mm long; bracts 1–2 mm long, similar to bracteoles in shape. Calyx lobes elongate-triangular, acute at apex, 3.5–5 by 1–1.5 mm; adaxial surface sparsely pubescent or merely papillose near apex; abaxial surface with few glandular-headed hairs. Corolla cylindrical-urceolate, weakly 5-ridged, 6–8(–8.5) by 4–5 mm, white. Filaments 4–6 mm long, geniculate, glabrous, \pm smooth. Style strongly impressed into apex of ovary. Capsule subglobose, 2.5–4 by 3.5–5.3 mm, glabrous; placentae appearing central to nearly basal with respect to capsule apex. Seeds angular-ovoid, 0.9–1.3 mm long, with testa of \pm isodiametric cells. (FIGURE 7; see also Hooker, 1837; Small, 1933; Lemon, 1945; Lemon & Voegel, 1962; Godfrey & Wooten, 1981.)

DISTRIBUTION AND ECOLOGY. Eastern United States from southeastern South Carolina to Florida, west to Mississippi. (MAP 3; see also Ingram, 1963; Duncan, 1967; Godfrey, 1969; Clark, 1971.) Coastal Plain species occurring

in *Taxodium ascendens* or *Chamaecyparis thyoides* swamps, less commonly in various broad-leaved swamps (of *Nyssa biflora*, *Acer rubrum*, *Magnolia virginiana*, *Cyrilla racemiflora*, or *Cliftonia monophylla*) or low pine-lands. Flowering chiefly late January through April.

COMMON NAMES. Climbing heath, climbing fetter-bush.

REPRESENTATIVE SPECIMENS. **United States.** SOUTH CAROLINA. Charleston Co.: 4.5 mi S of Santee R. along U. S. Rte. 17, *Godfrey 68211* (FSU). Colleton Co.: Moselle Swamp, W of Islandton, *Godfrey 68534* (FSU). GEORGIA. Atkinson Co.: S of Pearson, *Bozeman 9432* (E. FSU, GH, NO, NY). Berrien Co.: Alapaha, *Cooper s.n.*, 17 February 1946 (DUKE). Charlton Co.: Okfeenokee Swamp between Bugaboo Landing and Bugaboo Is., *R. M. Harper 1475* (A, E, GH, US). Early Co.: Big Cypress area, near Baker Co. line, *Thorne & Ford 1868* (NY, US). Lowndes Co.: 2 mi E of Valdosta, *R. M. Harper 2052* (A, GH, US). Screven Co.: 15 mi N of Statesboro, *Godfrey 68190* (FSU). Ware Co.: Waycross, *Williamson s.n.* (NY); Wheeler Co.: 1.2 mi NE of Lumber City, *Duncan et al. 16961* (GA). FLORIDA. Bay Co.: W of Panama City, *S32, T3S, R15W, Laessle s.n.*, 21 June 1962 (FLAS). Columbia Co.: 12 mi N of Lake City, *Arnold & West s.n.*, 29 February 1948 (FLAS). Franklin Co.: S16, T7S, R7W, *Conde s.n.*, Sept. 1976 (FLAS). Hamilton Co.: 5 mi E of Jasper, *West & Arnold s.n.*, 30 Sept. 1941 (FLAS). Jackson Co.: 6 mi W of Sneads, *Wiegand & Manning 2344* (GH). Lake Co.: Alexander Springs, *Lakela 26824* (GH). Leon Co.: 12 mi W of Tallahassee, *Godfrey 58002* (GH). Liberty Co.: S of Sumatra, *Reese 1142* (GH). Madison Co.: 5 mi E of Pinella, *Kral 6290* (FSU, GH). Marion Co.: 5 mi NE of Juniper Springs, *Ward & Will 3025* (FLAS, GH). Santa Rosa Co.: W of Milton, *Godfrey & Hawk 62560* (FLAS). Taylor Co.: 3 mi NW of Perry, *Godfrey 58046* (FSU, GH). Walton Co.: 4.5 mi W of Fort Walton, *Godfrey 68388* (FSU). ALABAMA. Geneva Co.: 6.4 mi S of Hartford, *McDaniel 7628* (FSU). Mobile Co.: pine barren streams, *Mohr s.n.*, 20 February 1894 (NY). MISSISSIPPI. Jackson Co.: Escatawpa, *Demaree 32688* (GH).

Pieris phillyreifolia is a very distinctive taxon immediately recognizable because of its often scandent habit and its strongly geniculate, glabrous filaments. It is probably most closely related to *P. cubensis*, which, however, is never a liana, and which has more or less straight filaments that are covered with unicellular hairs. *Pieris cubensis* also has calyx lobes that are densely pubescent adaxially.

The scandent habit of this species has been investigated by several botanists (Harper, 1903; Small, 1914; Lemon, 1945; Lemon & Voegel, 1962; and Hallé, Oldeman, & Tomlinson, 1978). *Pieris phillyreifolia* begins its growth on the ground, and shrubby specimens produce terete, horizontal, underground rhizomes bearing scalelike leaves with adventitious roots arising from their axils (just above the bud). These rhizomes (upon encountering a tree?) are able to ascend *Taxodium ascendens* or *Chamaecyparis thyoides* by climbing upward within the fibrous bark. (Less commonly, this species can be found climbing *Cyrilla racemiflora*, *Sabal palmetto*, or *Pinus elliotii*.) The modified climbing rhizomes are flattened and produce scale leaves. The shoot apex resembles a knifelike wedge and forces its way upward within the bark. In addition to these upward-growing rhizomes, branches are produced that break out into the air at intervals, producing normal photosynthetic leaves (see Lemon & Voegel, 1962). *Pieris phillyreifolia* may also exist as

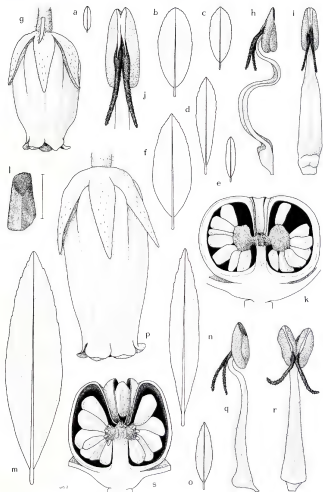
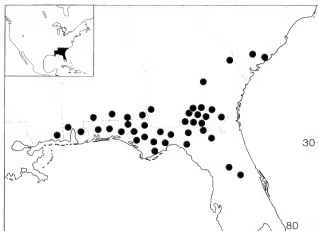


FIGURE 7. a-k, *Pieris phillyreifolia*: a-f, leaves, $\times .66$; g, flower, $\times 4$; h, i, stamens, $\times 8.5$; j, anther, $\times 17$; k, capsule, longitudinal section, $\times 8.5$; l, seed, bar = 1 mm. m-s, *P. cubensis*: m-o, leaves, $\times .66$; p, flower, $\times 4$; q, r, stamens, $\times 8.5$; s, capsule, longitudinal section, $\times 8.5$.



MAP 3. Distribution of *Pieris phillyreifolia*.

a low shrub on hummocks, old stumps, or fallen logs, or in moist openings of swamp forests.

This species is occasionally cultivated.

5. *Pieris cubensis* (Griseb.) Small, N. Am. Fl. **39**: 63. 1914.

Andromeda cubensis Griseb. Catal. Pl. Cubens. 51. 1866. TYPE: Cuba, Pinar del Río, ± La Palma, banks of rivulets, 4 July [1862], C. Wright 2198, in part (holotype, GOE!; isotypes, GH!, L(fragment)!, NY(3 sheets)!, S!).

Rhizomatous(?) shrub to ca. 2 m tall. Twigs terete to strongly angled with few scattered glandular-headed hairs, otherwise glabrous to sparsely pubescent. Buds ovoid to hemispheric, glabrous or with fringe of unicellular hairs along scale margins. Scales (2 or) 3 or 4, imbricate, apex rounded, acute, or slightly acuminate. Expanded leaves alternate; petiole 2–9 mm long, vascular bundle bifacial; blade elliptic to ovate or slightly obovate, 3.5–13 by 0.6–4 cm, coriaceous, the epidermis not lignified to slightly so, the apex slightly acuminate or acute to rounded, the base cuneate to attenuate, the margin plane to conspicuously revolute (especially toward base), entire except for few clear to obscure teeth near apex, the venation brochidodromous, 3° veins slightly visible and reticulate, the adaxial and abaxial surfaces with sparse glandular-headed hairs, ± glabrescent, sparsely pubescent on adaxial surface of midvein. Inflorescences axillary racemes from 1 to several buds usually near apex of branch, ± horizontal. Pedicels 2.5–7.5 mm long, with

few glandular-headed hairs, otherwise densely pubescent; bracteoles from lower 20 to upper 30% of pedicel, linear to narrowly triangular, 1–2.5 mm long; bracts 1.5–3.5 mm long, similar to bracteoles in shape. Calyx lobes elongate-triangular, acute at apex, 3–6.5 by 0.7–1.5 mm; adaxial surface densely pubescent; abaxial surface with few glandular-headed hairs, otherwise sparsely to densely pubescent. Corolla cylindrical-urceolate, weakly 5-ridged, 8–13 by 3–5 mm, white. Filaments 4–5 mm long, straight to very slightly geniculate, covered with unicellular hairs, especially near base. Style strongly impressed into apex of ovary. Capsule subglobose to short-ovoid or ovoid, 4–7 by 4.5–8 mm, glabrous or very sparsely pubescent; placentae appearing central to nearly basal with respect to capsule apex. Seeds angular-ovoid, 1.5–2 mm long, with testa composed of \pm isodiametric cells. (FIGURE 7; see also León & Alain, 1957.)

DISTRIBUTION AND ECOLOGY. Western Cuba (Pinar del Río) and Isle of Pines. (MAP 4.) Along banks of small streams (arroyos) or rivers. Flowering chiefly February to May.

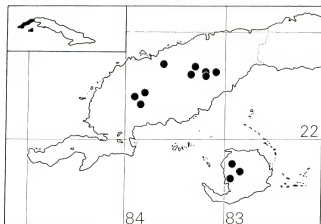
COMMON NAME. Clavellina.

REPRESENTATIVE SPECIMENS. **Cuba.** PINAR DEL RÍO: Sierra de Rangel, *Acuña* 4882 (NY); Santa Cruz de los Pinos, Valle of Taco-taco R., *Alain* 757 (GH, US); Lagunillas, Río San Sebastian, *Ekman* 13796 (s); Sierra Organos, grupo del Rosario, valley of Río Santa Cruz, *Ekman* 16387 (K, NY, s); near El Guama, *Palmer & Riley* 155 (NY, US); Arroyo del Sumidero, *Shafer & León* 13585 (NY, US); Arroyo Veinticinco, San Cristobal, Partir Palacios, *Wright* 2198, in part (GH, GOET, s). ISLA DE PINOS: vic. of Los Indios, *Britton et al.* 14240 (GH, MO, NY, s, US); S of Santa Bárbara, *Killip* 43100 (F, NY, s, US); between San Francisco de las Piedras and Cerro la Cañada, *Killip* 44617 (F, US).

Pieris cubensis is most closely related to *P. phillyreifolia*, from which it is easily distinguished by its nonclimbing habit, its more or less straight, pubescent filaments, its more sparsely toothed, often longer leaves, and its calyx lobes that are densely pubescent on the adaxial surface. Grisebach (1866), when he described this species, was aware of its close relationship to *P. phillyreifolia*. The similarities between these two species were also noticed by K. Lems (unpublished notes).

6. *Pieris swinhoei* Hemsley, Jour. Linn. Soc. Bot. **26**: 17. 1889. TYPE: China, Fukien prov., Amoy interior, June 1870, *R. Swinhoe* s.n. (holotype, K!; fragment of holotype, A!).

Rhizomatous(?) shrub or small tree to ca. 3 m tall, with brownish to gray, vertically furrowed bark. Twigs terete to slightly angled with few glandular-headed hairs, otherwise sparsely pubescent. Buds ovoid, glabrous or with few unicellular hairs along scale margins. Scales ca. 4, imbricate, apex acute to acuminate. Expanded leaves pseudovercillate; petiole 2–7 mm long, vascular bundle unifacial; blade narrowly obovate to elliptic, (2.5–)4–12.5 by (0.4–)0.7–1.7 cm, coriaceous, the epidermis not lignified to slightly so, the apex acute, the base narrowly cuneate to attenuate, the margin revolute (es-

MAP 4. Distribution of *Pieris cubensis*.

pecially toward base), conspicuously toothed on distal half, entire or very obscurely toothed in proximal half; the venation brochidodromous, 3° veins visible and \pm reticulate, the adaxial and abaxial surfaces with sparse glandular-headed hairs, sparsely to moderately pubescent on adaxial surface of midvein. Inflorescences axillary or terminal racemes, less commonly terminal panicles with lowermost lateral branches arising from axils of uppermost foliage leaves, erect to \pm horizontal (?). Pedicels 3.5–9 mm long, with few glandular-headed hairs, otherwise moderately to densely pubescent; bracteoles from upper 15–25% of pedicel, narrowly triangular to ovate, 1.3–4 mm long; bracts 4–10 mm long, similar to bracteoles in shape, rarely approaching leaves in shape and size. Calyx lobes elongate-triangular, acute at apex, 4.5–9 by 1.2–2 mm; adaxial surface moderately to densely pubescent, especially near apex; abaxial surface with few glandular-headed hairs, otherwise glabrous or sparsely pubescent near base. Corolla cylindrical-urceolate, weakly 5-ridged, 8–10 by 3.5–5 mm, white. Filaments 5–7.5 mm long, straight to very slightly geniculate, covered with unicellular hairs, especially near base. Style strongly impressed into apex of ovary. Capsule ovoid to globose, slightly subglobose, or slightly urceolate, 3.5–4.5 by 4–4.5 mm, densely to occasionally moderately pubescent; placentae appearing central to nearly basal with respect to capsule apex. Seeds angular-ovoid, 1–1.5 mm long, with testa of \pm isodiametric cells. (FIGURE 8; see also Anonymous, 1974.)

DISTRIBUTION AND ECOLOGY. Southeastern China (Kwangtung, Fukien), Hong Kong. (MAP 1.) Rare; along stream banks. Flowering in March.

COMMON NAMES. Ma-tsui-mi, maaui-mei-fa (China).

REPRESENTATIVE SPECIMENS. **China.** KWANGTUNG: Thai-Yong, 60 mi W from Port of Swatow, *Dalziel s.n.*, 16 July 1901 (E); Taai Yeung Shaan, *McClure 535* (A); North

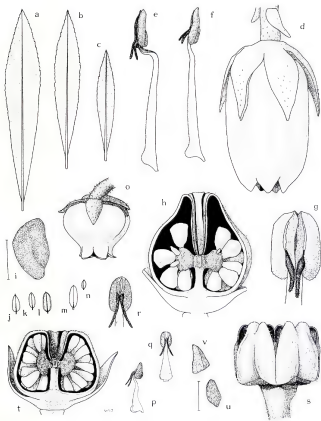


FIGURE 8. a-i, *Pieris swinhoei*: a-c, leaves, $\times .66$; d, flower, $\times 4$; e, f, stamens, $\times 8.5$; g, anther, $\times 17$; h, capsule, longitudinal section, $\times 8.5$; i, seed, bar = 1 mm. j-v, *P. nana*: j-n, leaves, $\times .66$; o, flower, $\times 4$; p, q, stamens, $\times 8.5$; r, anther, $\times 17$; s, capsule, $\times 8.5$; t, capsule, longitudinal section, $\times 8.5$; u, v, seeds, bar = 1 mm.

R., Ma Nui Pa, McClure 1429 (A, NA, UC). **Hong Kong:** Torrent des Ligularia, Poifu-lan, Bodinier 1407 (E).

Pieris swinhoei, a rare and little-collected species of southeastern China, is most closely related to *P. cubensis* and *P. phillyreifolia*. Like these species, it has capsules with the placenta appearing central to nearly basal with respect to the capsule apex, and seeds with more or less isodiametric testa cells. The characters best distinguishing the three species are listed in the key. *Pieris swinhoei* is easily distinguished from *P. japonica* by the above-mentioned characters, and by its larger flowers, its densely pubescent capsules, and its leaves with the secondary and prominent intersecondary veins diverging at often nearly right angles from the midvein and extending more or less straight to near the leaf margin, where they join adjacent secondary veins. In contrast, *P. japonica* has fewer and often less prominent secondary veins that diverge at more acute angles and extend more or less straight or in an upward curve toward the margin.

Pieris D. Don Subgenus **Arcterica** (Cov.) Judd, comb. nov.

Arcterica Cov. Proc. Acad. Sci. Washington 3: 573. 1901. TYPE SPECIES: *Pieris nana* (Maxim.) Makino.

Low shrubs to ca. 10 cm tall. Twigs with homogeneous pith. Leaves usually in whorls of 3, (3-)3.5-11 mm long; margin entire. Flowers in whorls of 3 in axillary or terminal racemes. Calyx lobes often deciduous in fruit, with stomata lacking on adaxial surface; corolla 3-5 mm long; filaments 1.5-2 mm long, roughened-papillose; anthers lacking or with only poorly developed disintegration tissue on back. Capsule with placenta appearing \pm central with respect to its apex.

DISTRIBUTION. Same as species.

NUMBER OF SPECIES: 1.

7. **Pieris nana** (Maxim.) Makino, Bot. Mag. Tokyo 8: 213. 1894.

Andromeda nana Maxim. Bull. Acad. Sci. St.-Petersb. 18: 47. 1872. *Arcterica nana* (Maxim.) Makino, Bot. Mag. Tokyo 20: 85. 1906. *Lyonia nana* (Maxim.) Makino, pro. syn., *ibid.* TYPE: Japan, prov. Nambu (Rikuchu), in high mountains, *Tschonoski s.n.* (holotype, LE, not seen). *Cassiope oxycoccoides* A. Gray, Proc. Am. Acad. n.s. 20: 300. 1885. *Arcterica oxycoccoides* (A. Gray) Cov. Proc. Acad. Sci. Washington 3: 573. 1901. TYPE: Bering Island, [ca. 300 ft alt. behind fishing village of Saranna, 22 August.] 1883, L. Stejneger s.n. (holotype, GH!).

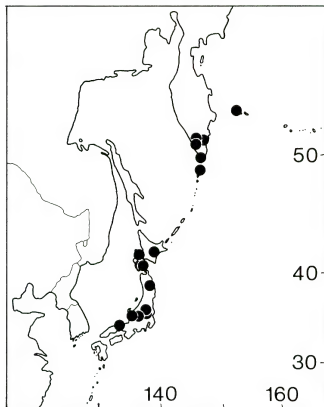
Low, rhizomatous shrub to ca. 10 cm tall. Twigs terete to slightly angled, with few glandular-headed hairs, otherwise moderately to densely pubescent. Buds flattened-ovoid, glabrous or with fringe of unicellular hairs along scale margins. Scales 3 or 4 (or 5), imbricate, apex rounded to acute. Leaves in whorls of 3, rarely opposite or alternate, scalelike and often alternate or opposite on horizontal rhizomes, alternate in seedlings; petiole 0.5-2 mm long,

vascular bundle unifacial; blade elliptic to slightly ovate, (3-)3.5-11 by 1.5-5 mm, coriaceous, the epidermis not lignified to slightly so, the apex acute to rounded, with knoblike, prominent mucro, the base rounded to very slightly cordate, the margin conspicuously revolute throughout, entire, the venation hypodromous to brochidodromous, 2° veins obscure to slightly visible, the adaxial surface with glandular-headed hairs, otherwise sparsely pubescent (on both blade and midvein), \pm glabrescent, the abaxial surface with only glandular-headed hairs. Inflorescences axillary or terminal racemes with flowers in 1 to 3 (rarely to 5) whorls of 3 flowers each, \pm horizontal to pendent but becoming erect as fruits mature. Pedicels 1.5-5 mm long, with few glandular-headed hairs, otherwise densely pubescent; bracteoles from near middle to apex of pedicel, ovate, 2-3 mm long; bracts \pm ovate, 2-5 mm long, often approaching leaves in shape and size. Calyx lobes triangular, acute at apex, 2.5-4 by 0.9-1.3 mm, often deciduous in fruit; adaxial surface sparsely to densely pubescent, especially near apex; abaxial surface with few glandular-headed hairs, otherwise glabrous or sparsely pubescent near base. Corolla urceolate, 3-5 by 2-5 mm, white. Filaments 1.5-2 mm long, straight, roughened-papillose, especially near base. Style strongly impressed into apex of ovary. Capsule short-ovoid or subglobose, 1.7-2.7 by 3-3.5 mm, glabrous to densely pubescent; placentae appearing \pm central with respect to capsule apex. Seeds angular-ovoid, ca. 0.5 mm long, with testa of \pm elongated cells. (FIGURE 8; see also Coville, 1904; Makino, 1961; Ingram, 1963.)

DISTRIBUTION AND ECOLOGY. Japan (central and northern Honshu, Hokkaido) northward to Kuril Islands, southern Kamchatka, Commander Islands (Bering Is.). (MAP 5; see also Hultén, 1930.) In Japan, ca. 1350-2700 m alt.; volcanic-rock areas, rocky peaks, exposed windswept cliffs and slopes, mountain summits, thickets, alpine scrub, dwarf-scrub heath; often with *Pinus pumila*, *Empetrum nigrum*, *Loiseleuria procumbens*, *Diapensia lapponica*, *Vaccinium uliginosum*, *Cassiope lycopodioides*, *Rhododendron camtschaticum* (see Numata, 1974). In more northern portions of range, frequently at lower elevations in low heaths or rocky windswept areas; often with mosses, lichens, *Bryanthus gmelinii*, *Loiseleuria procumbens*, *Oxytropis revoluta*, *Vaccinium vitis-idaea*. In Japan, flowering May through August (mainly July?); data insufficient to determine blooming period for other portions of range.

COMMON NAMES. Komeba-tsugazakura zoku, hama-zakura (Japan).

REPRESENTATIVE SPECIMENS. **Japan.** HOKKAIDO: Hokkaido pref., Mt. Hakamagoshi, Yamamoto s.n., 23 June 1924 (TAI), Mt. Shiribeshi, Wilson 7293 (A), Yezo, Faurie 6754 (A). NORTHERN HONSHU: Akita pref., Mt. Iwate, Furuse s.n., 27 July 1958 (A). CENTRAL HONSHU: Gumma pref., Mt. Shibutsu, Katashinamura, Nishida s.n., 17 July 1950 (A); Ishikawa pref., Mt. Hakusan, Shiota s.n., 4 Aug. 1921 (A); Nagano pref., Mt. Asama, Mizushima s.n., 17 Aug. 1951 (A), Mt. Yatsugatake, Matsuiama 2433 (A); Tochigi pref., Mt. Shirane, Mizushima s.n., 4 July 1952 (A); Tottori pref., Mt. Daisen, Wilson s.n., 30 Nov. 1914 (A).



MAP 5. Distribution of *Pieris nana*. (Distribution outside Japan based Hultén, 1930.)

Pieris nana is a very isolated taxon that is easily distinguished from all other *Pieris* species by its low habit, its small, entire-margined, usually whorled leaves, its roughened-papillose filaments, and its only poorly developed disintegration tissue. The phylogenetic isolation of this species (see Judd, 1979, and above) is expressed here by its being placed in a monotypic subgenus.

The species is occasionally cultivated.

TAXA EXCLUDED FROM PIERIS

- Pieris annamensis* Dop in Lecomte, Fl. Gén. Indo-chine **3**: 726. 1930 = **Lyonia ovalifolia** (Wallich) Drude var. **rubrovenia** (Merr.) Judd.
- Pieris bracteata* W. W. Sm. Notes Royal Bot. Gard. Edinburgh **19**: 116. 1916 = **Vaccinium sprengelii** (G. Don) Sleumer (Rehder, 1949).
- Pieris buxifolia* Lévl. Bull. Soc. Bot. France **53**: 203. 1906 = **Vaccinium triflorum** Rehder (Rehder, 1934; Chamberlain, 1977).
- Pieris cavaleriei* Lévl. & Vaniot, Bull. Soc. Bot. France **51**: 292. 1904 = **Leucothoe griffithiana** Clarke (Rehder, 1934; Chamberlain, 1977).
- Pieris chapaensis* Dop in Lecomte, Fl. Gén. Indo-chine **3**: 726. 1930 = **Lyonia chapaensis** (Dop) Merr.
- Pieris chapaensis* Dop var. *glabra* Dop & Trochain, Bull. Mus. Hist. Nat. Paris II. **4**: 719. 1932 = **Lyonia chapaensis** (Dop) Merr.
- Pieris compta* W. W. Sm. & Jeffrey, Notes Royal Bot. Gard. Edinburgh **9**: 116. 1916 = **Lyonia compta** (W. W. Sm. & Jeffrey) Hand.-Mazz.
- Pieris coreana* Lévl. Repert. Sp. Nov. **5**: 281. 1908 = **Vaccinium bracteatum** Thunb. (Rehder, 1934, 1949; Chamberlain, 1977).
- Pieris divaricata* Lévl. Bull. Acad. Géogr. Bot. **12**: 252. 1903 = **Vaccinium bracteatum** Thunb. (Rehder, 1934, 1949; Chamberlain, 1977).
- Pieris doyonensis* Hand.-Mazz. Anzeig. Akad. Wiss. Wien Math.-Naturwiss. Kl. **60**: 185. 1923 = **Lyonia ovalifolia** (Wallich) Drude var. **doyonensis** (Hand.-Mazz.) Judd.
- Pieris duclouxii* Lévl. Bull. Acad. Géogr. Bot. **12**: 253. 1903 = **Vaccinium sprengelii** (G. Don) Sleumer (Rehder, 1949; Chamberlain, 1977).
- Pieris elliptica* (Sieb. & Zucc.) Nakai, Bot. Mag. Tokyo **33**: 207. 1919. = **Lyonia ovalifolia** (Wallich) Drude var. **elliptica** (Sieb. & Zucc.) Hand.-Mazz.
- Pieris esquirolii* Lévl. & Vaniot, Bull. Soc. Bot. France **53**: 206. 1906, incl. var. **discolor** Lévl. & Vaniot = **Vaccinium sprengelii** (G. Don) Sleumer (Rehder, 1949; Chamberlain, 1977).
- Pieris fauriei* Lévl. Repert. Sp. Nov. **5**: 281. 1908 = **Vaccinium bracteatum** Thunb. (Rehder, 1934, 1949; Chamberlain, 1977).
- Pieris formosana* Komatsu in Matsumura, Ic. Pl. Koishikav. **3**: 71. t. 181. 1916 = **Lyonia ovalifolia** (Wallich) Drude var. **elliptica** (Sieb. & Zucc.) Hand.-Mazz.
- Pieris fortunati* Lévl. Bull. Soc. Bot. France **54**: 369. 1907 = **Gaultheria leucocarpa** Blume (Chamberlain, 1977).
- Pieris gagnepainiana* Lévl. Bull. Acad. Géogr. Bot. **12**: 251. 1903 = **Vaccinium fragile** Franchet (Rehder, 1934, 1949; Chamberlain, 1977).
- Pieris griffithiana* Hooker f., pro. syn., Clarke in Hooker f. Fl. Brit. India **3**: 460. 1882 = **Leucothoe griffithiana** Clarke.
- Pieris henryi* Lévl. Bull. Soc. Bot. France **53**: 204. 1906 = **Lyonia ovalifolia** (Wallich) Drude var. **hebecarpa** (Franchet ex Forbes & Hemsley) Chun.
- Pieris kouyangensis* Lévl. Bull. Acad. Géogr. Bot. **12**: 253. 1903 = **Lyonia ovalifolia** (Wallich) Drude var. **lanceolata** (Wallich) Hand.-Mazz.

- Pieris lanceolata* (Wallich) D. Don, Edinburgh New Philos. Jour. **17**: 159. 1834 = **Lyonia ovalifolia** (Wallich) Drude var. **lanceolata** (Wallich) Hand.-Mazz.
- Pieris longicornu* Lévl. & Vaniot, Bull. Soc. Bot. France **51**: 291. 1904 = **Vaccinium sprengelii** (G. Don) Sleumer (Rehder, 1949; Chamberlain, 1977).
- Pieris lucida* Lévl. Bull. Soc. Bot. France **53**: 207. 1906 = **Vaccinium bracteatum** Thunb. (Chamberlain, 1977).
- Pieris macrocalyx* Anthony, Notes Royal Bot. Gard. Edinburgh **15**: 241. 1927 = **Lyonia macrocalyx** (Anthony) Airy Shaw.
- Pieris mairei* Lévl. Bull. Acad. Géogr. Bot. **25**: 21. 1915 = **Lyonia ovalifolia** (Wallich) Drude var. **hebecarpa** (Franchet ex Forbes & Hemsley) Chun.
- Pieris mariana* (L.) Benthams & Hooker, Gen. Pl. **2**: 588. 1876 = **Lyonia mariana** (L.) D. Don.
- Pieris martinii* Lévl. Bull. Acad. Géogr. Bot. **12**: 252. 1903 = **Vaccinium dunalianum** Wight var. **urophyllum** Rehder & Wilson (Rehder, 1934; Chamberlain, 1977).
- Pieris nitida* (Bartram ex Marsh.) Benthams & Hooker, Gen. Pl. **2**: 588. 1876 = **Lyonia lucida** (Lam.) K. Koch.
- Pieris obliquinervis* Merr. & Chun, Sunyatsenia **5**: 157. 1940 = **Lyonia ovalifolia** (Wallich) Drude var. **rubrovenia** (Merr.) Judd.
- Pieris oligodonta* Lévl. Bull. Soc. Bot. France **54**: 369. 1907 = **Maesa japonica** (Thunb.) Moritzi (Myrsinaceae; Lauener, 1977).
- Pieris ovalifolia* (Wallich) D. Don, Edinburgh New Philos. Jour. **17**: 159. 1834 = **Lyonia ovalifolia** (Wallich) Drude var. **ovalifolia**.
- Pieris ovalifolia* (Wallich) D. Don var. **denticulata** Lévl. Bull. Soc. Bot. France **51**: 291. 1904 = **Vaccinium bracteatum** Thunb. (Chamberlain, 1977).
- Pieris ovalifolia* (Wallich) D. Don var. **elliptica** (Sieb. & Zucc.) Rehder & Wilson in Sargent, Pl. Wilson. **1**: 552. 1913 = **Lyonia ovalifolia** (Wallich) Drude var. **elliptica** (Sieb. & Zucc.) Hand.-Mazz.
- Pieris ovalifolia* (Wallich) Drude var. **hebecarpa** Franchet ex Forbes & Hemsley, Jour. Linn. Soc. Bot. **26**: 17. 1889 = **Lyonia ovalifolia** (Wallich) Drude var. **hebecarpa** (Franchet ex Forbes & Hemsley) Chun.
- Pieris ovalifolia* (Wallich) Drude var. **lanceolata** (Wallich) Clarke in J. D. Hooker, Fl. Brit. India **3**: 461. 1882 = **Lyonia ovalifolia** (Wallich) Drude var. **lanceolata** (Wallich) Hand.-Mazz.
- Pieris ovalifolia* (Wallich) D. Don var. **pubescens** Franchet, Nouv. Arch. Mus. Hist. Nat. Paris II. **10**: 44. 1887 = **Lyonia villosa** (Wallich ex Clarke) Hand.-Mazz. var. **pubescens** (Franchet) Judd.
- Pieris ovalifolia* (Wallich) D. Don var. **tomentosa** Fang, Contr. Biol. Lab. Sci. Soc. China Bot. **10**: 241. 1938 = **Lyonia ovalifolia** (Wallich) Drude var. **lanceolata** (Wallich) Hand.-Mazz.
- Pieris pilosa* Komatsu in Matsumura, Ic. Pl. Koishikav. **3**: 73. t. 182. 1916 = **Lyonia ovalifolia** (Wallich) Drude var. **elliptica** (Sieb. & Zucc.) Hand.-Mazz.

- Pieris repens* Lévl. Bull. Acad. Géogr. Bot. **12**: 252. 1903 = **Vaccinium fragile** Franchet (Rehder, 1949; Chamberlain, 1977).
- Pieris rubrovenia* Merr. Philip. Jour. Sci. **23**: 256. 1923 = **Lyonia ovalifolia** (Wallich) Drude var. **rubrovenia** (Merr.) Judd.
- Pieris shanica* W. W. Sm. Rec. Bot. Surv. India **4**: 277. 1911 = **Craibiodendron stellatum** (Pierre) W. W. Sm.
- Pieris sinensis* Sweet, Hortus Brit. ed. 3. 439. 1839 = *Vaccinium* sp.
- Pieris ulbrichii* Lévl. Bull. Soc. Bot. France **53**: 205. 1906 = **Lyonia ovalifolia** (Wallich) Drude var. **lanceolata** (Wallich) Hand.-Mazz.
- Pieris vaccinium* Lévl. Repert. Sp. Nov. **9**: 448. 1911 = **Gaultheria leucocarpa** Blume (Chamberlain, 1977).
- Pieris villosa* Wallich ex Clarke in J. D. Hooker, Fl. Brit. India **3**: 461. 1882 = **Lyonia villosa** (Wallich ex Clarke) Hand.-Mazz.
- Pieris villosa* Wallich ex Clarke var. *pubescens* (Franchet) Rehder & Wilson in Sargent, Pl. Wilson. **1**: 554. 1913 = **Lyonia villosa** (Wallich ex Clarke) Hand.-Mazz. var. **pubescens** (Franchet) Judd.

NOMINA AMBIGUA

- Pieris compacta* W. W. Sm. in Anonymous, Ic. Corm. Sin. **3**: 174. 1974.
- Pieris langbianensis* A. Chev. ex Dop in Lecomte, Fl. Gén. Indo-chine **3**: 728. 1930. The placement of this name awaits an examination of the type.
- Pieris rolissonii* Lavallée, Arb. Segrez. 149. 1877.
- Pieris scrobiculata* Hollick, Maryland Geol. Survey, Miocene Vol. 486. fig. 1, g. 1904. A fossilized leaf of the Miocene, Calvert Formation, Prince George's Co., Maryland. Not a *Pieris*. True affinities unknown.

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STEM STRUCTURE OF THE NEW WORLD MENISPERMACEAE

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SINCE PUBLISHING a taxonomic study on the Menispermaceae (Krukoff & Moldenke, 1938), B. A. Krukoff has remained interested in this family. He has published numerous papers, both alone and as a joint venture with R. Barneby (for a bibliography see Barneby & Krukoff, 1971; see also Krukoff & Barneby, 1970, 1972, 1974, 1978), centering on the tribes Triclisieae and Anomospermeae. The neotropical Tinosporeae were revised by Barneby in 1970; New World species of the tribes Hyperbaeneae and Menispermaceae are currently being studied by others. Rhodes published a revision of *Cissampelos* in 1975.

Various menisperms are important as a source of ingredients for the drug curare. Thinking that still unknown alkaloids might be present in the bark and wood of many species of this family, Krukoff instigated the collection of additional wood samples associated with herbarium vouchers to provide material for both chemical and anatomic studies. The herbarium specimens of most of this material are located at the herbarium of the New York Botanical Garden.

The present study was undertaken at the suggestion of Krukoff, who provided a great number of the wood samples. Because the majority of the samples belong to the Triclisieae and Anomospermeae, the anatomic treatment presented here also centers on these two tribes. Additional information on the Hyperbaeneae, Tinosporeae, and Menispermaceae is based on rather scarce material, as is shown in TABLES 2 and 4 and in the APPENDIX. According to present taxonomy, the New World menisperms comprise five tribes and eighteen genera; this study is based on representatives of thirteen genera.

MATERIAL AND METHODS

All the wood samples used in the present investigation were received dry. Microtome sections were made in the usual way and were stained with safranin. Macerations were effectuated by placing chips in equal parts of glacial acetic acid and hydrogen peroxide at a temperature of 60°C for 24 hours. The macerated material was stained with lactic acid (cotton blue).

Pore diameters were measured tangentially. Due to the great variation in pore size, more attention was given to the widest vessels than to the small or intermediate ones, which are always present. Consequently, the mean width of the widest vessels was calculated rather than the average width of all vessels.

The average of the counts of all vessels in at least ten bundles was calculated instead of the usual average number of vessels per mm². The length of the imperforate elements, of the vessel elements, and of the parenchyma strands was measured in the macerations. For vessel elements and fiber-tracheids the average of 25 counts was taken, for the other elements the average of at least ten counts. The terminology of crystals follows Chattaway (1955, 1956). General terminology follows the International Association of Wood Anatomists' *Multilingual Glossary of Terms used in Wood Anatomy* (1964).

With the exception of *Borismene japurensis* and an unnamed species of *Cissampelos*, the genera and species do not show much variation in microscopic characters. Differences in sizes and numbers of elements may be even greater between species than among genera, as is shown in TABLE 3 by data from all the available material of *Abuta rufescens*. The general uniformity of the microscopic structure makes generic descriptions superfluous and preparation of a dichotomous key impossible. Instead, the presence of characteristic features is listed in synoptic tables, as advocated by Leenhouts (1966). The features included are the shape of the stems (discussed below), the gross aspect of the bark, and the macroscopic characters of the pith (discussed in the next section) (all shown in TABLE 1), and the distribution of crystals and silica grains in the stems (TABLE 2).

STEM MORPHOLOGY

Most menisperms are woody lianas or shrubs with scandent branches; some are slender vines that are woody only at the base. Exceptions include most species of *Hyperbaena* and the Asiatic *Cocculus laurifolius*, which are small trees or shrubs. *Abuta grandifolia* occurs as a shrub, a tree, or a liana.

Irrespective of the plant's habit, a transverse section of its wood usually shows a highly characteristic pattern of abnormal secondary growth consisting of fairly regular consecutive rings or partial rings of vascular bundles separated radially by wide interfascicular rays and tangentially by layers of mixed sclerenchymatous and parenchymatous cells. This special structure was first noticed by Decaisne (1839) in *Cissampelos pareira* and *Cocculus laurifolius*. His findings were later confirmed in representatives of many other menispermaceous genera by numerous botanists, including Radlkofer (1858), Eichler (1864), Blottière (1886), Schenck (1892, 1893), Solereder (1899), Maheu (1902), Diels (1910), Williams (1936), Chalk and Chattaway (1937), Metcalfe and Chalk (1950), Obaton (1960), and van der Walt and associates (1970).

Exceptions to the above-mentioned group of characteristics are known to exist: *Coccinium fenestratum*, a liana from Ceylon (Eichler (1864), Gamble (1881), Solereder (1899), Diels (1910), Zeijlstra (1911)); *Cocculus umbellatus*, from eastern Asia (Zeijlstra, 1911); and *Cissampelos capensis* (Blottière, 1886). Mention should also be made of Decaisne's (1839) statement regarding the structure of a half-inch-wide stem of *Menispermum canadense* in which only one ring of triangular bundles was present. Other exceptions have been mentioned by Dipasupil (1955) for several genera of menisperms

TABLE 1. General characters of the stems.

STEMS

Shape in cross section*

Centric: *Abuta candollei*, p.p., *A. grandifolia*, *A. pahnii*, *A. sandwithiana*, *A. solimoesensis*, p.p., *A. velutina*, p.p.; *Anomospermum bolivianum*, *A. chloranthum*, *A. matogrossense*; *Borismene japurensis*; *Caryomene olivascens*; *Chondrodendron tomentosum*; *Hyperbaena* sp.; *Odontocarya* aff. *wulfschlaegeli*; *Orthomene schomburgkii*; *Sciadotenia eichleriana*, p.p., *S. solimoesana*, p.p.; *Telotoxicum glaziovii*, p.p., *T. krukovi*.

Excentric, not strongly flattened: *Abuta brevifolia*, *A. candollei*, pp., *A. fluminum*, *A. grisebachii*, *A. imene*, *A. obovata*, *A. panurensis*, *A. rufescens*, *A. solimoesensis*, p.p., *A. velutina*, p.p.; *Anomospermum reticulatum*, *A. solimoesanum*; *Caryomene* sp.; *Sciadotenia eichleriana*, p.p., *S. solimoesana*, p.p., *S. toxifera*; *Telotoxicum glaziovii*, p.p., *T. minutiflorum*.

Excentric, strongly flattened, with only 1 or 2 complete rings around pith: *Curarea candicans*, *C. tecunarium*; *Sciadotenia solimoesana*, p.p.; *Chondrodendron microphyllum*, p.p.

Color of wood in transverse section

Yellowish green: *Abuta brevifolia*, *A. obovata*, p.p., *A. pahnii*, *A. panurensis*, *A. sandwithiana*, p.p.

Dull grayish brown: all other species.

BARK

Young twigs velvety, greenish brown: *Abuta rufescens*.

Young twigs neither velvety nor greenish.

Smooth: *Abuta brevifolia*, *A. bullata*, *A. panurensis*; *Anomospermum bolivianum*; *Sciadotenia toxifera*.

Grooved:

Thick, deeply grooved, grooves ca. 4 mm apart: *Anomospermum solimoesanum*.

Thick, superficially and narrowly grooved: *Borismene japurensis*.

Thin, narrowly grooved: all other species.

PITH

Hollow, ca. 5 mm wide: *Caryomene olivascens*, *Caryomene* sp.

Solid, 5 mm or more wide: *Abuta grandifolia*, p.p., *A. rufescens*; *Anomospermum bolivianum*; *Borismene japurensis*; *Elephantomene eburnea*; *Telotoxicum krukovi*.

Solid, usually 1.5–3 mm wide: all other species.

*Not all specimens cited in the Appendix could be assigned to a category, either because the pieces of large stems did not allow visualization of the section of a complete trunk or because only sections were present.

from the Philippines, and by Obaton (1960) for a liana from the Ivory coast.

It has generally been assumed (Record & Hess, 1943) that among New World representatives of the family no exceptions from the "normal" pattern occur. In the present investigation, however, three stems—one of a species of *Cissampelos* (as yet unnamed) and the other two of *Borismene japurensis*—also showed a different type of secondary growth.

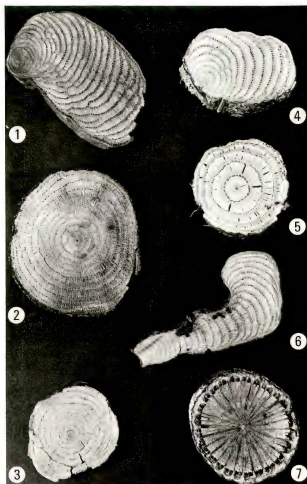
The typical pattern referred to above is illustrated by transverse sections

TABLE 2. Occurrence of silica and crystals.

TRIBE	TAXON	PRESENCE OF SILICA GRAINS	ABSENCE OF CRYSTALS	CRYSTAL TYPES			
				Large, rhomboid; solitary or twin	Small, rhomboid; one per cell	Rhomboid; large and small in same cell	Small, acicular
TRICLISIEAE	<i>Curarea candicans</i>			+ 1	+++ 1,2		
	<i>Curarea tecunarium</i>		p.p.		+ 1,2 p.p.		
	<i>Curarea toxicifera</i>			++ 1,2	+++ 1,2	+ 1	
	<i>Chondrodendron microphyllum</i>				+++ 1,2	+++ 1,2	
	<i>Chondrodendron tomentosum</i>			+ 1,2	++ 1,2	+++ 1,2	
	<i>Sciadotenia eichleriana</i>			++ 1,2		+++ 1,2	
	<i>Sciadotenia paraensis</i>			++ 1,2			
	<i>Sciadotenia solimoesana</i>			+ 1,2			
	<i>Sciadotenia sprucei</i>			+ 2			
	<i>Sciadotenia toxifera</i>			++ 1,2	+ 2	+ 1	
HYPER- BAENEAE	<i>Hyperbaena domingense</i>			+ 2	+++ 2	+ 2	
	<i>Hyperbaena</i> sp.			++ 1,2	+++ 2	++ 2	+++ 2
	<i>Telitoxicum glaziovii</i>			++ 1		+ 2	
	<i>Telitoxicum krukovii</i>		—				
	<i>Telitoxicum minutiflorum</i>		p.p.	+ 1			
	<i>Abuta brevifolia</i>			+ 1	+ 1		
	<i>Abuta candollei</i>			+ 1			
	<i>Abuta colombiana</i>			+ 1			
	<i>Abuta fluminum</i>			++ 1	++ 2		
	<i>Abuta grandifolia</i>		p.p.	+ 1			
	<i>Abuta grisebachii</i>						
	<i>Abuta imene</i>			++ 1,2			

ANOMOSPERMACEAE	<i>Abuta obovata</i>		+ 1			
	<i>Abuta pahnii</i>		+++ 1,2			
	<i>Abuta panurensis</i>		+ 1			
	<i>Abuta rufescens</i>	p.p.	+ 1,2	+ 2		
	<i>Abuta sandwithiana</i>		+ 1	++ 2		
	<i>Abuta solimoesensis</i>	—				
	<i>Abuta velutina</i>	—				
	<i>Caryomene olivascens</i>		+ 1			
	<i>Caryomene</i> sp.				+ 1	
	<i>Anomospermum bolivianum</i>	++ 2	—			
	<i>Anomospermum chloranthum</i>		++ 1			
	<i>Anomospermum chloranthum</i> subsp. <i>occidentale</i>		++ 1			
	<i>Anomospermum matogrossense</i>		++ 1,2			+ 1
	<i>Anomospermum reticulatum</i>		+++ 1,2			
	<i>Anomospermum reticulatum</i> subsp. <i>dielsianum</i>		+ 1			
	<i>Anomospermum solimoesanum</i>	++ 2,3	—			
TINO- SPORIEAE	<i>Orthomene prancei</i>		+ 1			
	<i>Orthomene schomburgkii</i>		++ 1,2			
MENI- SPERMACEAE	<i>Elephantomene eburnea</i>		+ 1			+ 2
	<i>Odontocarya</i> aff. <i>wulfschlaegelii</i>		++ 4	+ 4	++ 4	++ 4
	<i>Borismene japurensis</i>		+++ 4			++ 4
	<i>Cissampelos fasciculata</i>		+ 1	++++ 2	++ 1	
	<i>Cissampelos pareira</i>		+++ 1	++++ 2	++ 1	
	<i>Cissampelos</i> sp.				+	+++ 4

Explanation of symbols: (—) crystals absent, (p.p.) crystals only present in part of the specimens, (+, ++, +++, +++) the relative amount of crystals. Tissues in which the crystals occur: (1) parenchyma cells or sclerotic tissue of the "connective bands," (2) interfascicular rays, (3) vascular parenchyma bands, (4) wide medullary rays, particularly where they border on the fiber tissue.



FIGURES 1-7. Transverse sections of menisperm stems, $\times 1$: 1, *Abuta imene*, stem excentric; 2, *Telitoxicum glaziovii*, stem centric; 3, *Orthomene schomburgkii*, stem centric; 4, *Sciadotenia toxifera*, stem excentric; 5, *Chondrodendron tomentosum*, stem centric; 6, *Curarea tecunarium*, stem strongly excentric and comma shaped in cross section; 7, *Borismene japurensis*, showing wedge-shaped vascular bundles (instead of characteristic successive layers of bundles).

of stems of various genera (FIGURES 1-6, 20, 21). With the exception of *Borismene* (FIGURE 7), all show the concentric rings or partial rings of vascular bundles separated radially by rather wide interfascicular rays that are not continuous from one ring to the next. Tangential bands of connective tissue composed of parenchymatous and sclerotic cells separate one ring of bundles from the next.

Although spacing and width of the bundles are fairly regular in cross section, this is not the case for the outline of the stem sections. Stems can be strongly excentric, winged on one side, or even much flattened, as can be seen in FIGURES 1, 4, and 6. Maheu (1902) mentioned excentric growth of the stems for *Abuta rufescens*, *A. selleana*, *Anomospermum grandifolium*, *A. schomburgkii*, and *Chondrodendron tomentosum*. Schenck (1893) published a drawing of a double-winged stem of *Abuta rufescens* and stressed the fact that the form of a sectioned stem is not constant over its entire length. Some lianas that grow very thick and long (e.g., *A. rufescens*) may show different shapes in different places. Dimensions of the transverse sections, shown in the list of material studied (APPENDIX), give an idea of the sizes and shapes of the stems; where two dimensions are given, the form is elliptic.

WOODS WITH TYPICAL STRUCTURE

PITH. The pith is usually relatively small (1-3 mm in diameter), but in some cases it is up to 7 mm wide (see TABLE 1); sometimes the central part is hollow. An inner and an outer pith can usually be recognized. The inner part consists of a central core of large, more or less isodiametric, thin- or thick-walled parenchyma cells with large intercellular cavities (FIGURES 12-15). In dried material the cells are empty or are filled with starch; occasionally they contain crystals. Solitary or clustered stone cells may be found scattered among the parenchymatous cells. Secretory sacs, which Solereder (1899, 1908) noted for several, mostly Old World genera and which Santos (1928, 1931) mentioned for *Tinospora* sp., *Archangelisia flava*, and *Anamirta cocculus* (all collected in the Philippines), were seen only in material of *Abuta rufescens* and *Cissampelos* sp.

The inner pith gradually changes into the outer pith, where the parenchyma cells become smaller in diameter and more elongate in form; often septa are formed. Fiber "caps," originating in the pith opposite the protoxylem of the bundles and resembling the fiber "caps" on the outside of the phloem of the bundles, are characteristic of this zone. These fibers may be restricted to a small number, forming an unobtrusive group embedded among the parenchyma cells (FIGURE 14), or they may form crescent- or dome-shaped masses, as illustrated in FIGURES 13 and 15.

In *Borismene japurensis* and an unidentified specimen of *Cissampelos*, both characterized by a mode of growth different from the other menisperms, the parenchyma cell walls of the pith are not lignified and the cells contain numerous small, spindle-shaped, acicular crystals. The pith of *Borismene* is different in other aspects as well, as is discussed below.

VASCULAR BUNDLES. The number of vascular bundles around the pith varies considerably, usually fluctuating between 25 and 40, although 88 bundles

TABLE 3. Stem features in specimens of *Curarea tecunarium* (tribe Triclisieae) and *Abuta rufescens* (tribe Anomospermeae).

SPECIMEN NUMBER	DIMENSIONS (in cm) OF CROSS SECTION WOOD SAMPLE	LENGTH AND WIDTH (in mm) OF BUNDLES	NUMBER OF VESSELS PER BUNDLE (mean and range)	TANGENTIAL DIAMETER (in μ m) OF WIDEST VESSELS	NUMBER OF BUNDLES AROUND PITH
<i>Curarea tecunarium</i>					
Uw 18054	1 \times 3.5	2.6 \times 0.4	18 (12 to 25)	170-240	
Uw 18678	1 \times 3.5	1.7 \times 0.4	15 (8 to 19)	200	
Uw 18679	a	2.3 \times 0.3-0.4	17 (10 to 31)	190-250	
Uw 18680	a	2-2.8 \times 0.4-0.5	16 (8 to 28)	200-230	
Uw 18681	a	3.5 \times 0.3	22 (15 to 28)	170-240	
Uw 18682	1.5 \times 2.5	2.3-2.8 \times 0.35-0.45	18 (8 to 30)	200-240	
Uw 18683	2 \times 6	3-4 \times 0.3-0.48	29 (22 to 38)	160-190	
Uw 18684	2 \times 6	1.8 \times 0.35-0.55	15.5 (10 to 25)	180-230	
Uw 18685	2 \times 7	2.8-3.5 \times 0.5-0.75	30 (25 to 33)	200-220	
Uw 18686	1.5 \times 7	2.2-3 \times 0.4-0.5	15 (7 to 22)	200-220	
Uw 18687	2 \times 10	2-2.5 \times 0.3-0.4	14.3 (9 to 21)	230-280	
Uw 18688	a	2.5 \times 0.35-0.5	17 (14 to 21)	200-250	
Uw 18689	a	2.7 \times 0.2-0.5	12 (8 to 20)	230-300(-350)	
Uw 18690	a	2.4-3 \times 0.25-0.4	19 (10 to 26)	200-240	

Abuta rufescens	Uw 18692	0.5 × 6	1.5-1.7 × 0.3-0.4	11 (5 to 15)	180-200	
	Uw 18693	a	2 × 0.4-0.6	15 (10 to 27)	160-220	
	Uw 18747*	3 × 6	3 × 0.35-0.45	5 (2 to 9)	300-350	
	Uw 12356	1.4 × 1.4	2.5 × 0.24-0.3	6 (2 to 10)	80-120	50
	Uw 18058	2 × 4.5	2.3-2.5 × 0.4-0.5	10 (7 to 13)	300-360	80
	Uw 18071	1.5 × 4.5	2.2-2.5 × 0.45	9 (3 to 18)	300-360	62
	Uw 18079	2 × 5-6	2.5 × 0.5-0.6	6 (1 to 9)	300-360	31
	Uw 18519	1 × 1	1.1 × 0.4	4 (1 to 8)	120-140	60
	Uw 18623	1.3 × 6	2.2 × 0.45	9 (6 to 11)	260-330	>45
	Uw 18660	b	2.5-3.2 × 0.4-0.6	11 (5 to 15)	260-325	a
	Uw 18661	4 × 10	2.2-2.8 × 0.45	9 (5 to 13)	300-350	a
	Uw 18662	1 × 2	2-2.3 × 0.35-0.5	10 (3 to 17)	250-300	46
	Uw 18663	a	2-2.25 × 0.3-0.45	10 (4 to 15)	230-300	a
	Uw 18665	3 × 6	1.7-2 × 0.4	5.5 (3 to 9)	250-300	a
	Uw 18730	3.5 × 4.5	1.4-1.9 × 0.3-0.4	5 (2 to 9)	250-320	45
	Uw 18926	1.5 × 4.5	2 × 0.35-0.5	7 (4 to 10)	250-360	55
	Uw 21098	3.5 × 4	1.8-2.6 × 0.3-0.4	8 (2 to 14)	270-350	73

Explanation of symbols: (a) pith absent or only sections available, (b) strip of a stem over 7 cm wide.

*Probably not this species but an *Abuta*, as implied by the figures and also by the cross-sectional outline of the stem and the texture of the bark.

were recorded in *Elephantomene eburnea* and 44 in *Chondrodendron microphyllum*. An illustration of the considerable variation of this character within one species is given in TABLE 3 for *Abuta rufescens*, for which the numbers range between 31 and 80.

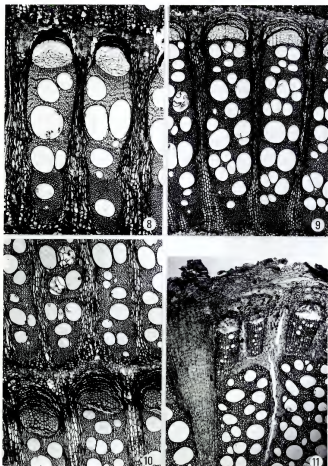
The medullary (primary) and secondary interfascicular rays separating the bundles of each ring are often very wide and very high, with considerable variation within each sample (e.g., in *Anomospermum reticulatum* (Uw 18614)). The wider rays are 25 cells (525 μ m) wide and over 2 cm high; the narrower ones are only 11 cells (200 μ m) wide. The cells are mainly procumbent and are of irregular dimensions as seen in radial and tangential sections. They are often filled with starch and may also contain crystals of different forms, or silica grains as is the case in two species of *Anomospermum* (see below). The rays are not continuous from ring to ring (FIGURES 16, 17, 20, 21).

As seen in transverse section, the vascular bundles are wedge shaped to nearly rectangular. Radially they measure from 1.5 to 5.5 mm; their widest tangential dimensions range from 0.3 to 0.8 mm. Usually some variation occurs within a stem, particularly in one that is excentric or otherwise irregular (FIGURES 1, 4).

In the first-formed ring of vascular bundles, the oldest, obliterated cell layers of the phloem are surrounded by one layer of thin-walled parenchymatous cells. Outside of these cells, there is a thick, crescent-shaped "cap" of thick-walled sclerenchymatous fibers. Beyond the "caps" a continuous cortical band of parenchyma stretches over both the "caps" and the medullary rays. In this zone the cambium is generated; this gives rise to the next ring of bundles. The difference between the first and the second and subsequent rings is that in the first ring the fiber "caps" are restricted to the connective tissue. The consecutive rings of bundles are separated from each other by a connective tissue consisting of a layer of parenchyma, a two- to four-cell-wide layer of stone cells, and an outer layer two to six cells wide of parenchyma. The layer of stone cells widens over the interfascicular rays and penetrates, wedgelike, into these rays usually as far as the vascular cambium (see FIGURES 8-10, 16).

The woody part of the bundles is composed of vessels, fiber-tracheids, and axial parenchyma; rays are extremely scarce. The radial dimensions of the woody part are highly variable, although they generally tend to be shorter in the *Anomospermeae* (1-2.5 mm) than in the *Triclisieae* (2.5-5 mm) (see FIGURES 20, 21; TABLE 3). In the phloem portion of the bundles, tangential bands of sieve tubes and companion cells occur alternately with bands of parenchyma cells; fibers are always absent. The oldest peripheral layers are arc shaped and composed of strongly flattened sieve tubes and intact paren-

FIGURES 8-11. Transverse sections, $\times 28$: 8, *Abuta rufescens* (Uw 18661), showing two vascular bundles with few large, solitary vessels and few small ones, active phloem parts "capped" by several obliterated cell layers, connective tissue on abaxial side consisting mainly of stone cells penetrating into interfascicular rays up to cambial



zone; 9, *Curarea tecunarium* (Uw 18682), with vessels more numerous and smaller; 10, *Sciadotenia eichleriana* (Uw 18658), showing same type of bundles as *Curarea*, fingerlike thin tyloses present in some vessels; 11, *Cissampelos* sp. (Uw 18072), showing different type of growth, without successive layers (wide, wedge-shaped interfascicular rays continuous from pith to bark; woody part has split during growth of stem).

chyma, resulting in a banded appearance of the phloem "cap" (see FIGURES 9 and 10). Sizes of the phloem portion vary from 500 to 700 μm tangentially and from 300 to 500 μm radially.

VESSELS. Although the vessels are mainly solitary, they sometimes occur in radial multiples of two, or in tangential groups of two or three with or without direct contact; the tangential arrangement is frequently continuous from one bundle to the next (FIGURE 21). In each bundle wide and narrow vessels are intermingled. Vessels are often absent in the adaxial part of a bundle, or sometimes only one or two extremely narrow ones are to be found; this feature occurs more frequently in the Anomospermeae than in the Triclisieae. The narrowest vessels are about 40 μm wide, the widest 350–400(–500) μm . The number of vessels per bundle is rather variable within a sample, but an average can be established with some confidence from a survey of a great number of bundles seen in cross section. These averages range from 14 to 34 per bundle for genera of the Triclisieae, and from 4 to 19 for the Anomospermeae (see TABLE 4, FIGURES 20, 21). A possible relation between taxonomy and the number and width of the vessels is discussed below.

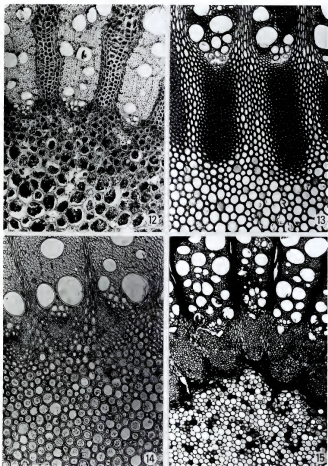
The perforations of the vessel elements are exclusively simple, with the perforation plates nearly horizontal. Intervascular pitting is irregular, with the pits from 6 to 11 μm wide and the apertures enclosed or confluent; near the end of a vessel member there are always clusters of very large, elongated

TABLE 4. Vessel characters.

TRIBE	GENUS	AVERAGE NUMBER OF VESSELS PER BUNDLE (range)	TANGENTIAL DIAMETER OF WIDEST VESSELS (in μm)
Triclisieae	<i>Chondrodendron</i> (2)*	14 to 34	300
	<i>Curarea</i> (3)	15 to 29	250
	<i>Sciadotenia</i> (5)	20 to 28	240
Hyperbaeneae	<i>Hyperbaena</i> (4)	8 to 24	210
Anomospermeae	<i>Telotoxicum</i> (3)	3.5 to 13 (to 40)	300–400
	<i>Abuta</i> (15)	4 to 19	350
	<i>Caryomene</i> (2)	16 to 19	350–400
	<i>Anomospermum</i> (5)	5 to 8	350–400
	<i>Orthomene</i> (1)	6 to 10	350
	<i>Elephantomene</i> (1)	4 to 9	500
Tinosporeae	<i>Odontocarya</i> (1)	14	400
	<i>Borismene</i> (1) [†]		400
Menispermeae	<i>Cissampelos</i> (2)	25 to 31	230
	<i>Cissampelos</i> sp. [†]		220

*The number of species investigated is cited in parentheses.

[†]Due to different stem structure in *Borismene* and one (unidentified) specimen of *Cissampelos*, data for number of vessels per bundle are not applicable.



FIGURES 12-15. Details of pith region: 12, *Abuta sandwithiana* (Uw 18739), $\times 70$; 13, *Elephantomene eburnea* (Uw 21079), $\times 70$, adaxial bundle "caps" of thick-walled fibers strongly developed; 14, *Sciadotenia sprucei* (Uw 18745), $\times 70$, pith cells relatively thick walled, adaxial "caps" unobtrusive; 15, *Chondrodendron tomentosum* (Uw 18694), $\times 28$, pith cells thin walled, adaxial bundle "caps" well developed.

pits with narrow borders (FIGURE 19). Vessel members average 230–500 μm long (including the short tails, if present). Tyloses occur frequently and are generally thin walled and fingerlike (FIGURES 9, 10, 16).

VASCULAR TRACHEIDS. Vascular tracheids of the same length as the vessel members are occasionally present, but in macerations they are often difficult to distinguish from the shortest fibers.

FIBER-TRACHEIDS. The fiber-tracheids are nonseptate, with numerous small, bordered pits on radial and tangential walls. Their mean tangential diameter is 16–24 μm . The walls are mostly 4–5 μm thick. The length varies considerably in each species, ranging from 400 to 1900 μm and averaging between 700 and 1300 μm .

PARENCHYMA. The axial xylem parenchyma of all species (with the exception of the aberrant *Borismene japurensis* and the unnamed species of *Cissampelos*) consists of numerous one-cell-wide, wavy, tangential bands. Sometimes vasicentric strands are also present, but they seldom form a complete ring. Strands are usually composed of two cells, but four-celled strands also occur; their mean length is 350 μm (range, 270–460 μm).

RAYS. Rays are very rare in the bundles, occurring only in the widest abaxial portions of the largest ones (e.g., *Curarea toxifera*); they are uniseriate and consist of upright cells.

WOODS WITH A DIFFERENT STRUCTURE

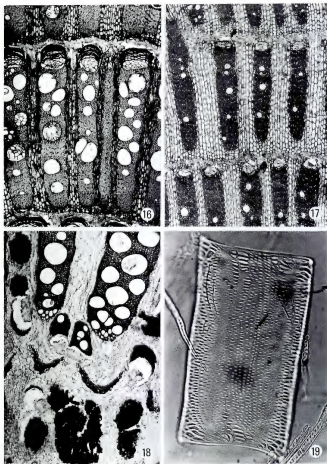
***Borismene japurensis* (Martius) Barneby**

FIGURES 7, 18.

MATERIAL: *J. Schunke* V. 5388 (Uw 20524), Peru. Stem diameter 3.8 cm, centric; bark grayish brown, 3 mm thick, the rhytidome with superficial, narrow grooves. *Plowman & Schunke* 7547 (Uw 25678), Peru. Liana 8 m tall; trunk terete, 2 cm in diameter; bark similar to that in preceding sample.

Pith narrow, 3 mm wide, consisting of large, unligified parenchymatous cells; dispersed among these cells are large, isolated or clustered stone cells. A number of small, irregularly distributed medullary bundles, 500 by ca. 200 μm , occur at the periphery of the pith in one sample (Uw 20524). These bundles are inversely oriented but are otherwise normally developed (FIGURE 18). The pith is surrounded by 27 main bundles in Uw 20524 and 20 in Uw 25678; at the circumference of the stem there are about twice that number of phloem "caps" due to dilation that results in a splitting of the main bundles near the pith. At this level in Uw 20524, the wood of all bundles is penetrated by transverse intrusions of parenchyma from the medullary rays. Beyond this irregular region, which contains only a few narrow vessels, a new wide ray is formed that divides the original bundle in two or sometimes three equal parts, whereupon normal growth is resumed. Although the intrusion of a few parenchyma cells may repeat itself at intervals, in the material at hand dilation was apparently not yet sufficient to induce renewed splitting of the bundles.

The elements of the wood are similar to those described in the preceding



FIGURES 16-19. 16, 17, transverse sections of *Abuta grandifolia*, $\times 28$: 16, Uw 18688, liana; 17, Uw 3361, small tree. 18, *Borismene japurensis* (Uw 20524), pith with inverted bundles and first ring of bundles, $\times 28$. 19, *Orthomene schomburgkii* (Uw 18075), maceration showing vessel member with large, elongated pits near perforation, $\times 180$.

paragraph. Vessels are up to 400 μm wide; thin- or thick-walled tyloses occur; pits are of irregular sizes, 8–16 μm wide, often with very large apertures. The fiber-tracheids are 24–30 μm wide, and the lumen is large. The medullary rays are from 10 to 40 cells wide (250–1200 μm), and the cells contain a large number of small and large crystals, mainly small, acicular ones in the interior ray cells, and rhombic ones in the cells adjacent to the bundles. Within the bundles uniseriate rays are occasionally present. One-cell-wide bands of axial parenchyma are scarce, short, and scattered.

The phloem of the bundles is capped by an arc of sclerenchyma; where the bundles are split, paired or tripled phloem is capped by a single arc.

***Cissampelos* sp.**

MATERIAL: *Barquero 1970/201* (Uw 18072), Costa Rica. Stem diameter 1 cm, centric; bark very thin, smooth.

The narrow pith is 800 μm wide and consists of large parenchymatous cells with thin, unlignified walls. The cells become gradually smaller near the outer part. The groups of fiberlike cells opposite the primary xylem are small. The pith is surrounded by 13 vascular bundles 3.6 mm by 800–1100 μm , some of which are radially divided by an ingrowth of parenchymatous cells. The bundles are separated by broad, wedge-shaped, nonlignified medullary rays up to 1400 μm wide. The vessels are often more or less tangentially arranged in rows of 4 to 6 and have a maximum width of 200–220 μm ; tyloses are absent. Axial xylem parenchyma is scarce and in tangential patches or irregular, very short, tangential bands.

This species differs from material of *Cissampelos pareira* L. (Uw 5437) and another (unidentified) specimen (*Gill 20a*) in the absence of successive rings of bundles, in the splitting of some of the bundles, and in the unlignified cells of the pith and medullary rays. The numerous large and small rhomboid crystals found in the interfascicular rays and the connective tissue of these two specimens are also absent in the specimen described above.

OCURRENCE OF CRYSTALS AND SILICA

Crystals of various forms are of general occurrence in menisperms; silica inclusions, on the contrary, are very rare and in the present material are restricted to two species of *Anomospermum*: *A. bolivianum* and *A. solimoesanum*. In these two species the silica grains are mainly in the cells of the parenchyma bands of the vascular bundles and, to a lesser degree, in the cells of the interfascicular rays; in the other genera and in other species of *Anomospermum*, crystals never occur in the cells of the bundle parenchyma but are found in those of the connective tissue and the interfascicular rays.

The variation in the form of the crystals was described by Solereder (1899, 1908), who reported their presence in the tissues of the leaves. Krafft (1907), in his thesis on the anatomy of the leaves of the Menispermaceae, stressed the importance of the occurrence of various types of crystals, such as spiculae and the small and large rhomboid calcium oxalate crystals. In addition, he mentioned the probability that the presence of sclerotic elements and the for-

mation of crystals are related since the two often occur close together. Such a relation was also found in the wood specimens examined in this study. Crystals are most frequently found in the parenchymatous cells bordering the sclereids of the conjunctive tissue.

In a single species can be found large, single rhomboid crystals of calcium oxalate completely filling the cells, twin crystals or one large and several small ones in the same cell, or one or two rodlike or acicular crystals (terminology follows Chattaway, 1955, 1956). Alternatively, there may be such a profusion of small crystals that they might be called crystal sand.

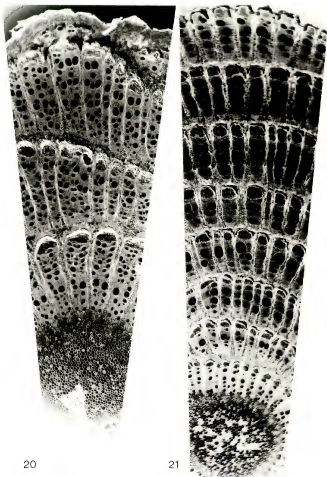
As is seen in TABLE 2, the presence and quantity of a special type of crystal is characteristic of some genera or species; for example the abundance of nearly all types of crystals in *Chondrodendron*, as well as in two species of *Curarea*, *Sciadotenia eichleriana*, *Cissampelos fasciculata* and *C. pareira*, *Hyperbaena*, and *Odontocarya* aff. *wulfschlaegeli*. Small, acicular, spindle-shaped crystals are particularly characteristic of *Borismene* and *Cissampelos* sp.

DISCUSSION

In the Menispermaceae it is not possible to separate the genera on the basis of their wood anatomy. One can, however, suggest tribal characteristics that make it possible to assign material to either the Anomospermeae or the Triclisieae, and perhaps to the Hyperbaeneae. *Borismene*, however, stands by itself.

When this study was initiated with limited material of the tribes Triclisieae and Anomospermeae, it appeared that *Chondrodendron*, *Curarea*, and *Sciadotenia* formed one group and *Abuta*, *Anomospermum*, *Caryomene*, *Orthomene*, and *Teletoxicum* another, as shown in FIGURES 20 and 21. In the Triclisieae the vascular bundles, as seen in cross sections of the stems, are mostly relatively long, narrow, and wedge shaped adaxially, containing numerous vessels of various widths (maximum width usually 250–300 μ m). Besides the three New World genera represented by many samples, a specimen of *Tiliacora funigera*, also belonging to tribe Triclisieae, has the same type of bundles. The Anomospermeae, on the other hand, are characterized by bundles with less radial extension and more rectangular form; the number of vessels is smaller, and some have a larger (300–400 μ m) diameter. The initial impression of two structural types was somewhat altered when more material became available, because individual samples of some species represented by a large number of specimens did not fit the overall picture of the tribes.

The discrepancies among samples are partly due to the different habits of the individual plants, such as shrub or tree versus liana (see below). They may also arise from sampling different portions of a plant—for example, a thick, full-grown stem of a liana or a younger, less-developed flowering branch—particulars that are generally not mentioned on the accompanying labels. In other cases (e.g., with *Chondrodendron microphyllum* (Uw 18061) and *Curarea tecunarium* (Uw 18747) of the Triclisieae, and *Teletoxicum*



FIGURES 20, 21. Transverse sections, $\times 16$: 20, *Sciadotenia paraensis* (Uw 18068), showing pattern characteristic of tribe Triclisieae; 21, *Abuta grisebachii* (Uw 18666), showing pattern characteristic of tribe Anomospermeae.

minutiflorum (Uw 18673) and *Anomospermum bolivianum* (Uw 18672, of the Anomospermeae) no obvious reason could be found for the diverging patterns. Confusion of herbarium and wood samples cannot always entirely be excluded. It is sometimes particularly difficult when collecting material of lianas to sort out the tangled masses of stems dangling from the trees from the flowering or fruiting branches that may be growing farther away. In Gill's material of *Curarea tecunarium* (Uw 18747 = Gill 35), such an error has most likely taken place: not only are the number and the width of the vessels different from those of the other samples (see TABLE 3), but the form of the stem—comma shaped as seen in cross section—is more suggestive of *Abuta* (*Curarea* has very flat, strap-shaped stems). In the other specimens cited above, confusion during collection is not as likely because the data are intermediate between the two groups.

In spite of the exceptions, if one considers the large number of samples seen in both tribes, the impression seems justified that a general anatomic trend exists in each of the two tribes. This trend can be used with some confidence as a means to assign a specimen to one tribe or the other.

A circumscription of these two tribes is not flawless, and the delimitation of the Hyperbaeneae in a similar way is even more uncertain. From the scarce material available, supplemented by data forwarded by the late Dr. L. Chalk for samples of *Hyperbaena domingensis* (a liana) and *H. winzerlingii* (a tree), *Hyperbaena* might be considered to be an intermediate genus. The average number of vessels per bundle is from 15 to 25, and the average size for the widest vessels 150(–200) μm , but often less. The largest vessel size, together with the same average number of vessels per bundle, can also be found in specimens belonging to genera of the Triclisieae, to which members of tribe Hyperbaeneae show the closest affinities.

Structural affinities to the Triclisieae are also shown by species of *Cissampelos*, a genus of the tribe Menispermeae. Of the three stems investigated, two resemble the Triclisieae in number of vessels (average, 25 to 31 per bundle) but differ in having a slightly lower value for the greatest width (ca. 200 μm). A third specimen, Barquero 1970/201, does not conform to the others because only one ring of bundles is formed. Although the diameter of the sample is only 1 cm, in other samples this size a second ring is usually present. Furthermore, the splitting of some of the bundles by radial parenchyma intrusion is indicative of another type of secondary growth. Solereder (1899, citing Hérail) and Schenck (1893) also doubted the constancy of the menisperm type of abnormal secondary growth in some species of *Cissampelos*.

The usual menisperm pattern is also absent in tribe Tinosporeae, which is represented in the New World by four genera. Of these, wood samples were available only for one species of *Odontocarya*, and for *Borismene*, a monotypic genus. Unfortunately, the specimen of *Odontocarya wulfschlaegelii* was very small and was in poor condition due to fungal attack. This species was illustrated and briefly described by Eichler (1864) under the name *Somphoxylon Wulfschlaegeli*. The stem that he saw was of the same diameter as the present sample. In both stems only one ring of bundles has been formed.

The interfascicular rays are very wide—wider than usual in stems of this size. The bundles are nearly triangular, thus resulting in a cross-sectional pattern differing from the one usually present in menisperms. Material of larger-sized stems (if these plants grow any larger—which is questionable since other species described by Barneby (1972) are also stated to have stems ca. 1 cm in diameter) will be necessary for elucidating the problem should the wood structure not follow the usual trend. On the other hand, in *Borismene* (FIGURE 7), the other representative of this tribe, there is clearly another form of secondary growth—one without supernumerary cambia. Radial splitting of the bundles by parenchymatous plates, described above in one sample of *Cissampelos* (Uw 18072) and in *Borismene* (Uw 20524, 25678), was noted by Obaton (1960) for *Rhigiocarya racemifera*, an African liana of the tribe Tinosporeae.

A mode of growth even more similar to that occurring in *Borismene* is shown by the Philippine *Stephania japonica* of the tribe Menispermaceae, recorded by Dipasupil (1955) as having tangential intrusions of parenchyma from the medullary rays. Decaisne (1839) described and illustrated the wood of a half-inch-wide stem of *Menispermum canadense* as having secondary growth normal although with very wide medullary rays.

In the tribe Anamirteae, not represented in the New World, *Anamirta* shows the familiar menisperm structure, although *Coscinium fenestratum* has a normal uninterrupted woody cylinder dissected radially by very wide medullary rays. Apparently in the Anamirteae, the Tinosporeae (including the Fibraureae according to Barneby (1972)), and the Menispermaceae, some species or perhaps genera do not follow the general structural trend, while in the Triclisieae (with the possible exception of *Pycnarrhena manillensis*, studied by Dipasupil (1955)), the Anomospermeae, and the Hyperbaeneae the wood always shows the concentric layers of bundles in cross section.

RELATION BETWEEN HABIT AND ANATOMY

In families that include numerous climbing species among their members, plants of a single species may grow either as a tree or as a liana. In the Menispermaceae this is the case with *Abuta grandifolia*, a species very well represented among our material (see APPENDIX). To correlate variation in anatomic characters with habit, data were compiled for vessel width, length of vessel elements, length of fiber-tracheids, and ratio of these lengths for specimens for which the growth habit was known. The results are shown in TABLE 5.

One of the obvious dissimilarities between the arborescent and the vining specimens of *Abuta grandifolia* is the difference in vessel width, shown in FIGURES 16 and 17: narrower vessels occur in the trees than in the lianas. The length of the vessel elements is about the same in both groups. The fiber-tracheids, on the contrary, show a distinct difference in average length, being longer in the arborescent specimens. Apparently length of the imperforate elements is habit related, while that of the vessel members is not. The ratio of fiber-tracheid length to vessel member length also differs with habit, ranging from 3.7 to 5 for the trees and from 2 to 3.1 for the lianas. In the

TABLE 5. Comparison of *Abuta grandifolia* growing as a shrub or tree and as a liana.

SPECIMEN NUMBER	HABIT	RANGE OF WIDEST VESSELS (in μm)	MEAN LENGTH AND RANGE (in μm)		RATIO OF FIBER- TRACHEID LENGTH TO VESSEL LENGTH
			VESSELS	FIBER-TRACHEIDS	
Uw 1612	Shrub	40-70	350 (170-550)	1400 (1150-1625)	4.0
Uw 3361	Treelet	30-90	350 (150-480)	1660 (1250-1840)	4.8
Uw 3341	Shrub	40-70	320 (180-440)	1296 (1000-1700)	4.0
Uw 18750	Tree	30-120	283 (140-430)	1405 (1050-1950)	5.0
Uw 18753	Tree	110-140	375 (225-540)	1790 (1375-2150)	4.8
Uw 18754	Tree	60-120	294 (150-440)	1560 (900-2250)	5.3
Uw 18755	Tree	40-100	314 (250-500)	1600 (1075-1980)	5.1
Uw 18757	Shrub	30-100	366 (300-485)	1570 (1250-1900)	4.3
Uw 19026	Treelet	70-80	403 (220-750)	1816 (1500-2050)	4.5
Uw 20189	Tree	100-140	386 (210-600)	1412 (920-2000)	3.7
Uw 18736	Liana	150-250	434 (250-550)	880 (500-1400)	2.0
Uw 22771	Liana	120-200	350 (250-470)	933 (650-1200)	2.7
Uw 22804	Liana	130-220	420 (240-550)	1293 (750-1650)	3.1
Uw 23258	Liana	100-300	374 (230-550)	1006 (710-1260)	2.7

wood of the vines, the fiber-tracheids are not only shorter but also have a slightly wider lumen and a slightly thinner wall with more numerous bordered pits, particularly on the tangential walls; furthermore, they are often crooked and twisted. The occurrence of shorter, thin-walled, more densely pitted fiber-tracheids in the vining specimens of *A. grandifolia* is in accordance with the general trend for imperforate elements of climbing dicotyledons, as pointed out by Carlquist (1975). Within a family such differences in trends between lianas and trees are usually encountered in different members of a genus (e.g., *Strychnos*) (Mennega, 1980). In this case it is interesting to observe two trends within the same species.

PHYLOGENETIC TENDENCIES

From an evolutionary point of view, little can be offered. The difficulties of comparing woods (particularly lianas) with abnormal secondary growth with normal wood has been pointed out before (see, for example, Garratt (1933)). Ayensu and Stern (1964), in their paper on the anatomy and ontogeny of the stem of the Passifloraceae, discuss at some length the physiological adaptation of the stem in the climbing species. They consider the broad vessels, the relatively short vessel members, and the presence of fiber-tracheids and tracheids to be related to the special problems of the water-conducting system in lianas. They indicate that the wood structure of the trees of the family must be examined for anatomic modifications related to phylogenetic specialization.

Among the Menispermaceae, as in the Passifloraceae, trees, shrubs, and lianas occur. In the menisperms, however, abnormal structure is present in the arborescent species as well as in the vines. If the species with abnormal growth (in the sense of the presence of supernumerary cambia) are compared to those without it, there are no important differences in the structure of the secondary wood or in the cellular components of the tissues.

The vessels in the arborescent species show only a few indications of a primitive state. For example, scalariform perforation plates—seldom present in lianas (Carlquist, 1975) and therefore hardly to be expected in the climbing species—are not present in the arborescent species. Other indications of a less advanced state, such as scalariform or opposite intervacular pitting, are also absent, and the vessel elements are not particularly long. The predominance of isolated vessels is a primitive character, as are the fiber-tracheids that constitute the imperforate tracheary elements. The absence of rays within the bundles cannot be compared to a complete absence of rays, usually considered to be a character of high specialization, but as Barghoorn (1941) discussed in his paper on the loss of rays and anomalous secondary growth, here it cannot be considered as an indication of specialization. Although rays are very scarce, one or two narrow ones may occasionally be present in the widest bundles of some species, giving the impression that it is the influence exerted by the neighboring cells that induces the formation of some ray tissue.

Thus the Menispermaceae, considered as one of the basal families in most classifications, has few really primitive features in its wood anatomy, unless the wide rays of the species without abnormal secondary growth are considered to be a less advanced character.

RELATIONSHIP WITH OTHER FAMILIES

According to most systems of classification, the Menispermaceae are placed near the Berberidaceae and the Lardizabalaceae in the order Ranales. At first glance, the resemblance between the Berberidaceae and the Menispermaceae is not striking except for the unusual yellowish green color that woods of a number of menisperms from various genera (TABLE I) have in common with the Berberidaceae. However, when other features (e.g., the occurrence and more or less pronounced tangential arrangement of large and narrow vessels, and the large rays composed of irregularly sized procumbent cells, which never border on the vessels) are examined, more similarities between the two families become evident. Also, the pith of the woody members of the Berberidaceae consists of two different layers: a large-celled central core and, on the periphery, smaller cells with thicker, pitted walls. In herbaceous genera of the family (e.g., *Podophyllum*), the vascular bundles are scattered in the pith (Metcalf & Chalk, 1950). The few scattered bundles noticed in the pith of *Borismene* may indicate relationship.

In the Lardizabalaceae the stem anatomy (particularly the form of the bundles, the structure of the pith, and the large medullary rays) of the liana *Akebia* closely resembles that of a young menisperm. However, new cambia are not formed. Another difference is found in the scarcity of the paren-

chyma, which is restricted to a few scattered and occasional paratracheal strands.

Additionally, the large, gashlike pits near the ends of the vessel members, which are so characteristic for all menisperms, are absent in both the Berberidaceae and the Lardizabalaceae. Such pits are, however, known in *Ocotea rodiaei* and *O. venenosa* (Kostermans *et al.*, 1969) of the less closely related Lauraceae.

SIMILARITY IN WOOD PATTERN WITH SPECIES FROM OTHER FAMILIES

The typical menispermaceous pattern as seen in cross section is also present in the lianas of the genus *Gnetum* (Gnetaceae). For example, on inspection with a hand lens, the wood of *G. nodiflorum* matches that of the menisperms quite well; the chief difference is that in *Gnetum* the parenchyma is lacking.

Another species showing some resemblance with menisperms in cross-sectional pattern is *Leretic cordata* of the Icacinaceae. In this liana the vascular bundles are, however, not as regularly arranged, and the fascicular rays between the bundles show a far greater diversity in width. Furthermore, the phloem "caps" are smaller and less sharply demarcated than in the Menispermaceae.

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APPENDIX. Material studied.*

- Abuta brevifolia* Krukoff & Moldenke. BRAZIL: *N. T. Silva* 844 (Uw 18069), 1 × 2 cm; *N. T. Silva* 847 (Uw 18066), 1 × 1.2 cm; *N. T. Silva* 3432 (Uw 18515), 1 × 2 cm; *Prance* 11627 (Uw 18735), 1 × 1.5 cm; *Prance* 12121 (Uw 18737), 3 cm.
- A. candollei* Triana & Planchon. SURINAM: *Pulle* 337 (Uw 10651), 1.5 cm; *van Donselaar* 2364 (Uw 11295), 6 cm; *van Donselaar* 2374 (Uw 11304), 3 cm; *van Donselaar* 2960 (Uw 11948), 3.5 × 6 cm.
- A. colombiana* Moldenke. COLOMBIA: *Cuatrecasas* 14028 (Uw 18758) (type), 30 cm.
- A. fluminum* Krukoff & Barneby. PERU: *J. Schunke* V. 1971/34 (Uw 18619), 3.5 × 5 cm.
- A. grandifolia* (Martius) Sandwith. SURINAM: *Lanjouw & Lindeman* 2098 (Uw 1612), 2.5 cm, shrub; *Lindeman* 4931 (Uw 3361), 3 cm, treelet; *Lindeman* 5076 (Uw 3441), 1.5 cm, shrub; *Lindeman & Heyde* 139 (Uw 22771), 2 cm; *Lindeman & Heyde* 193 (Uw 22804), 1.5 × 2 cm; *Heyde* 651 (Uw 23258), 6 cm. BRAZIL: *Forero* 6321 (Uw 18060), 2 cm; *Krukoff* 7812 (Uw 18668), 5 cm; *Krukoff* 7641 (Uw 18748), 1.5 cm; *Krukoff* 5786 (Uw 20189), material from tree of unknown diameter; *INPA-Manaus X-4100* (Uw 18866), 4.5 cm; *Prance* 12116 (Uw 18736), 3.5 cm; *Prance* 13948 (Uw 19026), 5 cm, tree; *Prance* 18090 (Uw 20890), 2.5 cm. BOLIVIA: *Krukoff* 10954 (Uw 18757), 4 cm, shrub. PERU: *Ll. Williams* 8013 (Uw 18750), 7.5 cm, tree; *Ll. Williams* 3500 (Uw 18753), 8 cm, tree; *Ll. Williams* 4713 (Uw 18754), 6.5 cm, tree; *Ll. Williams* 2435 (Uw 18755), 7.5 cm, tree; *J. Schunke* V. 1970/25 (Uw 18074), 1 cm.
- A. grisebachii* Triana & Planchon. BRAZIL: *Krukoff* 7822 (Uw 18667), 2.3 × 2.5 cm; *Krukoff* 8660 (Uw 18664), 3 × 5.5 cm; *Krukoff* 7960 (Uw 18666). PERU: *J. Schunke* V. 3498 (Uw 20523), 2.5 × 4 cm.

*Unless otherwise stated, material is from lianas. The diameter of the stems is indicated in cm; for asymmetric stems the largest and smallest dimensions of the cross sections are given.

†Sections only.

- A. imene* (Martius) Eichler. SURINAM: *Lindeman 6985* (Uw 4700), 4 cm. BRAZIL: *Krukoff 8605* (Uw 18691), 10 cm. PERU: *Mathias & D. Taylor 3660* (Uw 18520), 2 × 3.5 cm.
- A. obovata* Diels. SURINAM: *van Donselaar 3171* (Uw 12020), 3 × 8 cm. BRAZIL: *Prance 12437* (Uw 18738), 1.5 × 3.5 cm.
- A. pahnii* (Martius) Krukoff & Barneby. PERU: *J. Schunke V. 1970/28* (Uw 18613), 9 cm.
- A. panurensis* Eichler. BRAZIL: *Prance 14973* (Uw 18924), 3.4 × 6 cm; *Prance 11575* (Uw 18734), 0.5 cm.
- A. rufescens* Aublet. FRENCH GUIANA: *Maas, Mennega, & Koek 2188* (Uw 21098), 4 cm. SURINAM: *van Donselaar 3832* (Uw 12356), 1.4 cm; *Maas, Mennega, & Koek 2364* (Uw 21263), 1 cm. BRAZIL: *Krukoff 8030* (Uw 18665), 3 × 6 cm; *Krukoff 10652*^a (Uw 18663); *Krukoff 10866* (Uw 18662), 1 × 2 cm; *Krukoff 10927* (Uw 18661), 4 × 10 cm; *Krukoff 11083* (Uw 18660) (type), no exact dimensions available, stem over 7 cm wide; *Prance et al. 5367* (Uw 18058), 2 × 4.5 cm; *Prance 11036* (Uw 18730), 4.5 cm; *N. T. Silva 3125* (Uw 18079), 5 × 6 cm; *N. T. Silva 3433* (Uw 18519), 1 cm. PERU: *J. Schunke V. 5168* (Uw 18926), 1.5 × 4.5 cm; *J. Schunke V. 1970/23* (Uw 18071), 1.5 × 4.5 cm; *J. Schunke V. 1971/38* (Uw 18623), 1.3 × 6 cm.
- A. sandwihiana* Krukoff & Barneby. SURINAM: *van Donselaar 2928* (Uw 11941), 3.5 cm. BRAZIL: *Prance 12461* (Uw 18739), 1 cm; *Krukoff 7640* (Uw 18756), 3 cm.
- A. solimoensis* Krukoff & Barneby. BRAZIL: *N. T. Silva 842* (Uw 18064), 2 × 4.5 cm. PERU: *J. Schunke V. 5185* (Uw 18927), 3 cm; *J. Schunke V. 1971/31* (Uw 18616), 1.5 × 1.8 cm.
- A. velutina* Gleason. BRAZIL: *Prance & Maas 15185* (Uw 19133), 4 × 8 cm. PERU: *J. Schunke V. 1969/18* (Uw 18076), 2 × 2.4 cm.
- Abuta* sp. PERU: *J. Schunke V. 1971/33* (Uw 18618), 5 × 7 cm.
- Anomospermum bolivianum* Krukoff & Moldenke. BRAZIL: *N. T. Silva 843* (Uw 18056), 1.5 cm; *N. T. Silva 3431* (Uw 18518), 2.3 cm. BOLIVIA: *Krukoff 10773* (Uw 18672) (type), 2.7 cm, climbing shrub.
- A. chloranthum* Diels subsp. *chloranthum*. BOLIVIA: *Krukoff 10639*^a (Uw 18671).
- A. chloranthum* Diels subsp. *occidentale* (Cuatrecasas) Krukoff & Barneby. COLOMBIA: *Cuatrecasas 15628* (Uw 18759), 3 cm.
- A. matogrossense* Krukoff & Barneby. BRAZIL: *Maguire et al. 56807* (Uw 16524) (type), 10 cm.
- A. reticulatum* (Martius) Eichler subsp. *dielsianum* (Moldenke) Krukoff & Barneby. BRAZIL: *Prance 12562* (Uw 18742), 2.5 cm.
- A. reticulatum* (Martius) Eichler subsp. *reticulatum*. PERU: *J. Schunke V. 1970/29* (Uw 18614), 7 × 10 cm.
- A. solimoense* (Moldenke) Krukoff & Barneby. BRAZIL: *Prance 5366* (Uw 18057), 4 cm.
- Anomospermum* sp. BRAZIL: *Krukoff 7565* (Uw 18761), 5 × 7 cm.
- Borismene japurensis* (Martius) Barneby. PERU: *J. Schunke V. 5388* (Uw 20524), 4 cm; *Plowman & J. Schunke V. 7547* (Uw 25678), 3.5 cm.
- Carymene olivascens* Barneby & Krukoff. BRAZIL: *N. T. Silva 3117* (Uw 18070), 2 × 2.5 cm.
- Carymene* sp. PERU: *J. Schunke V. 1970/21* (Uw 18078), 1.5 × 2.5 cm; *J. Schunke V. 1970/26* (Uw 18059), 2 cm.
- Chondrodendron microphyllum* (Eichler) Moldenke. BRAZIL: *Belem 3505* (Uw 18061), 0.6 × 1.5 cm; *Belem 3721* (Uw 18063), 1.5 × 2.5 cm.
- C. tomentosum* Ruiz & Pavon. PERU: *J. Schunke V. 1970/19* (Uw 18073), 3.5 cm. ECUADOR: *Gill 20*^a (Uw 18694); *Gill 1* (Uw 18806), 2 × 3.5 cm.
- Cissampelos fasciculata* Benth. ECUADOR: *Gill 20a*^a (Uw 18695).
- C. pareira* L. Locality unknown: *Anonymous s.n.* (Uw 5437), 2.5 cm.
- Cissampelos* sp. BRAZIL: *Barquero 1970/201* (Uw 18072), 1 cm.

- Cocculus laurifolius* DC. Locality unknown: *Anonymous s.n.* (Uw 5436), 4 cm.
- Coscinium fenestration* Colebrooke. INDIA: *Anonymous s.n.* (Uw 18746), 3 cm. SRI LANKA: *Anonymous s.n.* (MADw 273610, Uw 18752), 5 cm.
- Curarea candicans* (L. C. Richard) Barneby & Krukoff. SURINAM: *Pulle 408* (Uw 13861), 1 × 5 cm; *LBB11304* (Uw 14670), 1 × 2.5 cm.
- C. tecunarianum* Barneby & Krukoff. BRAZIL: *Krukoff 74* (Uw 18678), 1 × 3.5 cm; *Krukoff 7535¹* (Uw 18679); *Krukoff 7576¹* (Uw 18680); *Krukoff 7579¹* (Uw 18681); *Krukoff 7823* (Uw 18682), 1.5 × 2.5 cm; *Krukoff 7824* (Uw 18683), 2 × 6 cm; *Krukoff 7825* (Uw 18684), 2 × 6 cm; *Krukoff 7826* (Uw 18685), 2 × 7 cm; *Krukoff 7828* (Uw 18686), 1.5 × over 7 cm; *Krukoff 8522* (Uw 18687), 2 × 10 cm; *Krukoff 8549¹* (Uw 18688); *Krukoff 8713¹* (Uw 18689); *Krukoff 8370¹* (Uw 18690). PERU: *J. Schunke V. 1970/24* (Uw 18054), 1 × 2.8 cm. ECUADOR: *Gill 6* (Uw 18692), 0.5 × 6 cm; *Gill 12* (Uw 18693), 0.6 × 6 cm; *Gill 35* (Uw 18747), 3 × 6 cm.
- C. toxicofera* (Weddell) Krukoff & Barneby. BRAZIL: *Prance 11272* (Uw 18732), 1 cm. VENEZUELA: *Plowman 7712* (Uw 25681), 3 cm.
- Elephantomene eburnea* Barneby & Krukoff. FRENCH GUIANA: *Oldeman B-3925* (Uw 21079) (type), 1 cm; *De Granville s.n.* (Uw 22251), piece of a trunk of unknown dimensions.
- Hyperbaena* sp. PERU: *J. Schunke V. 1971/35* (Uw 18620), 3 × 3.5 cm; *J. Schunke V. 1971/37* (Uw 18622), 1.5 cm.
- Odontocarya* aff. *wulfschlaegellii* (Eichler) Barneby. BRAZIL: *Prance 12545* (Uw 18741), 1 cm.
- Orthomene prancei* Barneby & Krukoff. BRAZIL: *Prance et al. 5011* (Uw 18062) (type), 0.4 cm.
- O. schomburgkii* (Miers) Barneby & Krukoff. VENEZUELA: *Breteler 3756* (Uw 11758), 3 × 4 cm. PERU: *J. Schunke V. 1970/20* (Uw 18075), 1.3 × 1.7 cm. BOLIVIA: *Krukoff 10923* (Uw 18670), 4 cm.
- Sciadotenia eichleriana* Moldenke. BRAZIL: *Krukoff 8279* (Uw 18658) (type), 5.5 cm.
- S. paraensis* (Eichler) Diels. BRAZIL: *N. T. Silva 841* (Uw 18068), 0.8 × 1 cm; *N. T. Silva 846* (Uw 18067), 0.6 cm; *N. T. Silva 851* (Uw 18065), 1 cm.
- S. solimoesana* Moldenke. BRAZIL: *Krukoff 8243* (Uw 18751), 3 cm; *Krukoff 8385* (Uw 18656) (type), 1 × 2.5 cm.
- S. sprucei* Diels. BRAZIL: *Krukoff 8020* (Uw 18657) (section only); *Prance s.n.*, collected in 1971, under *a* (Uw 18744), 0.5 cm, and *b* (Uw 18745), 0.5 cm.
- S. toxifera* Krukoff & A. C. Smith. ECUADOR: *Gill 11* (Uw 18655), 1.5 × 3 cm. PERU: *J. Schunke V. 5024* (Uw 18925), 2 × 2.5 cm; *J. Schunke V. 1971/30* (Uw 18615), 2.5 × 4 cm; *J. Schunke V. 1971/32* (Uw 18617), 1.6 × 2.5 cm; *Plowman & J. Schunke V. 7537* (Uw 25680), 1 × 2.2 cm.
- Telotoxicum glaziovii* Moldenke. BRAZIL: *N. T. Silva 3120* (Uw 18052), 3.5 cm; *N. T. Silva 3122* (Uw 18053), 5 cm; *N. T. Silva 3423* (Uw 18516), 5.5 × 5.5 cm; *N. T. Silva 3434* (Uw 18517), 5.5 × 6.5 cm.
- T. krukoffii* Moldenke. BRAZIL: *Krukoff 6912* (Uw 8041) (type), over 8 cm. PERU: *J. Schunke V. 1970/27* (Uw 18055), 2.5 cm.
- T. minutiflorum* (Diels) Moldenke. BRAZIL: *Krukoff 7536* (Uw 18673), diameter unknown; *Krukoff 7564¹* (Uw 18676); *Krukoff 7566* (Uw 18677), 2.4 × over 5 cm; *Krukoff 7956* (Uw 18749), 2 × 4.5 cm; *Krukoff 8033* (Uw 18675), 2 × 6 cm; *Krukoff 8840¹* (Uw 18674).
- Telotoxicum* sp. PERU: *J. Schunke V. 1971/36* (Uw 18621), 2.5 × 5 cm.



OBSERVATIONS OF REACTION FIBERS IN LEAVES OF
DICOTYLEDONS

JOHN S. SPERRY

HALLÉ, OLDEMAN, AND TOMLINSON (1978) have discussed the transference of function between compound leaves and plagiotropic branches in the context of tree architecture. In trees conforming to Cook's model (see Hallé, Oldeman, & Tomlinson, 1978), plagiotropic branches resemble compound leaves in their determinate growth and their periodic abscission. Conversely, certain trees (primarily in the Meliaceae) have compound leaves that behave like plagiotropic branches. The rachis of such a leaf grows indeterminately, sometimes reaching lengths of up to 6 m (Sinia, cited in Hallé, Oldeman, & Tomlinson, 1978). The leaves persist on the tree for several years, in some species even forming growth rings in the extensive secondary xylem of the rachis (Skutch, 1946). The present study was stimulated by the observation of another branchlike feature of these leaves—the presence of reaction wood in the rachis. This paper describes reaction fibers in dicotyledonous leaves and presents speculations on the extent to which their function in leaves is similar to their known function in branches.

Reaction fibers have been extensively studied in the secondary xylem of roots and shoots and have been found in primary phloem (Scurfield, 1964) and nonvascular tissue (Staff, 1974). There is strong circumstantial evidence that individual reaction fibers contract during development, generating a contractile force in the axis (Wardrop, 1964). Thus, the distribution of reaction fibers in an axis correlates positively with the distribution of contractile forces in the axis. The contraction associated with the presence of reaction fibers in shoots assists in secondary orientation, and in aerial roots of *Ficus benjamina* L. aids in anchoring the plant (Fisher & Stevenson, 1981; Wardrop, 1964; Wardrop, Tomlinson, & Zimmermann, 1964). Reaction-fiber contraction is probably a consequence of the characteristic structure of the reaction-fiber wall. Scurfield (1973) has proposed a mechanism for this contraction based on the relationship between cellulose microfibril orientation in the layers of the fiber wall and the differential lignification of these layers.

Although the contractile forces involved in secondary orientation are often associated with the presence of reaction fibers, this is not always the case. There are many plant families (e.g., in the order Malvales; Kucera & Philipson, 1977) in which reaction fibers have never been observed. In their investigation of the role of reaction fibers in tree architecture, Fisher and Stevenson (1981) found that pronounced changes in the orientation of woody branches, which are characteristic of certain architectural models, occur in

many tree species that lack reaction fibers. Other modifications of the secondary xylem and/or secondary phloem that correlated with the observed changes in woody-branch orientation were found in most of these species. Thus, the reaction fiber is only one anatomic feature associated with contractile forces and secondary orientation in plants.

Despite the extensive study of reaction fibers, there is apparently no previous account of their occurrence in dicotyledonous leaves. Although Patel (1964), writing on gelatinous fibers in root wood, made brief mention of similar fibers in the petiole of *Cercis* and the leaf rachis of *Caragana*, he gave no details of their origin, distribution, or structure. Extra-xylary reaction fibers have been found in the leaves of the Australian monocotyledon *Xanthorrhoea australis* R. Br. (Xanthorrhoeaceae) by Staff (1974); this is the only known occurrence of reaction fibers in monocotyledons.

Reaction fibers in dicotyledonous leaves could be identified because of their structural similarity to reaction fibers in stems of the same plant. Speculations on the function of these fibers in leaves were based on the observed arrangement of the fibers in the leaf axis; the assumption was made that individual reaction fibers contract by virtue of their structure. The observations presented in this paper indicate that in certain species reaction fibers in leaves appear to function in the same manner as they do in branches and their presence may be correlated with an over-all branchlike appearance and behavior of the leaf; thus, the transference of function between leaf and branch appears to be an anatomic as well as a morphological phenomenon. In the leaves of other species, however, reaction fibers do not function as they do in branches, and there is no obvious modification of the leaf into a branchlike structure; a unique function for reaction fibers in these axes is suggested.

MATERIALS AND METHODS

The species examined are listed in TABLE 1. Transverse sections were cut by hand at various levels of the axes of fresh leaves, and the sections were stained in phloroglucinol and concentrated HCl. Sections were examined under the microscope in normal and polarized light.

Four species (*Rhus typhina* L., *Wisteria sinensis* Sweet, *Cercis canadensis* L., and *Robinia pseudoacacia* L.) were selected for more detailed study. Within a single plant of each species, the reaction fibers in the leaves were compared with those occurring in a branch and were contrasted with fibers in a vertical shoot. Material was fixed in FAA, embedded in paraffin, and sectioned on a rotary microtome at 7 and 10 μ m. Sections were stained with safranin and counterstained with chlorazol black E by a method modified from Robards and Purvis (1964). Some sections were left unstained for observation under polarized light.

Xylem reaction fibers were identified by the presence of a so-called gelatinous or S(G) layer in the secondary wall of the fiber; this unique layer can be distinguished from the first (S_1), second (S_2), and third (S_3) layers of normal xylem fibers. The S(G) layer is typically the innermost layer of the

TABLE 1. Taxa investigated.

TAXON	REACTION FIBERS		LEAF TYPE
	Xylem	Phloem	
Anacardiaceae			
<i>Rhus typhina</i> L.	+	+	Compound
Juglandaceae			
<i>Juglans cinerea</i> L.	-	-	Compound
Leguminosae			
<i>Caragana arborescens</i> Lam.	-	+	Compound
<i>Cercis canadensis</i> L.	+	+	Simple
<i>Delonix regia</i> Bojer	+	+	Compound
<i>Gleditsia triacanthos</i> L.	+	+	Compound
<i>Inga paterne</i> Harms	+	+	Compound
<i>Robinia pseudoacacia</i> L.	+	+	Compound
<i>Wisteria sinensis</i> Sweet	+	+	Compound
Magnoliaceae			
<i>Liriodendron tulipifera</i> L.	-	-	Simple
Meliaceae			
<i>Azadirachta indica</i> Juss.	-	-	Compound
<i>Carapa gualanensis</i> Aublet	+	+	Compound
<i>Cedrela fissilis</i> Vell.	+	?	Compound
<i>Guarea glabra</i> Vahl	+	?	Compound
<i>Swietenia mahagani</i> (L.) Jacq.	-	-	Compound
Oleaceae			
<i>Fraxinus americana</i> L.	-	-	Compound
Rosaceae			
<i>Crataegus</i> sp.	-	-	Simple
Rutaceae			
<i>Phellodendron</i> sp.	-	-	Compound
Simaroubaceae			
<i>Ailanthus altissima</i> (Miller) Swingle	-	-	Compound
Tiliaceae			
<i>Tilia cordata</i> Miller	-	-	Simple
Ulmaceae			
<i>Ulmus americana</i> L.	-	-	Simple

secondary wall and is either a second ($S_2(G)$) or third ($S_3(G)$) layer of the wall. The $S(G)$ layer is unlignified and has a high cellulose content; thus it is unstained in a phloroglucinol/HCl stain and stains black in chlorazol black E. Because cellulose microfibrils in the $S(G)$ layer run axially, the layer is isotropic or slightly birefringent when viewed in transverse section under polarized light (Wardrop, 1964). The $S(G)$ layer is weakly adherent to the adjacent layer, often causing it to pull away in sectioning. A well-developed $S(G)$ layer may be so thick as to occlude the cell lumen.

Phloem reaction fibers were identified by the presence of a secondary wall layer identical in staining, position, adherence, and isotropy to the $S(G)$ layer of xylem reaction fibers. The structural similarity between phloem fibers with this layer and xylem reaction fibers presumably reflects similar contractile

properties and justifies classification of these phloem fibers as reaction fibers. Although the S(G) layer was originally used to denote reference to the "gelatinous" layer of the xylem reaction fibers, Staff (1974) has applied the term to analogous layers in extra-xylary fibers in his description of primary reaction fibers in *Xanthorrhoea australis*; this precedent will be followed in referring to the S(G) layer of phloem reaction fibers.

OBSERVATIONS

GENERAL. TABLE 1 indicates the diversity of taxa in which xylem and phloem reaction fibers were found in the leaves. Although leaf reaction fibers were generally observed in species with large compound leaves, they were not always found in such species (e.g., *Ailanthus altissima* (Miller) Swingle). The seemingly common occurrence of reaction fibers in leaves of the Meliaceae and Leguminosae suggests that, at one level, the presence of leaf reaction fibers correlates more closely with taxonomic grouping than with compound leaf structure or leaf size.

Within the Meliaceae and Leguminosae, however, correlations were observed between leaf size and reaction fiber distribution in the leaf axis. In the Meliaceae the small (rachis < 25 cm) compound leaves of *Swietenia mahagani* (L.) Jacq. and *Azadirachta indica* Juss. lack reaction fibers, whereas the much larger (rachis > 40 cm) compound leaves of *Guarea glabra* Vahl, *Carapa guianensis* Aublet, and *Cedrela fissilis* Vell. have them (see TABLE 1). In these larger compound leaves, reaction fibers (whether in the xylem or the primary phloem) were consistently found on the side of the rachis facing upward with respect to gravity. (This upper side is not always the same as the morphologically adaxial surface of the leaf axis.) Reaction fibers uppermost in the rachis were also observed in *Rhus typhina* (FIGURE 1, A).

In the Leguminosae both large- and small-leaved species have leaf reaction fibers. The distribution of these fibers in the leaf axis, however, varies according to the size of the leaf. The large (rachis 15–25 cm) compound leaves of the tropical species *Delonix regia* Bojer and *Inga paterne* Harms generally have leaf reaction fibers toward the upper surface of the rachis, as do the large leaves of the Meliaceae and *Rhus typhina*. In the smaller-leaved temperate leguminosae (*Wisteria sinensis*, *Caragana arborescens* Lam., *Gleditsia triacanthos* L., *Cercis canadensis*, *Robinia pseudoacacia*) there was no consistent distribution of the leaf reaction fibers with respect to either gravity or the adaxial surface of the leaf axis. FIGURE 1, B shows them scattered above and below with respect to gravity in a rachis of *Wisteria sinensis*. In other small-leaved species they were found in a wide sector of the leaf axis at right angles to the force of gravity, and they occasionally occurred around the entire circumference.

Certain aspects of reaction-fiber distribution in leaves were consistent in all species. Where xylem and phloem reaction fibers occurred together, they were always found on the same side of the rachis, with the phloem reaction fibers occupying the wider sector (see FIGURE 1, A, B). Phloem reaction fibers were always found throughout the length of the rachis; xylem reaction

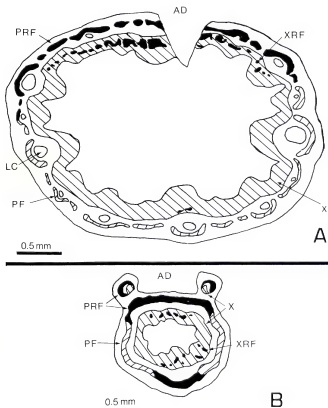


FIGURE 1. Reaction-fiber distribution in leaf axes: A, *Rhus typhina*, proximal section of rachis, notch made to mark upper side prior to sectioning; B, *Wisteria sinensis*, proximal section of rachis. AD = adaxial side of axis (in these examples corresponding with uppermost side of rachis with respect to gravity), PF = primary phloem fibers, PRF = phloem reaction fibers, X = xylem, XRF = xylem reaction fibers, LC = latex canal.

fibers were seen only in the proximal half. Reaction fibers were absent from the pulvinus in all species examined.

RHUS TYPHINA, *WISTERIA SINENSIS*, *ROBINIA PSEUDOACACIA*, *CERCIS CANADENSIS*. Xylem reaction fibers in stems of these species showed similar distributions.

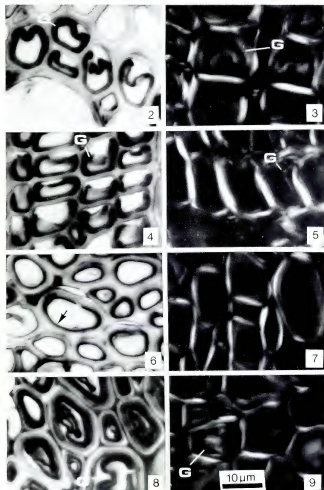
Inclined or horizontal branches had xylem reaction fibers in thick bands uppermost in the axis. Smaller numbers of reaction fibers were found in the xylem of vertical shoots either in a single unilateral band or in bands that overlap radially in wood of different ages. Phloem reaction fibers, although present in the leaves of all four species, were found only in the stems of *Rhus typhina*.

Xylem reaction fibers in the leaves and stems of these four species had the same wall structure. FIGURES 2-5, 10-13, and 20-23 show the S_1 - S_2 - S_3 (G) layering of xylem reaction fibers in leaves and stems. Occasional reaction fibers with an S_1 - S_3 (G) structure were seen in both organs. The birefringence of the S(G) layer varied from slight in the *Rhus* stem (FIGURE 5) and the *Robinia* leaf (FIGURE 11) to nearly as bright as that of the S_2 layer in the *Wisteria* leaf (FIGURE 21). Scurfield and Wardrop (1962) found that in secondary xylem reaction fibers of *Tristania conferta* R. Br. and *Grevillea robusta* A. Cunn., the S(G) layer is birefringent early in development and loses this birefringence as the layer matures. Perhaps the variation in S(G) birefringence observed in the present study has the same explanation. The diameter of reaction fibers varies considerably (compare FIGURES 10 and 22) but does not appear to be correlated with whether the fiber is in a leaf or a stem.

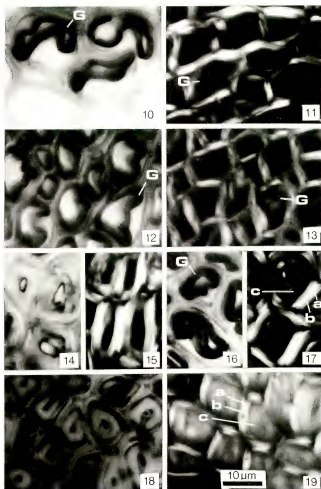
Phloem reaction fibers were primary in origin in these species. Like xylem reaction fibers, they had an S_1 - S_2 - S_3 (G) wall structure (FIGURES 8, 9, 16, 17, 25, 26). The similarity between xylem and phloem reaction fibers is indicated in a comparison of *Robinia* phloem reaction fibers (FIGURES 16, 17) with *Wisteria* xylem reaction fibers (FIGURE 23). Although in the four species investigated phloem reaction fibers generally had larger diameters than xylem reaction fibers, in some cases (e.g., *Rhus* leaf, FIGURE 2) the diameters were equal. As in xylem reaction fibers, the birefringence of the S(G) layer in phloem reaction fibers varied somewhat, perhaps related to fiber development. Some of this birefringence could be due to the rearrangement of the S(G) layer during preparation.

FURTHER OBSERVATIONS OF PRIMARY PHLOEM REACTION FIBERS. Because primary phloem reaction fibers have never been reported from leaves and have only rarely been studied in stems, their occurrence in *Rhus typhina*, *Wisteria sinensis*, *Robinia pseudoacacia*, and *Cercis canadensis* will be described in more detail. In *Rhus typhina*, primary phloem reaction fibers with an identical structure were present in both stems and leaves (FIGURES 8, 9). The two convoluted, black-staining layers evident in FIGURE 8 are typical. Because both layers have the same weak birefringence indicating a common, near-axial microfibril orientation, they are probably laminations of a single S_3 (G) layer. FIGURES 6 and 7 show nonreaction phloem fibers from the underside of a rachis. Although they lack the thick, convoluted S(G) layer of the reaction fibers, they have a thin, adherent, isotropic, black-staining layer (ar-

FIGURES 2-9. *Rhus typhina*, transverse sections. In each pair of illustrations, left photograph shows section stained in chlorazol black in normal light, right shows unstained section between crossed polarizers. G = S(G) layer of reaction fibers. 2, 3,



xylem reaction fibers in rachis; 4, 5, xylem reaction fibers in stem; 6, 7, nonreaction phloem fibers in rachis (arrow in 6 indicates narrow black layer apparently homologous with S(G) layer in reaction phloem fibers); 8, 9, reaction phloem fibers in rachis.



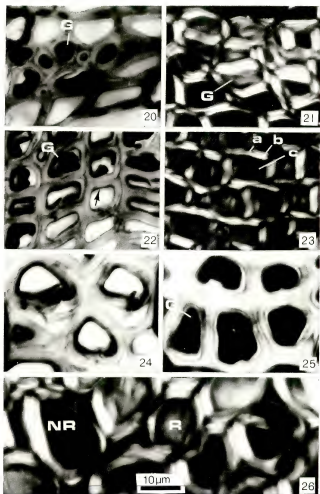
FIGURES 10-19. *Robinia pseudoacacia*, transverse sections. In each pair of illustrations, left photograph shows section stained in chlorazol black in normal light, right shows unstained section between crossed polarizers. G = S(G) layer of reaction fibers. 10, 11, xylem reaction fibers in rachis; 12, 13, xylem reaction fibers in stem;

row, FIGURE 6) that appears from its position and birefringence to be homologous with an S(G) layer. This apparent homology is best seen on the side of the rachis where the two fiber types intergrade. An analogous situation in xylem reaction fibers is shown in FIGURE 22. The arrow indicates a narrow, black layer that is probably homologous to the thick S(G) layers of adjacent fibers.

In a study of primary phloem reaction fibers in stems of *Lagunaria patersonii* G. Don, Scurfield (1964) found that phloem reaction fibers occurring uppermost in inclined branches differed from nonreaction phloem fibers in the underside of the branch only in the greater development within individual reaction fibers of an isotropic, unligified layer. This situation is identical to that in *Rhus typhina*. Scurfield interpreted this to indicate that both reaction and nonreaction phloem fibers conform to the same developmental plan: the nonreaction fiber with its narrow isotropic layer represents an immature state, and the reaction fiber with its thickened S(G) layer represents the mature one. Scurfield suggested that the phloem fibers uppermost in an inclined branch at a given level develop more rapidly than the phloem fibers in the underside of the branch at the same level. This hypothesis was supported by the fact that all primary phloem fibers in the older stems of *Lagunaria patersonii* are reaction fibers. Since this is also true of old stems in *Rhus typhina*, Scurfield's explanation of the origin of phloem reaction fibers in *Lagunaria patersonii* may also apply to these primary fibers in *Rhus typhina*.

In the three leguminous species (*Cercis canadensis*, *Robinia pseudoacacia*, and *Wisteria sinensis*) primary phloem reaction fibers were found only in leaves. Within the leaf the relation of reaction to nonreaction fibers was the same as in *Rhus typhina*: the two fiber types appear to differ only in the degree of development of an S₁ layer (FIGURES 14-17, 24-26). In the leaf the difference between reaction and nonreaction phloem fibers may also be interpreted in terms of rates of development. Primary phloem fibers in the stem, however, are not reaction fibers and apparently develop differently than those in the leaves. FIGURES 14-19 show the difference between primary phloem fibers in the stem and leaf of *Robinia pseudoacacia*. The S₁ layer in the leaf appears to be a G layer of varying thickness that stains black in chlorazol black (FIGURES 14-17), whereas the corresponding layer in the stem is consistently thick and birefringent and stains gray in the same stain (FIGURES 18, 19). Secondary phloem fibers were only sporadically present in the rather small (1-2 cm in diameter) stems examined and were absent from the leaves of all four species. Secondary phloem fibers do occur in the leaf rachis of some Meliaceae (J. Fisher, pers. comm.).

14, 15, nonreaction phloem fibers in rachis; 16, 17, reaction phloem fibers in rachis (in 17, a = very birefringent S₁ layer, b = moderately birefringent S₂ layer, c = weakly and unevenly birefringent S₃(G) layer); 18, 19, phloem fibers in stem (in 19, a = S₁ layer, b = S₂ layer, c = S₃ layer). Note difference in wall structure (especially birefringence and form of S₃ layer) between stem phloem fibers in 14-17 and leaf phloem fibers in 18, 19.



FIGURES 20-26. Transverse sections. 20-23, *Wisteria sinensis*: 20, 21, xylem reaction fibers in rachis; 22, 23, xylem reaction fibers in stem (in 23, a = very birefringent S₁ layer, b = birefringent S₂ layer, c = weakly birefringent S₃(G) layer). 24-26, *Cercis canadensis*, petiole: 24, nonreaction phloem fibers; 25, reaction

DISCUSSION

The observation of xylem and phloem reaction fibers in leaves raises the question of how their functions compare in leaves and shoots. In this context observations concerning reaction-fiber distribution in leaves and shoots are relevant. In shoots examined in this study, reaction fibers were found where their contraction could assist either in holding branches at a given position or in maintaining the position of vertical axes. This is consistent with the general finding that stem reaction fibers function in secondary orientation. Orientation seems to be the function of reaction fibers in some leaves but not in others.

The consistent distribution of leaf reaction fibers uppermost in the rachis of the larger-leaved species in the Leguminosae and the Meliaceae, as well as in *Rhus typhina*, argues for an orientation function for leaf reaction fibers in these species; a branchlike distribution of reaction fibers is correlated with the maintenance of the horizontal position of the leaf. Although reaction fibers were absent from the pulvinus of these species, this area is sufficiently rigid and broad based in each species to provide a fixed support for the rachis. A rigid connection with the parent axis makes it possible for the reaction fibers in the rachis to aid in the horizontal positioning of the leaf.

The apparent participation of reaction fibers in the transference of function between leaf and branch in these large compound leaves is especially evident in *Guarea glabra* (Meliaceae). In this species the branchlike distribution of reaction fibers in the rachis is accompanied by other branchlike features of considerable secondary growth, indeterminate extension growth, and prolonged longevity. It is interesting to note that there are very few reaction fibers in the highly modified, leaflike branches of *Phyllanthus acidus* Skeels and *P. grandifolius* L. (Euphorbiaceae—pers. obs.).

In discussing the role of reaction fibers in the transference of function between leaf and branch, it is important to remember that not all branches and large compound leaves have reaction fibers. Reaction fibers were not found in the large leaves of *Ailanthus altissima* or *Juglans cinerea* L. (TABLE 1), and they appear to be absent from several woody plant families (Kucera & Philipson, 1977). In plants or parts of plant framework that lack reaction fibers, there can be other anatomic features that generate the contractile forces required to control secondary orientation (see Fisher & Stevenson, 1981). Reaction fibers represent a branchlike modification in leaves only if they are also present in the branches of the same plant.

In addition to assisting in the maintenance of leaf orientation with respect to gravity, reaction fibers in the larger, pinnately compound leaves of *Inga paterne* (Leguminosae) may have consequences for another aspect of leaf positioning. Due to the highly variable orientation of the parent axis, the adaxial surface of the rachis often faces as much as 90 to 180 degrees away

phloem fibers; 26, nonreaction (NR) and reaction (R) phloem fibers. 20, 22, 24, 25, sections stained in chlorazol black, photographed in normal light; 21, 23, 26, unstained sections between crossed polarizers; G = S(G) layer in reaction fibers.

from its upward-facing surface. Between the rachis base and the first few leaflet nodes, however, the rachis is frequently twisted so that the adaxial and uppermost surfaces nearly coincide. This orientation results in the full display of leaflets to the sun. Throughout the twisted rachis, reaction fibers occur in the uppermost sector. This naturally suggests that reaction fibers may aid in maintaining the leaf at a given position with respect to gravity. However, the reaction fibers are distributed in a spiral opposite to that of the twist in the rachis. The contraction of reaction fibers distributed in this fashion may thus also aid in maintaining the twist. Developmental studies are needed to clarify whether the twist in the rachis is primary and is later reinforced by development of reaction fibers, or if the reaction fibers themselves effect a reorientation in the axis.

The relationship between reaction fibers and the orientation of branchlike axes does not seem to apply to the presence of reaction fibers in the smaller leaves of the Leguminosae studied (*Wisteria sinensis*, *Robinia pseudoacacia*, *Cercis canadensis*, *Caranga arborescens*, *Gleditsia triacanthos*). Reaction fibers were not only inconsistently distributed with respect to the upper side of horizontally positioned leaves and often positioned on opposite sides of the axis at a given level, but were also found in quantity in leaves that were hanging vertically. This circumstantial evidence suggests that reaction fibers are not influential in leaf orientation; developmental evidence would be necessary to substantiate such a conjecture. Active orientation, although apparently not mediated by reaction fibers, does occur in these leaves, as indicated by the great variation in the angle that different leaf axes make with the stem; it is probably controlled by the flexible, cylindrical pulvini, which lack reaction fibers. Pulvinal action is probably a more responsive mechanism of orientation than reaction-fiber contraction for these medium-sized leaves. The inconsistent distribution of reaction fibers with respect to gravity in these leaves, as well as the absence of any secondary orientation of the leaf axis that can be correlated with reaction-fiber distribution, suggests that their distribution might produce a balanced tension in the slender leaf axis (assuming that the fibers differentiate concurrently), which might help to provide a firm support for the leaf. In contrast to their apparent function in the secondary orientation of larger leaves in both the Leguminosae and the large-leaved species of the Meliaceae, this possible function of leaf reaction fibers in small-leaved leguminous species does not resemble the function of reaction fibers in branches.

The presence of reaction fibers in leaves provides another example of the independent and flexible relationship between tissues and organs in plants. In large compound leaves, most strikingly those of *Guarea glabra*, distribution of reaction fibers like that found in branches accompanies morphological modifications of the leaf into a branchlike structure. Conversely, in the small-leaved Leguminosae studied, the distribution of reaction fibers in the leaf axis is not similar to that in branches and may serve a unique function in the context of the morphology of typical leaves. In addition, the entire absence of reaction fibers in the branches and large compound leaves of many species exemplifies the flexible relationship between structure and function

in plants. The control of secondary orientation is evidently related to more than one anatomic structure.

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THE TAXONOMY AND CHEMISTRY
OF PINUS ESTEVEZII

J. P. PERRY, JR.

IN HIS ORIGINAL DESCRIPTION of *Pinus pseudostrobus* var. *estevezii* Martínez, Martínez (1945, p. 188) pointed out that "this pine, from its general aspect, resembles *P. pseudostrobus* Lindl. and *P. montezumae* Lamb. but presents some characteristics, principally in the cone, that in my opinion merit its consideration as a variety of the first" (author's translation). Loock (1950) generally followed Martínez's description of *P. pseudostrobus* var. *estevezii* and also noted (p. 156) that the species is "related to both *P. montezumae* and *P. pseudostrobus*, but more closely to the latter in that the bark of the young trees and upper part of the stems is smooth." Zobel and Cech (1957) collected *P. pseudostrobus* var. *estevezii* in the state of Nuevo León and noted the difficulty they experienced in classifying the five-needled hard pines, primarily because of the many intermediate or intergrading forms. Gausson (1960) elevated *P. pseudostrobus* var. *estevezii* to specific status, but the change in rank is invalid since he did not refer to the original publication. Mirov (1961) followed Martínez and Loock in his treatment of *P. pseudostrobus* var. *estevezii*. Shaw (1909, 1914), Standley (1929), Miranda and Hernández (1963), Rojas-Mendoza (1965), Critchfield and Little (1966), and J. Rzedowski (1978) made no mention of the variety.

In this paper both morphological and biochemical characteristics are used as a basis for elevating *Pinus pseudostrobus* var. *estevezii* to specific rank. There is now considerable precedence for such an approach. Mirov (1948, 1958, 1961), Zobel (1951), Williams and Bannister (1962), Smith (1967), and Rockwood (1973) used chemical composition of turpentine as an important diagnostic character in their studies of different species of pines, their hybrids, and their classification. Evidence (discussed below) that I have collected from numerous field observations, morphological studies, and chemical analyses of stem oleoresins from *Pinus montezumae*, *P. pseudostrobus*, and *P. pseudostrobus* var. *estevezii* strongly indicates that var. *estevezii* should be considered as a distinct species.

***Pinus estevezii* (Martínez) Perry, comb. et stat. nov.**

FIGURE 1.

Pinus pseudostrobus var. *estevezii* Martínez, Las Pinaceas Mexicanas 1: 188-192, figs. 158-160, 1945. TYPE: Mexico, Nuevo León, Santa Catarina, Cañon de las Mieleras, June, 1941, Martínez 3433 (holotype, MEXU).

Tree 15-20 m tall, d.b.h. .75-1 m; branches large, often rather low on



FIGURE 1. *Pinus estevezii* growing near town of Iturbide, Nuevo León, Mexico.

stem, horizontal to slightly ascending, crown often dense and rounded. Bark on mature trees reddish brown, thick, divided into longitudinal plates by deep vertical and horizontal fissures. In young trees upper part of stem quite smooth since bases of needle bracts not decurrent and soon merging into bark. Leaves in fascicles of 5 (rarely less), bright green, 20–30(–35) cm long, ca. 1 mm thick, stiff, edges finely serrate; stomata present on all 3 faces; hypoderm irregular, 2 to 4 layers of cells with many shallow penetrations into chlorenchyma; resin canals 3 to 5, medial; endodermis with thickened outer cell walls; vascular bundles 2, quite distinct; fascicle sheath ca. 20 mm long, persistent, pale brown, not gummy or resinous. Conelets erect, reddish purple, subterminal, solitary or borne 2 to 4 together; scales thick, bearing strong, up-curved prickle. Cones yellowish brown to brown, 10–13 by 7–8 cm, long-ovoid or conoid, asymmetric, often reflexed (occasionally erect and symmetrical); opening at maturity, generally in December and January; borne on thick, strong peduncles ca. 1 cm long that remain attached to branchlet along with few basal cone scales when cone falls. Scales hard, strong, 25–30 by 12–15 mm, apex slightly rounded to pointed, apophysis subpyramidal, with prominent transverse keel, the umbo raised, prominent, grayish, armed with strong, persistent prickle most often curved upward

(FIGURE 2). Seeds dark brown, ovoid to long-ovoid, 6–7 mm long; wing detachable, brown, ca. 25 by 7–9 mm.

TYPIFICATION

In his original description of *Pinus pseudostrabus* var. *estevezii*, Martínez (1945, p. 189) stated "habitat in Cañon de las Mieleras, Santa Catarina, Nuevo León, Typus in Herb. Instituto de Biología, Mexico"; he did not specify a date or a collection number. His illustrations were apparently taken from the type specimen. He also cited (p. 191) collections from "Sierra de Santa Catarina, N.L. en los Picachos de Sabinas, N.L. y en Los Lirios, Arteaga, Coah."; collectors' names and numbers were again not given. While in Mexico City in 1979, I found a specimen at the Herbario Nacional del Instituto de Biología, Universidad Nacional Autónoma de México, bearing a glued label that reads (handwritten) "*Pinus pseudostrabus* var. *Estevezii* Martínez; Cañon de Mieleras, Sta. Catarina, N.L. var. nova, tipo, Junio 1941, Num: 3433" and (printed) "Prof. Maximino Martínez." This specimen, consisting of a single branchlet bearing needles and two mature, open cones, can reasonably be considered the holotype of *Pinus pseudostrabus* var. *estevezii* Martínez.

DISTRIBUTION

I have collected and observed *Pinus estevezii* in the type locality. In Nuevo León I have also seen it northeast of Galeana, near the village of Dieziocho



FIGURE 2. *Pinus estevezii*: cones, conelets, foliage, and branchlets.

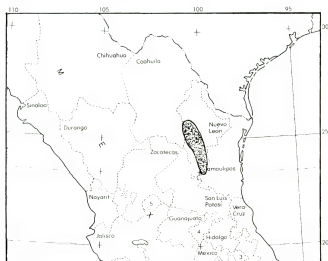
de Marzo, at the foot of Cerro Potosí in association with *P. cembroides* Zucc., *P. arizonica* Engelm. ex Rothr. var. *stormiae* Martínez, and south of Zaragoza. In 1978 I collected it in the state of Tamaulipas at 1800 m alt. near the dirt road from Palmillas to Miquihuana. This was a small, scattered stand of trees growing in association with *P. cembroides* and *Quercus* spp. At all of these locations the site was generally dry, rocky, and overgrazed.

Loock (1950) and Mirov (1967) reported *Pinus estevezii* occurring in the states of Coahuila and Nuevo León. Zobel and Cech (1957) collected *P. estevezii* west of Iturbide, Nuevo León, and Mittak (pers. comm.) reported a collection (Mittak 8921) from 47 km west of Linares, Nuevo León, at 1420 m alt. Other records of the species are as follows: Mexico, Nuevo León: Dulces Nombres, and E to border into Tamaulipas, 1800 m, *F. G. Meyer & D. J. Rogers* 3087 (GH); Sierra Madre above Monterrey, 770–1220 m, *Pringle* 10170 (GH); Sierra Madre, Monterrey, *C. H. Mueller & C. T. Mueller* 33 (A).

Thus the range of *Pinus estevezii* extends from near the city of Monterrey, south along the Sierra Madre Oriental, into the southeastern corner of the state of Tamaulipas near the town of Miquihuana (MAP 1).

DISTINCTION BETWEEN *PINUS ESTEVEZII*, *P. MONTEZUMAE*, AND *P. PSEUDOSTROBUS*

Martínez (1945) and Loock (1950) agreed regarding differences between the cones, stems, and branchlets of *Pinus pseudostrobus* and its variety *es-*



MAP 1. Distribution of *Pinus estevezii* in Mexico.

tevezii (see Martínez, 1945, pp. 190, 191, *figs. 159, 160*; Loock, 1950, pp. 156, 157, *pl. A*). Loock (1950) showed the differences between branchlets of *P. montezumae* and *P. pseudostrobus*, and between the cones and cone scales of *P. pseudostrobus* and its varieties.

Regarding differences between *Pinus pseudostrobus* var. *estevezii* and *P. montezumae*, both Loock and Martínez stressed that in *P. montezumae* bases of the leaf bracts are decurrent, leaving the branchlets and stems of young trees very rough and scaly, while in *P. pseudostrobus* var. *estevezii* (hereafter in this paper referred to as *P. estevezii*) the leaf bract bases on stems of young trees are not decurrent and soon merge into the bark, leaving the stems smooth (FIGURE 3). On the older branchlets of *P. estevezii*, leaf bract bases are raised and prominent, but they are neither scaly nor as rough as in *P. montezumae*.

There are other differences between the three taxa. Mature trees of *Pinus estevezii* rarely attain a height of 20 m, and the crowns are generally low and broad, often with the lower branches extending almost to the ground. In sharp contrast, both *P. pseudostrobus* and *P. montezumae* attain heights of 30–40 m and have characteristically long, clear boles and rounded crowns. In addition, bark of *P. estevezii* is reddish brown and furrowed by deep fissures into long, rectangular plates; that of mature *P. montezumae* and *P. pseudostrobus* is dark grayish brown and has smaller plates.

Differences between the cones of *Pinus pseudostrobus* and *P. estevezii* are generally quite consistent. Cones of *P. pseudostrobus* range in length from 8 to 10 cm, while those of *P. estevezii* are 10–13 cm. Cone scales of *P. pseudostrobus* are not as stiff and strong as those of *P. estevezii*. Apophyses



FIGURE 3. Above, *Pinus montezumae*, decurrent leaf bract bases on stem of young plant. Below, *P. estevezii*, nondecurrent leaf bract bases. Both $\times 0.9$.

TABLE 1. Summary of differences between *Pinus estevezii*, *P. pseudostrobus*, and *P. montezumae*.

CHARACTER	SPECIES		
	<i>P. estevezii</i>	<i>P. pseudostrobus</i>	<i>P. montezumae</i>
CONES	10-13 by 7-8 cm, long-ovoid or conoid	8-10 by 5-7 cm, generally ovoid	13-15 by 7-10 cm, ovoid or conoid
CONE SCALES	Hard, strong, thick; apophyses raised to subpyramidal, with prominent transverse keel; umbo raised, armed with strong, persistent prickles, generally curved upward toward apex	Neither as hard nor as thick as in <i>P. estevezii</i> ; apophyses slightly keeled; umbo small, occasionally depressed, armed with small, deciduous prickles	Scales hard, strong, thick; apophyses raised, subpyramidal, with strong transverse keel; umbo slightly raised, armed with small, deciduous prickles
LEAVES			
DIMENSIONS	20-30(-35) cm long, 1 mm thick	20-25(-30) cm long, ca. 0.7 mm thick	15-25(-30) cm long, 0.7-1 mm thick
HABIT	Stiff, erect	Slender, flexible, generally drooping	Variable from slender and flexible to stiff and erect

INTERNAL STRUCTURE	Hypoderm irregular, with many shallow penetrations into chlorenchyma; resin canals 3 (to 5), medial	Hypoderm uniform to irregular, with few shallow penetrations into chlorenchyma; resin canals 2 or 3 (or 4), medial	Hypoderm uniform to irregular, with few slight penetrations into chlorenchyma; resin canals 3 to 5 (or 6), medial
STEM OF YOUNG TREE	Smooth; bases of leaf bracts not decurrent, merging into bark, leaving stem smooth	Smooth; bases of leaf bracts not decurrent, merging into bark, leaving stem smooth	Rough; bases of leaf bracts decurrent, leaving stem rough and scaly
FORM OF MATURE TREE	15-20 m tall; often with large, low branches; crown dense, broadly rounded	30-40 m tall; stem clear; crown narrow, rounded	30-40 m tall; stem clear; crown narrow, rounded
TURPENTINE	Usually high amounts of heptane and small amounts of nonane; often with high α -pinene; sometimes with high myrcene, limonene, methyl chavicol, and β -phellandrene	Usually with very high amounts of α -pinene, rarely with high myrcene; heptane, octane, and nonane usually absent	Usually with very high amounts of α -pinene, rarely with high myrcene; heptane, octane, and nonane usually absent
ALTITUDINAL RANGE (m)	800-1800	1600-3200	1700-3400

of *P. estevezii* cones are strongly keeled, while those of *P. pseudostrobus* are not. The prickles of *P. pseudostrobus* scales is small, weak, and early deciduous; that of *P. estevezii* is prominent, curved upward, and persistent.

The cones of *Pinus montezumae* are slightly longer than those of *P. estevezii* (13–15 cm vs. 10–13 cm). Cone scales in both species are hard, strong, and thick, with apophyses raised to subpyramidal. However, the umbo is armed with a small, deciduous prickle in *P. montezumae*, but with a strong, persistent prickle that is generally curved upward in *P. estevezii*.

Differences in altitudinal range are also quite marked. *Pinus estevezii* is generally found growing at 800–1500 m alt., while *P. pseudostrobus* usually occurs at 1600–3200 m, and *P. montezumae* at 1700–3400 m. TABLE 1 summarizes the differences between the three species.

RELATIONSHIPS OF *PINUS ESTEVEZII*

Both Martínez (1945) and Loock (1950) postulated a close relationship between *Pinus pseudostrobus*, *P. estevezii*, and *P. montezumae*. Martínez (1945) showed the relationships between the Montezuma, Ponderosa, and Pseudostrobus pine groups. His fig. 169 shows *P. pseudostrobus* var. *estevezii* and *P. pseudostrobus* var. *coatepecensis* Martínez forming a connecting link between the *P. pseudostrobus* and *P. montezumae* groups. Mirov (1967) referred to three great pine complexes of America: A, the *P. ponderosa* Lawson complex; B, the *P. montezumae* complex; and C, the *P. pseudostrobus* complex. His fig. 9-4, almost identical to Martínez's fig. 169, also showed *P. pseudostrobus* var. *estevezii* and *P. pseudostrobus* var. *coatepecensis* forming connecting links between the *P. pseudostrobus* and *P. montezumae* groups.

In an effort to clarify these relationships, I collected samples of xylem oleoresin from trees of *Pinus pseudostrobus*, *P. montezumae*, and *P. estevezii*. These have now been analyzed, and the results are shown in TABLE 2. Information regarding collection and analysis of the oleoresins is given in the APPENDIX.

It can be seen that turpentine of *Pinus estevezii* has an entirely different composition than that of *P. pseudostrobus* and *P. montezumae* (TABLE 2). Turpentine of *P. pseudostrobus* and *P. montezumae* is almost entirely α -pinene. In both species there were a few trees with a large proportion of myrcene. In sharp contrast, *P. estevezii* consistently had high heptane and a smaller but very consistent percentage of nonane. These light hydrocarbons were found in neither *P. pseudostrobus* nor *P. montezumae*. In addition, there were trees of *P. estevezii* with significant amounts of five other compounds: α -pinene (61% of the trees had high amounts); myrcene (30%); limonene (8%); β -phellandrene (15%); and methyl chavicol (15%).

These are the first published data on analyses of turpentine from *Pinus estevezii*. However, Iriarte (1946) analyzed the turpentine of *P. pseudostrobus* from Mexico and found it to consist almost entirely (over 90%) of d- α -pinene, and this was confirmed by Brummer's (1978) analysis of turpentine from Guatemalan specimens. Both investigators reported a complete absence of the light hydrocarbons (heptane, octane, and nonane).

TABLE 2. Turpentine composition* of xylem oleoresin from *Pinus estevezii*, *P. pseudostrobus*, and *P. montezumae*.

Species	Sample number	Heptane	Octane	Nonane	α -Pinene	Camphene	β -Pinene	β -Caryophyllene	α -Terpinene	Limonene	β -Phellandrene	β -Cymene	Terpinolene	α -Fenchol	Terpinolene-4-ol	β -Caryophyllene	Methyl chavicol	α -Terpinol
<i>P. estevezii</i>	H1	69		12	5	4	2	1	1									
	H2	36		18	14		TR ¹	1	26									6
	H3	24	6	8	4			2	1	23								3
	H4	30	12	13	5			3	1	13		26	3					2
	H5	15	6	7	22	3	4	3	35		15		4					4
	H6	49		18	15				3		TR		2					3
	H7	33		10	5	4	TR		1		7							2
	H8	46		9	25	5	4		2	1	1							10
	H9	42	9	6	11	4	6	2	3		2							7
	H10	40		11	28	4	4	TR	3		1							13
	H11	27		6	53		6		2		TR	1						8
	H12	49		16	18	4	3											6
	H13	28		11	38	5	7		5		1							8
	H14																	6
% High ¹		100	0	55	61	0	0	0	30	8	15	0			0	15		
<i>P. pseudostrobus</i>	1				58	1	2	2	31			TR						1
	2				81	1	TR	1	12		TR							1
	3				83	1	5	TR	6		4							1
	4				57	1	3	2	29		TR							2
	5				91	1	TR	1	2		1							2
	6				94	1	TR	1	3		1							2
	7				92	1	3	1	3		1							1
	8				92	1	3	1	3		1							1
	9				68	1	3	2	22		1	TR	1					TR
	10				87	3	3	1	3		1							1
% High ¹					89	1	3	1	3		1	TR			1			1
% High ¹					100	0	0	0	40	0	0	0	0	0	0	0	0	0
<i>P. montezumae</i>	M150			86	6	2	3			2								
	M152			96	2	1												
	M153			92	3	2	1		1		TR							1
	M154			89	5	2	1		1		TR							2
	M155			70	2	1		19		6								
	M158			98	2													
	M160			92	4	2	1		1		TR							1
	M161			91	4	2	1		1		TR							TR
	M162			89	3	2	1		5		TR							TR
	M163			93	1	5												
% High ¹					100	0	0	0	10	0	0	0						0

*Percent of total terpenes.

¹Percent of trees having relatively high amounts.²TR = trace.

Both Iriarte (1946) and Mirov (1951) reported that turpentine collected from *Pinus montezumae* from the state of Michoacán, Mexico, was 96–98% d- α -pinene. Neither author reported the presence of any light hydrocarbons.

More recently, with the development of gas chromatography, studies of the chemical composition of pine turpentine have greatly expanded. Squillace (1976) provided an outstanding summary of investigations in this field and noted (p. 120) that "genetic studies have shown that monoterpene composition varies greatly among trees within species and is strongly inherited." He also pointed out (p. 121) that "high versus low levels of some monoterpenes are controlled by single genes. Such traits are very useful as gene markers for identification of hybrids and relatives and for studies of the degree of natural inbreeding and of population structure."

As noted earlier in this paper, Martínez (1945), Loock (1950), and Mirov (1967) stated that *Pinus estevezii* is closely related to *P. pseudostrobus* and *P. montezumae*. However, the distinctive chemical differences between its turpentine and that of *P. montezumae* and *P. pseudostrobus* clearly rule out the possibility of a hybrid origin of *P. estevezii* involving *P. montezumae* or *P. pseudostrobus* as the parental species.

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APPENDIX. Collection and analysis of oleoresins.

COLLECTION

Samples of xylem oleoresin were collected from 14 trees of *Pinus estevezii* growing near the highway from Linares to Galeana, 2 km west of Iturbide, Nuevo León, Mexico. This was an open, rather scattered stand of pines at 1650 m alt. on gravelly-rocky, heavily grazed slope. No other species of pines was associated with this group. The trees sampled were 35-70 cm d.b.h. and 15-20 m high. A hole ca. 0.5 cm in diameter was drilled into the stem of each tree about 75 cm from the ground (October 25, 1978), and a threaded glass vial was immediately screwed tightly into the hole. The next day the vials were collected and each one was covered with a threaded, gasketed cap. Resin flow from all trees was abundant and uniformly pale amber in color. Specimen number *J. P. Perry MEX 78-1043* was collected as a composite voucher for these trees and has been deposited in the herbarium at nsc.

Samples of xylem oleoresin were collected from *Pinus pseudostrobus* trees by Biol. Xavier Madrigal Sanchez at Puenteillas near the village of Dos Aguas, Coalcomán, Michoacán, Mexico. The trees were growing on a gravelly clay slope at 2370 m alt. Associated species were *Pinus michoacana* var. *cornuta* Martínez, *Pinus douglasiana* Martínez, and *Quercus* spp. The sample trees were 30-54 cm in diameter and 25-30 m high. The sampling procedure was the same as for *P. estevezii*. Vials were placed on ten trees on February 8, 1979, and were collected on February 12. Resin flow from all trees was abundant and uniformly clear white in color. *X. Madrigal Sanchez CIFO 3226* (deposited at the herbarium of the Centro de Investigación Forestal Oeste, Uruapan, Michoacán, Mexico) was collected as a voucher for the trees.

Samples of xylem oleoresin were collected from ten *Pinus montezumae* trees growing near the Mexico City-Toluca highway, adjacent to the federal park, Desierto de Los Leones, México, D. F. This was a fully stocked stand of mature trees growing at 2750 m alt. in a gently sloping area of deep volcanic soil. Associated tree species were *P. patula* Schlecht. & Cham., *Abies religiosa* (H.B.K.) Schlecht. & Cham., and *Quercus* spp. The ten sample trees were 40-60 cm in diameter and 25-35 m high. Oleoresin samples were obtained in the same manner as those taken from *P.*

estevezii and *P. pseudostrobus*. Vials were placed on the trees on January 27, 1980, and collected on January 29. Resin flow from all trees was abundant and uniformly clear white in color. *J. P. Perry MEX-150* was collected as a composite voucher for these trees and has been deposited in the herbarium at NSC.

ANALYSIS

Most of the analyses were performed by a single chemical consulting laboratory; however, a few samples were analyzed by another laboratory. The following gas chromatographic conditions and equipment were used for analysis of most of the pine resin samples.

Turpentine from each sample was separated from the resin and extraneous matter by steam distillation (kept alkaline to prevent acid isomerization).

The chromatograph used was a Varian Series 1700 with a thermal conductivity detector. A stainless steel column $10' \times \frac{1}{8}"$ diameter packed with 15% carbowax 20M on "chromosorb W" was injected with 1.5 μ l of sample. Injector temperature was 210°C, detector temperature 225°C, and the column oven programmed from 75° to 220°C with a 4°C/minute temperature rise. The carrier gas used was helium.

Samples were identified by comparison of elution times and relative positions against standard chromatographs made from combinations of pure compounds. When a question arose as to the identity of a compound, the sample was "spiked"—i.e., reshot with known components added until the presence of overlapping peaks or increase in peak size eliminated any uncertainty.

For the few samples sent to another laboratory, the gas chromatographic conditions and equipment used were as follows:

Gas chromatograph: Perkin Elmer 3920

Columns: 50' stainless-steel support, open tubular columns coated with SP-2100 or OV-17

Carrier gas: helium at 10 psi

Initial temperature: 30°C

Program rate: 8°C/minute

Final temperature: 200°C with infinite hold

Injector temperature: 250°C

Detector temperature: 250°C

Data acquisition with a Spectro-Physics AutoLab System 1 or a Perkin Elmer Sigma 10

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MORE ADDITIONS TO THE FLORA OF JAMAICA

GEORGE R. PROCTOR

THE PUBLICATION of C. D. Adams's *Flowering Plants of Jamaica* in 1972 was an important milestone in the history of Jamaican botany. Among its useful contributions to knowledge was the enumeration and description of some 2888 species of flowering plants either indigenous to Jamaica or considered to be fully naturalized. It was stated in the Introduction (p. 22) that 784 (27%) of these "are in the state of our present knowledge thought to be endemic to the island." It was further stated (p. 24) that "some additions to the flora are inevitable in the future," but that "the main phase of exploration is virtually closed." While this may be generally true (and unusually so for a tropical country), the local distribution of native plants is so remarkably complex, and often so narrowly localized, that until virtually every wooded hilltop, cliff-face, mossy woodland, boggy wetland, dry thornscrub, or other special habitat has been thoroughly examined at different seasons of the year, our knowledge of the Jamaican flora will be incomplete. Further, anyone who makes really thorough collections in any more or less undisturbed or uncollected habitat, particularly at favorable seasons (which may not occur every year!), is likely to turn up new records and even species new to science. In this context, we still do not have a complete inventory of the Jamaican vegetation, and we do not yet have adequate knowledge of the local distribution of many individual species. It is surprising how many species are recorded on the basis of but one collection. For these reasons I have continued to investigate new localities, to revisit old ones, and to collect fresh material for the Institute of Jamaica Herbarium. The present publication arises from this work and summarizes a portion of the new information that has accumulated since 1972; it also includes a few overlooked or unpublished older records. It can be considered an informal supplement to Adams's volume.

A few of the new species proposed herein were included without names (for example, as "sp. A" or "sp. B") under various genera in *Flowering*

Plants of Jamaica. Their publication is long overdue. However, not all the taxa in this category can be dealt with at the present time.

This paper, as its title suggests, is a sequel to one that I published in 1967, and it has a somewhat similar format. The sequence of families, however, has been altered to conform with that of *Flowering Plants of Jamaica* (Adams, 1972). All specimens cited are deposited in the Institute of Jamaica Herbarium (IJ), unless indicated otherwise. Duplicates of most of these, and several cited holotypes, can be found in the Harvard University Herbaria (A and GH).

As a matter of statistical interest, this paper adds 2 families, 14 genera, 115 species, and 6 varieties to the known Jamaican flora growing outside of cultivation. Of these, 44 species and 5 varieties are new to science. Added to the figure cited by Adams (see above), the flowering plants of Jamaica now total 3003 species.

ORDER OF FAMILIES

MONOCOTS	Viscaceae	Thymelaeaceae
Calyciferae	Rafflesiaceae	Flacourtiaceae
Hydrocharitaceae	Polygonaceae	Turneraceae
Commelinaceae	Chenopodiaceae	Passifloraceae
Bromeliaceae	Amaranthaceae	Begoniaceae
Marantaceae	Nyctaginaceae	Lythraceae
	Phytolaccaceae	Myrtaceae
	Portulacaceae	Onagraceae
Corolliferae	Caryophyllaceae	Haloragidaceae
Araceae	Cactaceae	
Lemnaceae	Lauraceae	Sympetalae
Hypoxidaceae	Nymphaeaceae	Primulaceae
Orchidaceae	Ceratophyllaceae	Sapotaceae
	Theaceae	Oleaceae
Glumiflorae	Guttiferae	Gentianaceae
Cyperaceae	Droseraceae	Apocynaceae
Gramineae	Sarraceniacae	Asclepiadaceae
	Leguminosae	Convolvulaceae
	Rutaceae	Boraginaceae
	Burseraceae	Solanaceae
DICOTS	Malpighiaceae	Scrophulariaceae
Polypetalae	Polygalaceae	Bignoniaceae
Piperaceae	Euphorbiaceae	Lentibulariaceae
Moraceae	Celastraceae	Acanthaceae
Olcaceae	Staphyleaceae	Rubiaceae
	Malvaceae	Compositae

HYDROCHARITACEAE

Hydrilla L. C. Rich.

Hydrilla verticillata (L. f.) Royle, Illus. Bot. Nat. Hist. Himalayan Mts. 376, 1839.

Genus and species new to Jamaica. **St. Andrew:**¹ 0.5 mi² due E of Newcastle in small artificial pool, ca. 3700 ft, *Proctor 38141*, May 1, 1979. **St. Catherine:** near head of Fresh R., ca. 1.3 mi due WNW of Caymanas Factory, near sea level, *Proctor 38203*, June 19, 1979; Rio Cobre just S of Central Village, ca. 10 ft, *Proctor 36808*, April 30, 1977, *Proctor 37221*, Sept. 4, 1977.

It is possible that Adams's (1972) record of *Elodea* in Jamaica was based in part on misidentified material of *Hydrilla*, the existence of which in Jamaica was not suspected at that time.

This rampant aquatic species, widely distributed in the warmer parts of the Old World, particularly in tropical Asia and Indonesia, has become naturalized in several widely separated New World localities and can be expected to increase in range. It was collected in Aruba, Netherlands Antilles, in October, 1969 (*Arnoldo-Broeder 3815-b*, GH), and was recorded from central and southern Florida by Long and Lakela (1971), from Panama by Croat (1978), and from various southern states by Godfrey and Wooten (1979). Croat was incorrect in stating that his collections were the first from the Americas.

Hydrilla is closely related to *Egeria* and *Elodea*, and all of them might reasonably be united in a single genus. *Hydrilla* is, however, usually distinguished without difficulty from the other two by its more prominently toothed leaf margins, and especially by the toothlike projections of the midribs on the under-surfaces of its leaves. From *Egeria* it is also differentiated by its smaller leaves (less than 2 cm long, averaging ca. 1.5 cm, vs. 2–3 cm). Floral differences are distinctive but seldom observable.

COMMELINACEAE

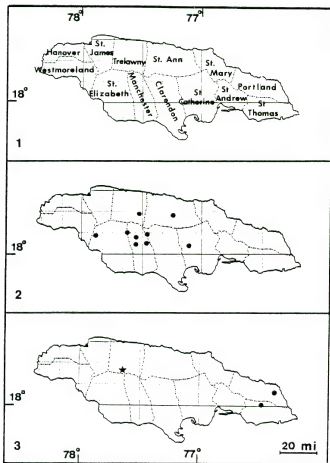
Callisia Loebl.

Callisia fragrans (Lindley) Woodson, Ann. Missouri Bot. Gard. **29**: 154. 1942. MAP 2.

New to Jamaica. **St. Catherine:** Browns Town distr., 1 mi N of Watermount P.O., ca. 1500 ft, *Proctor 37646*, Feb. 9, 1978. **Clarendon:** ca. 1 mi due ESE of Spaldings, ca. 2800 ft, *Proctor 37472*, Dec. 4, 1977. **Manchester:** Keynsham distr., ca. 1 mi by road N of St. Paul's, ca. 1100 ft, *Proctor 37677*, Feb. 19, 1978; Mike Town distr., ca. 3 mi NW of Mandeville, ca. 2200 ft, *Proctor 37587*, Jan. 17, 1978; Marshalls Pen., ca. 2.25 mi due NW of Mandeville, ca. 2100 ft, *Proctor 38636*, March 5, 1980; along road between Bellefield and Banana Ground, ca. 2000 ft, *Proctor 37591*, Jan. 18, 1978; 0.5 mi due NW of Grove Place, ca. 1700 ft, *Proctor 38548*, Jan. 19, 1980. **St. Elizabeth:** 1.5 mi by road SE of Newmarket, ca. 1200 ft, *Proctor 37625*, Feb. 5, 1978. **Trelawny:** Alps distr., ca. 2 mi NNE of Ulster

¹Specimens are cited according to parishes (see MAP 1); these are the basic political divisions of Jamaica.

²Elevations and local map distances are expressed in feet and miles because these are the official units of measurement used on Jamaican maps.



MAPS 1-3. 1, Jamaica, showing location of parishes (specimens are cited according to parishes where collected). 2, 3, distributions: 2, *Callisia fragrans*; 3, *Aechmea decurva* (dots), *Tillandsia trelawniensis* (star).

Springs, ca. 1400 ft, *Proctor* 37584, Jan. 9, 1978. **St. Ann:** vic. of Albion, ca. 2000 ft, *Proctor* 37693, Feb. 25, 1978.

As can be seen from these citations, the Mexican species *Callisia fragrans* has become widely and extensively naturalized in Jamaica.

BROMELIACEAE

Aechmea Ruiz & Pavon

Aechmea decurva Proctor, sp. nov.

MAP 3.

Aechmea paniculigera affinis, sed in foliis spinis brevioribus angustioribusque, scapo decurvato, paniculis brevioribus indumento tomentoso melius evoluto, sepalis brevioribus indumento tomentoso praeditis marginibus ciliatis, et petalis purpureis brevioribus, differt.

Solitary epiphyte. Leaves to 80 cm long and 7 cm broad above expanded base, minutely lepidote, the margins with sharp, narrowly deltate, straight or upcurved spines to 2.5 mm long and 1 mm wide at base. Scape densely arachnoid-tomentose, decurved and projecting below leaves, bearing along upper part several bright pink, reflexed, narrowly lanceolate bracts up to 17 by 2.5 cm; panicle ascending, 15–20 cm long, whitish-tomentose throughout, densely flowered. Branches of panicle in clusters of 2 or 3, each 3- to 5-flowered, flowers sessile. Sepals whitish-tomentose, with spiny-ciliate margins, 3.5–4 mm long excluding apical spines, the spines 1.5–2 mm long, oblique or bent horizontally, tomentose at base; petals purple, ca. 8 mm long at anthesis; ovary ca. 6 mm long, densely whitish-tomentose. Fruits not seen.

Portland: John Crow Mts., ca. 6 mi by road S of Sherwood Forest, 1200–1500 ft, *Proctor* 37294, Sept. 25, 1977 (holotype, λ). **St. Thomas:** along E arm of Morant R. SE of Macungo Hill, ca. 1500 ft, *Proctor* 28642, May 14, 1968.

This species is confined to the mountain rainforests at the eastern end of Jamaica, where it is rare. It is always an epiphyte, unlike *Aechmea paniculigera* (Sw.) Griseb., its only Jamaican congener, which most often grows on shaded rocks although it is occasionally an epiphyte. *Aechmea decurva* is obviously related to *A. paniculigera* of central and western Jamaica but differs in its shorter and narrower leaf-spines; its invariably decurved (vs. erect) scapes; its narrower scape bracts; its shorter (15–20 vs. 30–50 cm), much more pubescent panicles; its shorter (3.5–4 vs. 4.5–6.5 mm, excluding the spines), whitish-tomentose sepals with spiny-ciliate instead of entire margins; its oblique to horizontally bent calyx spines, these tomentose at base instead of glabrous; and its purple (vs. pink, mauve, or light blue) corolla ca. 8 (vs. 10) mm long at anthesis.

Tillandsia L.

Tillandsia adamsii R. W. Read, *Phytologia* 28: 21. pl. 1. 1974.

This species related to *Tillandsia canescens* Sw. was recognized as new too late to be included in *Flowering Plants of Jamaica* (Adams, 1972). It has been recorded from the parishes of St. James and Trelawny.

Tillandsia trelawniensis Proctor, sp. nov.

MAP 3.

Herba epiphytica sessilis a *Tillandsia polystachia* in foliis circa 55 (versus 17) omnis plantis; vaginis basalibus foliarum atrobrunneis (haud pallidis ferrugineis); laminis pallida lepidotis, squamis densis minutis peltatis marginibus elevatis; bracteis basibus ovatis; et bracteis floralibus hebetibus roseo-purpureis, haud viridibus, differt.

Plant stemless, rather massive. Leaves numerous (40 to 70, averaging 55), 20–32 cm long, straight to slightly recurved, forming dense, erect to subspreading rosette, very densely pale-lepidote throughout, peltate scales completely concealing epidermis; sheaths flat, broadly oblong or ovate-oblong, up to 4 cm broad, dark brown; blades narrowly triangular-attenuate, nearly filiform toward apex, 1–1.5 cm broad near base, more or less involute. Inflorescence shorter than or exceeding leaves, 15–35 cm long; scape erect; scape bracts foliaceous, densely grayish lepidote, with loosely imbricate or slightly separated ovate sheaths, terminated by erect, attenuate-acuminate blades; primary bracts ovate-attenuate, much shorter than spikes; spikes 6 to 12, erect, short-stipitate, rather densely subdigitate at apex of scape, mostly 5–10 cm long, complanate, linear-oblongate, ca. 1 cm broad above middle; floral bracts dull rosy purple, red-marginate, coriaceous, erect, more or less imbricate, ovate, acute and mucronate, 15–20 mm long, glabrous, smooth or very faintly striate, subcarinate toward apex. Flowers at anthesis and mature fruits not seen.

Trelawny: near Crown Lands road extension 4.5–5 mi NW of Troy, ca. 2000 ft, Proctor 34713, Jan. 26, 1975 (holotype).

This species superficially resembles *Tillandsia polystachia* (L.) L. in the size, shape, and arrangement of the spikes. However, it differs markedly from that species in its much more massive growth: *T. trelawniensis* averages 55 leaves per plant, whereas *T. polystachia* averages 17, with a range of 12 to 24. Further, the basal sheaths of this new species are dark brown instead of "pale-ferruginous" as in *T. polystachia*, and the leaves are densely pale-lepidote throughout, the minute peltate scales having raised margins (the punctate scales of *T. polystachia* are so minute that the leaf surface superficially appears smooth and glabrous). *Tillandsia trelawniensis* also differs in the ovate bases of its scape bracts and primary bracts, and in the dull rosy purple (instead of green) color of the floral bracts.

MARANTACEAE

Calathea G. F. W. Meyer

Calathea lutea (Aublet) G. F. W. Meyer, Prim. Fl. Esseq. 10. 1818.

Portland: between Millbank and Bowden Pen, 500–1000 ft, *Proctor* 28629, April 21, 1968. **St. Thomas:** Spring Bank distr., ca. 1200 ft, *Proctor* 27842, March 20, 1967.

Adams (1972, p. 60) briefly mentioned *Calathea lutea* ("native of Guyana") as "naturalized" in the parish of St. Thomas. This species, although originally described from Guyana, has a circum-Caribbean range, occurring on the continent from southern Mexico southward throughout Central America, and from Puerto Rico through the Lesser Antilles to Trinidad. In South America it is recorded from as far south as Peru. This distribution is consistent with its occurrence in Jamaica being natural. There is no evidence of its introduction to Jamaica by humans, at least in modern times. On the other hand, the widespread use in Central America of the leaf blades of *C. lutea* for wrapping food suggests the possibility of aboriginal introduction by Mayan sea-traders, who are known to have visited Jamaica in pre-Columbian times. It is doubtful, however, that any evidence exists for this hypothesis. The occurrence of this species in Jamaica on wet slopes and in open riverine marshes of the upper Rio Grande valley, and at isolated sites on the southern side of the same watershed, suggests that it has grown here for a long time. Certainly this species should be included as part of the present noncultivated flora of Jamaica.

The large leaves of *Calathea lutea* bear on their underside a white, flaky material called "cauassú wax," which is said to have considerable commercial value for high-quality polishes. Because of ease of propagation in wet, swampy soils and relatively high yield (one hectare will potentially grow 75,000 plants, which will yield 800 kg of wax per year after the second year), this species should be investigated as an agricultural crop for suitable Jamaican localities.

ARACEAE

Alocasia Schott

Alocasia macrorhiza (L.) Schott, Österr. Bot. Wochenbl. 4: 409. 1854; Prodr. 146. 1860. FIGURE 1.

Genus and species new to Jamaica. **St. Catherine:** vic. of Spanish Town, *N. L. Britton* 3107, Aug. 30–Sept. 3, 1908 (sterile) (det. D. H. Nicolson) (ny). **Portland:** Sherwood Forest, ca. 700 ft, *Proctor* 38498, Dec. 27, 1979 (sterile).

This species is one of the commonest and most widespread of its family



FIGURE 1. *Alocasia macrorrhiza* at Sherwood Forest, Jamaica.

in Jamaica and probably occurs in all parishes. Although its total absence from the literature on the Jamaican flora is therefore astonishing, it can perhaps be accounted for by the fact that plants of this species apparently never flower in Jamaica. Botanical collectors tend to neglect the Araceae in any case, and it seems that scarcely anyone ever bothers to gather large, unwieldy leaves of sterile plants, especially if their sap is irritating to the skin! There is no mention of this species by Adams (1972). Britton's collection at New York remained unidentified until 1962 and has not been cited until now. Britton and Wilson (1926, p. 335) reported this species from Puerto Rico and stated that "we have been unable to find it flowering . . .," although it was abundantly naturalized in moist ground. It would be interesting to

ascertain if *Alocasia macrorrhiza* ever flowers under West Indian conditions. The species occurs in Cuba and Hispaniola as well as in Puerto Rico.

Alocasia macrorrhiza is indigenous to tropical Asia; the circumstances and date of its introduction to Jamaica do not seem to be known. It is locally called "scratch-coco," and the large, starchy rhizomes are often fed to pigs.

Anthurium Schott

Anthurium cubense Engler, Bot. Jahrb. 25: 364. 1898.

New to Jamaica. **St. Andrew:** Salt Hill, ca. 3000 ft, *Proctor 32760*.

This plant was found on a wooded rocky mountainside by Mrs. Vernon James some time prior to 1965. She brought it into cultivation at her Pine Grove Hotel, where I saw it in 1970. At that time, Mrs. James gave me an offshoot of her plant, which has since been growing in a pot at my home. A leaf and inflorescence taken from this plant have been placed in the Institute of Jamaica Herbarium as *Proctor 32760*. This species has heretofore been considered endemic to Cuba; its identity and natural occurrence in Jamaica require further confirmation.

Anthurium gracile (Rudge) Lindley, Bot. Register 19: 1635. 1833, *excl. fig.*

New to Jamaica. **Portland:** along the Buff Bay-Hardwar Gap road above Cedar Valley, ca. 2000 ft, *Proctor 23033*.

A wild population of this species was found at the above site by Dr. G. E. Valentine prior to 1960; this station was subsequently destroyed by road-widening. However, Dr. Valentine had taken a number of the plants into cultivation and has distributed a few of these to friends interested in horticulture. I obtained two leaves and an inflorescence of this population from Mr. L. Hendrickson on Dec. 9, 1962, and these were deposited in the Institute of Jamaica Herbarium as *Proctor 23033*.

Anthurium gracile has a wide continental distribution from Belize southward into South America and has also been found in Hispaniola, so its natural occurrence in Jamaica is not surprising.

LEMNACEAE

In treating this family, Adams (1972) recognized two genera: *Lemna* L., with two species; and *Wolffia* Horkel ex Schleiden, with one. Subsequent collecting, as well as a reappraisal of available material, indicates that at least three more species occur in Jamaica, one of which represents a previously unreported genus. Although Adams followed the practice of most British authors in not recognizing *Spirodela* as a genus separate from *Lemna*, all monographers of the family have taken a contrary view. If *Spirodela* is accepted as valid, then Jamaica must be credited with a total of four genera

in this family. These can be keyed out as follows, using the classification presented by den Hartog and van der Plas (1970):

- A. Roots present; flowers enclosed by a spathe; anthers bilocular; tissue containing raphides.
 - B. Each thallus with several roots, a dorsal and a ventral scale, and 5 or more nerves. *Spirodela*.
 - B. Each thallus with 1 root, no dorsal or ventral scale, and 0, 1, or 3 nerves. *Lemna*.
- A. Roots absent; flowers not enclosed by a spathe; anthers unilocular; tissue without raphides.
 - C. Plant body a flat, recurved thallus 5–6 mm long; inflorescences 2 per thallus. *Wolffiella*.
 - C. Plant body globular to ellipsoid, 0.5–1 mm long; inflorescence 1 per thallus. *Wolffia*.

***Spirodela* Schleiden**

***Spirodela polyrhiza* (L.) Schleiden, Linnaea 13: 392. 1839.**

Lemna polyrhiza L. Sp. Pl. 2: 970. 1753; Adams, 1972.

***Lemna* L.**

Three species are now known to occur in Jamaica. Adams (1972) listed only *Lemna perpusilla* Torrey (excluding *L. polyrhiza*, now separated in *Spirodela*), although Daubs (1965) had cited a Jamaican collection of *L. valdiviana* (Harris 10837, us). Recent studies by Dr. E. Landolt have shown that the plants called *L. perpusilla* by Adams should instead be known as *L. aequinoctialis* Welw., and examination of Harris 10837 at us has revealed that it was misidentified by Daubs and also represents *L. aequinoctialis*. Thus my collections of authentic *L. valdiviana* are in fact a new record for Jamaica. The Jamaican species can be keyed as follows:

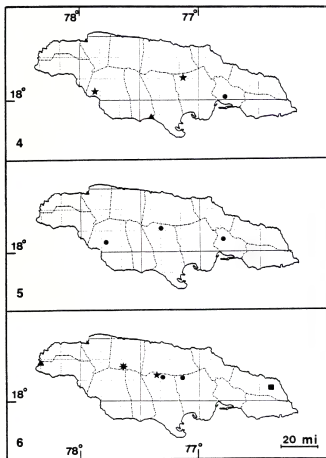
- A. Thallus 3-nerved, broadly oblong, obovate, or suborbicular, not much longer than broad. *L. aequinoctialis*.
- A. Thallus obscurely 1-nerved or apparently nerveless, narrowly oblong, usually at least twice as long as broad when mature.
 - B. Thallus 2.5–4.5 mm long, inequilateral and often subfalcate, submerged; epidermis without evident cystoliths. *L. valdiviana*.
 - B. Thallus 1–1.5 mm long, equilateral, floating; epidermis with minute, linear, whitish cystoliths. *L. minuscula*.

***Lemna aequinoctialis* Welw. Añaes Conselho Ultramar. 55: 543. 1858.**

Lemna perpusilla of Adams, Fl. Pl. Jamaica, 71. 1972, not Torrey, 1843.

***Lemna minuscula* Herter, Revista Sudam. Bot. 9: 185. 1954. MAP 4.**

New to Jamaica. **St. Andrew:** garden pool on Clieveden Ave., ca. 400 ft, Proctor 37942-a, Dec. 17, 1978.



MAPS 4-6. Distributions: 4, *Lemna minuscula* (dot), *L. valdiviana* (triangle), *Woi-fiella welwitschii* (stars); 5, *Curculigo scorzonrifolia*; 6, *Epidendrum blanchianum* (dots), *E. scalpelligerum* (star), *Liparis adamsii* and *Stelis scabrada* together (asterisk), *S. scabrada* alone (square), *Zeuxine straeumatica* (triangle).

These minute plants were associated with scattered groups of *Salvinia* and may have been introduced with them. This species is known chiefly from the southwestern United States (especially California), Guatemala, and several countries in South America; so far as can be ascertained, it has not previously been reported from the West Indies.

Lemna valdiviana Phil. *Linnaea* **33**: 239. 1864.

MAP 4.

New to Jamaica. **Manchester**: Alligator Hole R., sea level, *Proctor* 35373, Oct. 22, 1975, *Proctor* 38198, June 17, 1979 (coll. and det. R. M. Lowden).

This species is widely distributed in temperate and tropical America. The constantly submerged growth-habit that it maintains in Jamaica is not mentioned in any literature I have seen and apparently does not occur in populations elsewhere.

Wolffiella Hegelm.

Wolffiella welwitschii (Hegelm.) Monod, *Mém. Soc. Hist. Nat. Afrique N.*, hors-sér. **2**: 229, 242. 1949.

MAP 4.

Wolffia welwitschii Hegelm. *Jour. Bot. London* **3**: 114. 1865.

Wolffiopsis welwitschii (Hegelm.) den Hartog & van der Plas, *Blumea* **18**: 366. 1970.

Genus and species new to Jamaica. **St. Catherine**: Charlton, shallow weedy lake 1 mi W of Ewarton, ca. 1000 ft, *Proctor* 37943, Dec. 20, 1978. **St. Elizabeth**: weed-filled seasonal pond in pasture ca. 1 mi N of Black River, near sea level, *Proctor* 35444, Nov. 8, 1975 (det. R. M. Lowden).

This species was first described from tropical west Africa; its sporadic tropical American distribution includes the West Indian islands of Cuba, Jamaica, Hispaniola, and Guadeloupe, and the continental countries of Guatemala, Suriname, Venezuela, Colombia, and Ecuador.

Wolffia Horkel ex Schleiden

Wolffia brasiliensis Weddell, *Ann. Sci. Nat.* III. **12**: 170. 1849.

Wolffia punctata Griseb. *Fl. Brit. W. Indian Is.* 512. 1864; Adams, 1972.

The earlier Weddell name is here taken up for the Jamaican species following the recent publication of Landolt (1980).

HYPOXIDACEAE

Curculigo Gaertner

Curculigo scorzonerifolia (Lam.) Baker, *Jour. Linn. Soc. Bot.* **17**: 124. 1878.

MAP 5.

This species was listed by Adams (1972, p. 82) as "very rare (St. Andr.), in grassy places on heavy clay soil; 800–1000 ft. . . ." Subsequent collections have considerably extended the known local range and altitudinal span, but *Curculigo scorzonnerifolia* must still be considered very rare. However, this is a plant unlikely to be noticed except when it is flowering, and the flowering season is very short.

St. Andrew: (*fide* Adams). **Clarendon:** Bunkers Hill Savanna, ca. 2000 ft, *Proctor 36843*, May 8, 1977. **St. Elizabeth:** Slipe distr., sea level, *Proctor 38180*, June 16, 1979.

ORCHIDACEAE

Epidendrum L.

Epidendrum blancheanum Urban, Ark. Bot. 17(7): 21. 1922. MAP 6

Epidendrum acuña Dressler, Am. Orchid Soc. Bull. 28: 358. 1959.

New to Jamaica. **St. Catherine:** Blue Mountain distr., S slope of Mt. Diablo, epiphytic on wooded limestone hillside, 2600–2700 ft, *Proctor 27901* (with R. W. Read), May 13, 1967 (originally det. as *E. acuña* by L. A. Garay). **Clarendon:** stream gully 0.9 mi by road E of Reckford, epiphytic on tree branch overhanging stream, ca. 2000 ft, *Proctor 38151*, May 2, 1979.

This species is otherwise known from Cuba, Hispaniola, Mexico, Guatemala, Honduras, and Panama. It can be distinguished from the superficially similar *Epidendrum ramosum* Jacq. and its relatives by its pendent unbranched foliage stems with short lateral flowering shoots, each initially bearing one flower, but later by renewed growth producing another flower, and so on, eventually becoming somewhat elongate.

Epidendrum scalpelligerum Reichenb. f. Flora 48: 278. 1865. MAP 6.

New to Jamaica. **St. Ann:** Greenock distr., 0.8 mi due SE of Cave Valley Square, epiphytic on citrus trees, ca. 1850 ft, *A. L. Gloudon s.n. (IJ 69180)*.

I discovered this rare and little-known species on March 30, 1975, only in sterile or juvenile condition; no herbarium specimen was collected. Later, at my suggestion, Mr. Gloudon searched the same locality and collected a number of live plants for cultivation, one of which flowered in his garden. This plant was pressed in August, 1978, and is the specimen recorded above.

Epidendrum scalpelligerum was originally described on the basis of a Wright specimen (3339) from eastern Cuba; to the best of my knowledge, it has never been found again until the present Jamaican discovery. Our specimen was identified by L. A. Garay in September, 1978. The species was listed by León (1947) as *Pleuranthium scalpelligerum* (Reichenb. f.) Cogn. Its growth form is unusual for an *Epidendrum*, consisting of a small, fan-shaped vertical rosette of overlapping leaves very similar in appearance to that of *Oncidium pusillum*. The inflorescence is a small raceme that is merely

an extension and narrowing of this rosette, bearing a few inconspicuous greenish flowers.

***Liparis* L. C. Rich.**

***Liparis adamsii* Proctor, sp. nov.**

MAP 6.

Affinis *Liparis harrisii*, sed pseudobulbis minoribus, foliis in ambitu differentibus minoribusque, sepalis brevioribus angustioribusque, labello valde diverso, et columna sine spissescensibus sub apice et ad basin ample differt.

Pseudobulbs of flowering scape ca. 10 by 4–6 mm, enlarging to ca. 15 by 9 mm. Leaves 2, flat, broadly ovate, acute at apex, subcordate at base; blade of upper leaf 2–2.5 by 1.5–2 cm, of lower leaf 5–6 by 3.2–4.8 cm. Peduncle 10–13 cm long, quadrangular, very narrowly 4-winged; raceme 3.5–6 cm long, bearing 6 to 10 or more flowers, the bracts linear-lanceolate, 4–7 mm long; pedicels 9–12 mm long. Sepals pale green, lanceolate, 6–7 mm long, ca. 1.5 mm wide near base; petals filiform, greenish, 7–11 mm long, usually exceeding sepals; lip broadly obovate or nearly rotund, 12–15 mm long, 8–12 mm wide above middle, abruptly and minutely acuminate at apex, cordate at base, translucent dull purple with very faint darker veins; column greenish, 3.5 mm long, curved near apex, diameter uniform throughout. Capsules not seen.

Trelawny: near Crown Lands road extension 4.5–5 mi NW of Troy, in humus on shaded limestone ledges, ca. 2000 ft, *Proctor 34165*, Sept. 7, 1974 (holotype).

This beautiful species seems clearly related to *Liparis harrisii* Fawcett & Rendle, from which it differs in having smaller pseudobulbs, smaller leaves of a different shape, shorter and narrower sepals exceeded by the filiform petals, a differently shaped lip (obovate and minutely acuminate vs. oblong and obtuse) of a translucent purple color, and a shorter column of uniform diameter. It is named for Dr. C. D. Adams in recognition of his important contributions to Jamaican botany.

***Stelis* Sw.**

Three species of this genus are now known to occur in Jamaica, although Adams (1972) listed but two definitely, one of these under an incorrect name. The Jamaican species can be designated as follows:

***Stelis micrantha* (Sw.) Sw. Jour. Bot. Schrader 1799(2): 240. 1800.**

***Stelis scabrida* Lindley, Ann. Nat. Hist. 5: 115. 1840. TYPE: Dominica.**
MAP 6.

New to Jamaica. **Portland:** NW slope of Joe Hill, 1000–2250 ft, *Proctor 15836*, Dec. 2, 1956. **Trelawny:** 5.5 mi NW of Troy, 2000 ft, *Adams 12833*, May 8, 1966. (Both specimens det. L. A. Garay.)

Until now this species was believed to be endemic to the Lesser Antilles, where the flowers are cited as being "yellow-green." The flowers of both Jamaican specimens are purple but are morphologically indistinguishable from those of the Lesser Antilles.

Stelis trigoniflora (Sw.) Garay, Bot. Mus. Leaflet. **26**(1): 25. 1978, based on *Epidendrum trigoniflorum* Sw., 1788, excl. syn.

This species has been widely but incorrectly known as *Stelis ophioglossoides* (Jacq.) Sw.

Zeuxine Lindley

Zeuxine strateumatica (L.) Schlecht. Feddes Repert. Beih. **1**: 77. 1911. MAP 6.

Westmoreland: near milepost 23, 2.5 mi NE of Negril, sea level, *Proctor 34694* (with Lester Dinnall), Jan. 15, 1975; near Middle R., 2.3 mi NE of Negril, sea level, *Proctor 34728*, Jan. 29, 1975.

First reported from Jamaica by Proctor (1975). It has been suggested that this diminutive annual species might have been accidentally introduced from Florida on the feet of tourists. This is an interesting variation of the theory of plant distribution by birds.

CYPERACEAE

It is probably not a matter of chance that this family has produced more new Jamaican records than any other except the Myrtaceae; the somewhat drab, grasslike appearance of these plants and their lack of economic importance have tended to deflect critical interest in the group.

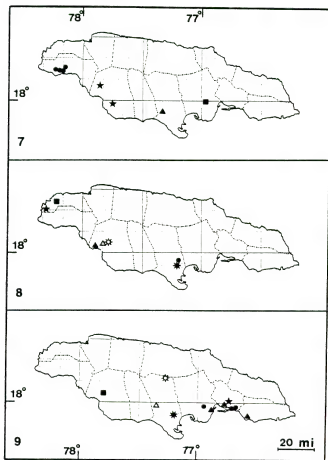
Cyperus L.

Some recent authors have treated the major subdivisions of this taxon as genera, but I prefer to view them as subgenera.

Cyperus cyperoides (L.) Kuntze, Rev. Gen. Pl. **3**(2): 333. 1898. MAP 7.

New to Jamaica. **St. Catherine:** Belle Vue near Spanish Town, in wet hollows in pasture, *Harris 12045*, May 24, 1915 (NY).

First reported from Jamaica by Koyama (in Howard, Fl. Lesser Antilles **3**: 277. 1979) as *Mariscus sumatrensis* (Retz.) J. Raynal, without data. This report was probably based on the above specimen. *Cyperus cyperoides* is indigenous to tropical Asia and Africa; in the New World it is recorded as an adventive in Grenada and Trinidad, as well as in Jamaica. It resembles the common *C. tenuis* Sw. but can easily be distinguished by the shorter spikelets (3–5 mm long vs. 7–10 mm for *C. tenuis*).



MAPS 7-9. Distributions: 7, *Cyperus cyperoides* (square), *C. floridanus* (stars), *C. iria* (triangle), *C. procerus* var. *lasiorrhachis* (dots); 8, *Eleocharis nigrescens* (dot), *Fimbristylis autumnalis* (solid triangle), *Rhynchospora tracyi* (star), *Scleria macrophylla* (hollow triangle), *S. reticularis* var. *pubescens* (square), *S. setuloso-ciliata* (hollow asterisk) (solid asterisk marks location of Harris Savanna); 9, *Paspalum botteri* (star), *Panicum exiguiflorum*, additional site (hollow triangle), *Reynaudia filiformis* (square), *Sacciolepis indica* (hollow asterisk), *Tragus berteronianus* (solid triangles), *T. racemosus* (dots) (solid asterisk marks location of Harris Savanna).

Cyperus floridanus Britton in Small, Fl. SE. U. S. 170, 1327, 1903.

MAP 7.

C. filiformis Sw. var. *densiceps* Kükenthal, Repert. Sp. Nov. 23: 190. 1926.

C. kingsii Adams ex Proctor, Sloanea 1: 1. 1977.

New to Jamaica. **St. Elizabeth:** Mt. Charles Estate, ca. 1 mi due SW of Giddy Hall P.O., 750–1000 ft, *Proctor 36399*, Oct. 2, 1976; 0.8 mile N of Mountainside, near sea level, *Proctor 37957*, Jan. 3, 1979.

Otherwise known from the Florida Keys, Bahamas, Cuba, and the Cayman Islands. This species belongs in subgenus *Torulinium* and is closely related to *Cyperus filiformis*, but it is definitely not conspecific with that entity.

Cyperus iria L. Sp. Pl. 1: 45. 1753.

MAP 7.

New to Jamaica. **Clarendon:** Ramble Pen, 1 mi NE of Pridees, in wet roadside ditch, 10–50 ft, *Proctor 32942*, Oct. 11, 1972.

This is a widespread species of the Old World tropics and subtropics, already well known as a naturalized plant in the southeastern United States, Cuba, and Hispaniola.

Cyperus procerus Rottb. var. *lasiorrhachis* C. B. Clarke in Hooker, Fl. Brit. India 6: 610. 1893; Kern, Fl. Males. 1. 7(3): 611. fig. 51. 1974.

MAP 7.

New to Jamaica. **Westmoreland:** near New Hope, sea level, *Proctor 33069*, Dec. 3, 1972; vic. of Big Bridge, WNW of Savanna-la-Mar, sea level, *Proctor 35340*, Oct. 7, 1975; near Little Bridge road crossing of Styx R., 2.5 mi ESE of Little London, sea level, *Proctor 33548*, Sept. 28, 1973; ca. 1.6 mi due SW of Georges Plain House, near sea level, *Proctor 37949*, Jan. 1, 1979.

This robust sedge of tropical Asia and Malesia has accidentally been introduced into Jamaica as a weed in rice-fields and is now thoroughly naturalized. So far as can be discovered, this species has not previously been recorded from anywhere in the Western Hemisphere.

Eleocharis R. Br.

Eleocharis atropurpurea (Retz.) Kunth, Enum. Pl. 2: 151. 1837.

New to Jamaica. **Clarendon:** Harris Savanna, in wet muddy ground among other sedges, 350 ft, *Proctor 34275*, Nov. 13, 1974, *Proctor 34312*, Nov. 15, 1974.

This is a pantropical species of somewhat sporadic distribution, apparently very rare in the West Indies. It occurs at a number of scattered localities in temperate North America. As an ephemeral annual, *Eleocharis atropurpurea* is probably often overlooked or only apparently absent; the achenes seem

able to live in a dormant state for a long time until growing conditions are favorable.

***Eleocharis nigrescens* (Nees) Steudel, Synopsis Pl. Glum. 2: 77. 1855.**
MAP 8.

E. minutiflora Böck. Bot. Jahrb. 7: 274. 1886.

E. nigrescens var. *minutiflora* (Böck.) Svensen, Rhodora 39: 226. 1937.

New to Jamaica. **Clarendon:** Lancewood Valley, in moist depression beside main highway, 50–200 ft, *Proctor 36521*, Nov. 11, 1976.

Like the previous species, this has a sporadic pantropical distribution; in North America it has been found as far north as South Carolina, where it is presumed to be introduced. *Eleocharis nigrescens* is very small and easily overlooked.

***Eleocharis oligantha* C. B. Clarke in Urban, Symb. Antill. 2: 69. 1900.**

New to Jamaica. **Clarendon:** Harris Savanna, on mud beside seasonal rain-pool, ca. 350 ft, *Proctor 34363*, Nov. 26, 1974, *Proctor 38029*, Feb. 10, 1979.

This species was previously known only from Cuba.

All three of the *Eleocharis* species newly reported from Jamaica would key out to the second half of Adams's (1972) key, in which *E. atropurpurea* is said to occur in the Cayman Islands. This section of the key can be rewritten as follows:

- (1. Spikelets less than 5 mm long, more or less ovoid, . . .)
 7. Achenes flattened; style 2-cleft; bristles conspicuous (8, 8; 9, 9; as in Adams's key).
 7. Achenes trigonous; style 3-cleft; bristles inconspicuous, much shorter than achene or absent.
 10. Achenes 1–1.2 mm long.
 11. Culms 0.2–0.4 mm in diameter; glumes mostly pale or greenish, at least along keel. *E. retroflexa*.
 11. Culms ca. 0.1 mm in diameter; glumes mostly purple-brown throughout. *E. oligantha*.
 10. Achenes 0.5–0.6 mm long.
 12. Bristles 3 to 5; spikelet subtended by linear bract more than half as long as spikelet; achenes grayish white, with rounded angles. *E. microcarpa*.
 12. Bristles lacking; spikelet subtended by bract similar to glumes; achenes yellowish brown, with ribbed angles. *E. nigrescens*.

Fimbristylis Vahl

***Fimbristylis autumnalis* (L.) Roemer & Schultes in L. Syst. Veg. 2: 97.**
1817. MAP 8.

New to Jamaica. **St. Elizabeth:** Police Rifle Range, 3.5 mi NW of Black River, in wet silica sand, near sea level, *Proctor 18447*, Dec. 11, 1958.

It was associated at this locality with another rare species, *Bacopa sessiliflora* (Bentham) Edwall of the Scrophulariaceae.

The record of this small annual species was overlooked and omitted by Adams (1972). *Fimbristylis autumnalis* also occurs in the Bahamas and Cuba, and it has a wide range in continental North America, as well as in the Old World tropics. This plant would key out in Adam's treatment to *F. complanata*, but it differs markedly from that species in its smaller stature (culms 10–20 vs. 20–60 cm tall), narrower leaves (0.8–1.5 vs. 2–3 mm wide), and smaller spikelets (2–5 vs. 5–10 mm long). The achenes of *F. autumnalis* are translucent and smooth or very faintly reticulate, whereas those of *F. complanata* are opaque and minutely papillose.

***Fimbristylis capillaris* (L.) A. Gray, Man. Bot. ed. 5. 567. 1848.**

Bulbostylis capillaris (L.) Kunth ex C. B. Clarke in Hooker f. Fl. Brit. India 6: 652. 1893.

New to Jamaica. **Clarendon:** Harris Savanna, ca. 350 ft, *Proctor 34279*, Nov. 13, 1974.

Of widespread occurrence in the United States, this species has also been recorded from Mexico, Belize, Honduras, Panama, and Cuba. *Fimbristylis arenaria*, a very similar species differing chiefly in its much darker achenes, has been recorded from pine forests in Cuba, Hispaniola, and Belize.

Fimbristylis capillaris, together with *F. papillosa* (Kükenthal) Alain (see Adams, 1972), belong to subg. BULBOSTYLIS, which is distinguished from subg. FIMBRISTYLIS by the persistent, caplike style-bases on the apex of the achenes, and also frequently by the finely wiry or filiform texture of the culms. These two species, however, are very different from each other in details. *Fimbristylis capillaris* is a small, soft-filiform, tufted annual with culms 5–20 cm tall; its spikelets are 2–7 mm long, and its transversely rugulose achenes are 0.75–0.9 mm long. *Fimbristylis papillosa*, on the other hand, is a perennial with a hard, often slightly bulbous base and filiform but rather wiry culms up to 60 cm or more tall; its spikelets are 7–12 mm long, and its densely papillose achenes are 1–1.1 mm long.

Rhynchospora Vahl

***Rhynchospora tracyi* Britton, Trans. N. Y. Acad. Sci. 11: 84. 1892.**

MAP 8.

New to Jamaica. **Hanover:** in Great Morass ca. 1.9 mi due SW of Logwood, open, wet, fresh-water "quaking" marsh (underlain with semiliquid peat), sea level, *Proctor 37135*, July 19, 1977, *Proctor 37517*, Dec. 20, 1977.

This species resembles *Rhynchospora cyperoides* (Sw.) Martius but differs from that taxon in its more slender and wiry culms, its fewer, larger heads,

and its much larger achenes (2.5 mm vs. 1 mm long).

Rhynchospora tracyi is otherwise known from the Bahamas, Cuba, Hispaniola, Belize, and along the coastal plain of southeastern United States from South Carolina to Florida and Mississippi.

Scleria Berg.

Scleria macrophylla C. Presl, Reliq. Haenk. 1: 200. 1838. MAP 8.

New to Jamaica. **St. Elizabeth:** in Black R. Morass near junction of Y.S. and Black rivers, sea level, *Proctor 24517*, Jan. 25, 1964 (det. John E. Fahey, III, too late to be included in Adams's *Flowering Plants of Jamaica* (1972)).

This species has a wide continental range from southern Mexico to Panama, Brazil, and Bolivia, but it has not previously been found in the West Indies. It is easily distinguished from all other *Scleria* species in Jamaica by its very broad leaves, which reach 4.5 cm in width.

Scleria reticularis Michaux var. **pubescens** Britton, Ann. N. Y. Acad. Sci. 3: 232. 1884. MAP 8.

New to Jamaica. **Hanover:** near Hog R., 1.7 mi due NW of Kingsvale P.O., ca. 500 ft, *Proctor 33577*, Oct. 31, 1973.

The variety has previously been known from southeastern United States, Cuba, and Haiti.

Scleria setuloso-ciliata Böck. Flora 65: 30. 1882. MAP 8.

New to Jamaica. **St. Elizabeth:** Slipe distr., sea level, *Proctor 33455*, July 22, 1973.

Originally described from Guatemala, this species is recorded from Cuba, scattered Central American localities, and Brazil.

GRAMINEAE

Panicum L.

Panicum exiguiflorum Griseb. Catal. Pl. Cubens. 234. 1866. MAP 9.

New to Jamaica. **Clarendon:** Harris Savanna, among sedges in open marshy ground, ca. 350 ft, *Proctor 34350*, Nov. 26, 1974; 0.8 mi by road E of Toll Gate, ca. 50 ft, *Proctor 37804*, May 5, 1978.

Otherwise known from the Bahamas, Cuba, and Haiti. This species is distinctive in its growth habit, the culms of well-developed plants becoming lax

and trailing. Unlike that in other species of this genus in Jamaica, the palea at maturity becomes much enlarged and of subcoriaceous texture, by its development forcing the spikelet open.

***Paspalum* L.**

***Paspalum botteri* (Fourn.) Chase, Jour. Wash. Acad. Sci. 13: 436. 1923. MAP 9.**

New to Jamaica. **St. Andrew:** campus of Univ. West Indies near Botany Dept., in open waste ground, ca. 600 ft, *C. D. Adams 13269*, Oct. 5, 1972 (v, ucw).

This perennial weed has somehow been introduced into Jamaica and is persisting; it will probably become naturalized. Its natural range is southern Mexico and Central America to Costa Rica.

***Paspalum clavuliferum* C. Wright, Anal. Acad. Ci. Habana 8: 203. 1871.**

New to Jamaica. **Clarendon:** Harris Savanna, in open ground among scattered sedges, ca. 350 ft, *Proctor 34432*, Dec. 10, 1974.

Otherwise known from Cuba, Hispaniola, and Puerto Rico; this species also has a wide range in continental tropical America from Mexico to South America.

***Paspalum pleostachyum* Döll in Martius, Fl. Brasil. 2(2): 58. 1877.**

New to Jamaica. **Clarendon:** Harris Savanna, among sedges and grasses in seasonally moist open ground, ca. 350 ft, *Proctor 35365*, Oct. 20, 1975.

Recorded by Hitchcock (1936) from Cuba, Haiti, and Grenada; also in South America south to Brazil.

***Paspalum rupestre* Trin. Linnæa 10: 293. 1836.**

New to Jamaica. **Clarendon:** Harris Savanna, in open ground among scattered sedges, ca. 350 ft, *Proctor 34400*, Dec. 7, 1974, *Proctor 34411* and *34411-a*, Dec. 10, 1974.

Otherwise known from Cuba, Hispaniola, and Puerto Rico. Some of the Harris Savanna plants were unusually robust for this species, but all show the characteristic slender, recumbent culms lying on the ground.

The addition of four more species of *Paspalum* to the 30 recorded by Adams (1972) hardly justifies rewriting his key. Interested persons are referred to Hitchcock (1936) for aid in identification.

Reynaudia Kunth**Reynaudia filiformis** Kunth, Révis. Gram. 195. 1830.

MAP 9.

This rare grass, not recorded from Jamaica since Wulfschlaegel collected it in the parish of Manchester in 1849, has now been rediscovered growing rather abundantly in a moist, savannalike pasture, where it was associated with a number of other rare species (see a partial listing of these under *Schultesia guianensis*).

St. Elizabeth: Slike distr., sea level, *Proctor* 33566, Oct. 26, 1973.

Sacciolepis Nash

Sacciolepis indica (L.) Chase, Proc. Biol. Soc. Washington **21**: 8. 1908.

MAP 9.

New to Jamaica. **Clarendon:** Mason River Field Sta., ca. 2.75 mi due NW of Kellits P.O., ca. 2300 ft, *Proctor* 37853, June 18, 1978, *Proctor* 38209, June 22, 1979 (duplicates of these numbers det. H. B. Correll).

In the West Indies this species has also been found in Guadeloupe (Gould, 1979). Its natural range is from tropical Asia through Malaysia to Australia and Polynesia, and its appearance in the Western Hemisphere has been comparatively recent. The earliest report I have seen is from Georgia (Hitchcock, 1935, p. 688): *Sacciolepis indica* is stated to have been "introduced in a Government pecan orchard, Thomasville." It has also been reported from Texas (Gould, 1975), Florida to North Carolina (Godfrey & Wooten, 1979), and North Carolina (Radford, Ahles, & Bell, 1968). The latter record is particularly interesting because it was based on two collections from Sampson County. It is probably more than a coincidence that the *Dionaea muscipula* plants now naturalized at the Jamaican locality of *S. indica* also originated from Sampson County, from where they were introduced in 1968. It seems reasonable to suppose that seeds of *S. indica* were accidentally introduced among the roots of the *Dionaea*.

Sacciolepis indica is easily distinguished from *S. striata*, the only other Jamaican species of this genus, by the very much smaller size of all its parts; *S. striata* also occurs only at very much lower elevations (below 400 ft).

Tragus Haller

Jamaica has always been credited with but one species of this genus, *Tragus berteronianus*; in fact, Hitchcock (1936) recorded no other species from the West Indies. It was therefore rather a surprise when a specimen of supposed *T. berteronianus*, sent with exchange material to Texas, was reported back by Dr. M. C. Johnston as *T. racemosus*. A close examination of the specimens of *Tragus* in the Institute of Jamaica Herbarium has subsequently

revealed several sheets of both species. These plants can be differentiated as follows:

- A. Spikelets 2–3 mm long, the apex blunt, scarcely projecting beyond spines, the bur nearly sessile. *T. berteronianus*.
 A. Spikelets 4–4.5 mm long, the apex acuminate, projecting beyond spines, the bur pedicellate. *T. racemosus*.

Tragus berteronianus Schultes, Mant. Syst. Veg. 2: 205. 1824. MAP 9.

Kingston: N end of Race Course [now National Heroes Circle], ca. 150 ft, *Proctor* 9358, Oct. 24, 1954. **St. Catherine:** Port Henderson Hill, *Miss P. B. Caws s.n.* (JJ 4352), Sept. 25, 1953. **St. Thomas:** near mouth of Yallahs R., ca. 50 ft, *Proctor* 9415, Oct. 31, 1954.

Tragus racemosus (L.) All. Fl. Pedem. 2: 241. 1785. MAP 9.

New to Jamaica. **St. Andrew:** near mouth of Hope R., 0–20 ft, *Proctor* 9288, Aug. 23, 1954 (cited by Adams (1972) as *T. berteronianus*); E of Cane R. above coastal highway bridge, ca. 20 ft, *Proctor* 25595, Oct. 25, 1964. **St. Catherine:** along Rio Cobre just S of Central Village, 10–40 ft, *Proctor* 36867, May 14, 1977.

This species occurs as an introduced, naturalized plant in the northeastern and southwestern United States. Its natural range extends from southern Europe eastward through Asia Minor to Iran and Afghanistan.

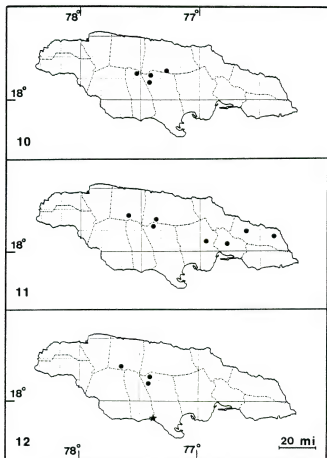
PIPERACEAE

Peperomia Ruiz & Pavon

Peperomia abdita Proctor, nom. et stat. nov. MAP 10.

Peperomia barbata C. DC. var. *puberula* Yuncker, Bull. Inst. Jamaica Sci. 11: 36. 1960; Adams, 1972, p. 206.

In describing this plant and assigning varietal status to it, Yuncker differentiated it solely by its minute, puberulous indument (vs. the dense villous hairs of typical *Peperomia barbata*). Working no doubt with insufficient material, he failed to note several other distinctive differences: the fruits of "var. *puberula*" are smaller (0.6 vs. 0.8 mm in diameter), are densely papillose-glandular (instead of smooth), have a symmetrical instead of a sub-oblique apex, and at maturity are exerted on a short, conical stalk instead of remaining sessile. Further, except at the type locality, "var. *puberula*" is consistently smaller in stature and leaf size. The two populations are only partly sympatric, and each may occur alone or somewhat near the other. Both occur in crevices on the sheltered sides of limestone cliffs, but "var. *puberula*" appears to require deeper shade and usually grows in the darkest, most hidden recesses of moist, rocky limestone hilltops. There appear to be



MAPS 10-12. Distributions: 10, *Peperomia abdita*; 11, *Pseudolmedia spuria*; 12, *Schoepfia harrisii* (dots), *S. obovata* (star).

no intermediate forms; therefore it is here proposed that Yuncker's "var. *puberula*" be raised to the rank of species. For this, a new name is required. The name *abdita*, which means "hidden" or "concealed," seems appropriate.

Clarendon: Peckham Woods, ca. 2500 ft, *Proctor 8218 p.p.*, March 10, 1954, 8419 p.p. (type); Glenwood Springs, along road between Balcarres and Sunbury, ca. 3100 ft, *Proctor 33636*, Nov. 30, 1973. **Manchester:** 1 mi SE of Pike, ca. 3100 ft, *Proctor 18316*, Oct. 25, 1958. **St. Ann:** Douglas Castle distr., ca. 2300 ft, *Proctor 26821*, Jan. 22, 1966.

Peperomia barbata var. *barbata* has been collected at some of the above localities, and also at others in the parishes of Trelawny and St. Catherine. *Peperomia abdita* has so far not been found in the latter two parishes.

Peperomia tetraphylla (G. Forster) Hooker & Arnott, Bot. Beechey Voy. 97, 1841.

Peperomia reflexa (L. f.) A. Dietr. in L. Sp. Pl. ed. 6. 1: 180. 1831, not Kunth in H.B.K., 1815.

The specific epithet *reflexa* as used by Yuncker (1960), Adams (1972), and most other authors of floristic works of the Antillean-Central American region is illegitimate. The name *tetraphylla* is the next available one.

MORACEAE

***Pseudolmedia* Trécul**

Pseudolmedia spuria (Sw.) Griseb. Fl. Brit. W. Indian Is. 152. 1860. MAP 11.

Adams (1972, p. 224) stated that this species is "rare and not recently collected." However, data now available suggest that it is in fact widely distributed and not uncommon. The Institute of Jamaica Herbarium has specimens from six parishes.

In the John Crow Mountains area this tree is known locally as "red breadnut."

St. Andrew: along Hermitage road above Red Gal Ring, 1000–1200 ft, *Proctor 31548*, Dec. 11, 1970 (sterile). **St. Catherine:** 1.5 mi due SE of Sligoville, 1800–1900 ft, *Proctor 31729* (♂), *Proctor 31730* (♀), both April 16, 1971. **Clarendon:** Broom Hall hills, 1.2 mi due SW of Cave Valley Square, 1800–2000 ft, *Proctor 36722*, Jan. 8, 1977 (sterile). **Trelawny:** Tyre distr., 2 mi N of Troy, ca. 1750 ft, *Proctor 9937*, March 14, 1955 (♂) (det. C. C. Berg). **St. Ann:** Cedar Valley distr., ca. 1.5 mi NE of Cave Valley Square, ca. 2000 ft, *Proctor 36699*, Dec. 18, 1976 (♀), *Goodfriend s.n.*, June 2, 1977 (♀). **Portland:** ca. 1 mi S of Chepstow, ca. 500 ft, *Proctor 36745*, March 20, 1977 (sterile); John Crow Mts. ca. 6 mi by road S of Sherwood Forest, 1200–1500 ft, *Proctor 38457*, Dec. 6, 1979 (sterile).

OLACACEAE

Schoepfia Schreber

Schoepfia obovata C. Wright ex Sauv. An. Acad. Ci. Habana 5: 289.
1868. MAP 12.

New to Jamaica. **Clarendon:** N slope of Round Hill, 500–1100 ft, *Proctor 9497*, Nov. 22, 1955, *Proctor 38257*, July 26, 1979.

The first of these two collections was cited by Adams (1972) as *Schoepfia harrisii*, but a reappraisal of this material shows that it is not the same as that species. *Schoepfia harrisii* is a straggling or even scrambling shrub confined to moist, wooded limestone crags at scattered localities around the perimeter of the Central Inlier (see MAP 12) at elevations of 2000–3000 ft. It has lanceolate, narrowly elliptic, or lance-ovate leaves up to 11.5 cm long and mostly 2–4 cm broad; they tend to be variable in shape, sometimes being inequilateral or bluntly acuminate, with petioles up to 8 mm long. The plant is cauliflorous along older stems (or with flowers occasionally originating from leaf axils), with floral peduncles 10–15 mm long, and its fruits are bright red. It is a rare and localized Jamaican endemic.

Schoepfia obovata, on the other hand, is an erect, sturdy shrub or tree up to 10 m tall that grows in dry limestone woodlands at much lower elevations. It has obovate, oblong, or elliptic leaves mostly 2–4 by 1.5–2 cm; they are quite regular in shape and always rounded or blunt at the apex, with very short petioles 1–3 mm long. Its flowers, on peduncles 2–8 mm long, always originate from leaf axils, and its fruits are yellow or dull red. This species has a broad West Indian range, being found in the Bahamas, Cuba, Hispaniola, and Puerto Rico. Its presence in suitable Jamaican habitats is therefore not surprising.

VISCACEAE

Following the proposals of Barlow (1964) and more particularly the careful analysis by Kuijt (1969), the genera *Dendrophthora* and *Phoradendron* are here considered members of the family Viscaceae instead of Loranthaceae. Adams (1972) treated all the mistletoes under Loranthaceae.

Dendrophthora Eichler

The publication of Kuijt's monograph of *Dendrophthora* (1961) made it possible for the first time to identify members of this genus with some degree of confidence. It is to be hoped that he (or someone as meticulous) will go on to bring order out of the chaos of *Phoradendron*.

Because Kuijt did not examine the material in the Institute of Jamaica Herbarium, he did not realize that the nearly complete personal collection of W. Buch from Haiti is now preserved there; he assumed that since the

holotype of *Dendrophthora brachystachys* Urban at Berlin "is probably no more extant" (p. 37), it was necessary to designate a neotype. However, the Buch collection in question (no. 811) is represented at *u* and should be designated lectotype of this species.

Recent field work in Jamaica has revealed the presence of an undescribed species of *Dendrophthora* that is related to *D. flagelliformis* (Lam.) Krug & Urban of Cuba, Hispaniola, and Puerto Rico. Dr. Kuijt has kindly examined this material and has confirmed that it is distinct; I am indebted to him for providing some helpful notes on these specimens.

***Dendrophthora nuda* Proctor, sp. nov.**

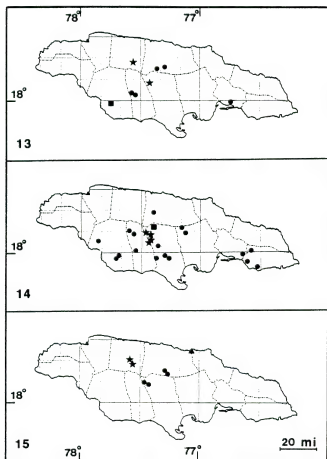
FIGURE 2, MAP 13.

Frutex aphyllus dioecius parasitatur in *Tabebuia angustata*, a speciebus aliis *Dendrophthora Jamaicensis* et a *D. flagelliformis* in ramulis elongatis teretibus et inflorescentiis compositis, inflorescentiis staminatis internodiis quadrangularibus et floribus numerosis congestus, inflorescentiis pistillatis floribus 2 vel 4 uterque nodo praeditis, differt.

Leafless dioecious shrub parasitic on *Tabebuia angustata* Britton; stems terete, glabrous, pendulous but firm, up to 1 m long, with numerous branches; cataphylls absent; basal appendages minute, transverse. Spikes elongate and apparently of indeterminate growth, curved, arranged in loose compound inflorescences with axes similar in appearance to ordinary stems except for nodal scales. Fertile staminate internodes up to 11 per division, each internode 5–18 by 0.8–1.7 mm, flattened-quadrangular in cross section,



FIGURE 2. *Dendrophthora nuda*, pistillate inflorescence with fruits.



MAPS 13–15. Distributions: 13, *Dendrophthora nuda* (square), *Phoradendron berterianum* (stars), *P. campbellii* (dots); 14, *P. crenulatum* (dots), *P. solandrae* (stars), *Pilostyles globosa* (square); 15, *Coccoloba priorii* (dots), *C. longifolia* × *C. tenuifolia* (stars), *C. uvifera* × *C. longifolia* (triangle).

with 5 to 15 crowded flowers borne in straight row on both narrow sides of each internode; staminate flowers ca. 0.7 mm in diameter. Fertile pistillate internodes up to 8 per division, each internode 5–18 by 0.7–2 mm, terete, with 1 or 2 pairs of flowers per internode (if 2, these widely separated); pistillate flowers ca. 1.5 mm in diameter. Fruits pale orange, oblong, 4–4.5 by 2–2.3 mm.

St. Elizabeth: 0.8 mi N of Mountainside, sea level, *Proctor 38034*, Feb. 17, 1979 (♀) (holotype), *Proctor 37959* (♂), *Proctor 37960* (♀), both Jan. 3, 1979.

Dendrophthora nuda is easily distinguished from the two other Jamaican species by its elongate terete stems and its compound unisexual inflorescences, of which the staminate have flattened-quadragular internodes with numerous small, crowded flowers, and the pistillate have only 1 or 2 pairs of flowers per internode. These characters also separate it from *D. flagelliformis* of Cuba and Hispaniola, seemingly its closest relative elsewhere. *Dendrophthora nuda* is the only Jamaican mistletoe to have been found parasitic on *Tabebuia*; it is also unusual in its genus for occurring at sea level.

Phoradendron Nutt.

The mistletoes have generally been neglected by collectors, and there is still much to be learned about the Jamaican species. The present contribution adds a new record and a new species to the local roster and presents augmented locality data on two others that have been little known.

Phoradendron berterianum (DC.) Nutt. Jour. Acad. Nat. Sci. Philadelphia 1: 185. 1847. MAP 13.

P. dichotomum (Bert.) Krug & Urban, Bot. Jahrb. 24: 48. 1897.

New to Jamaica. **Clarendon:** Glenwood Springs, along road between Balcarras and Sunbury, ca. 3100 ft, on *Ateramnus integer*, *Proctor 33646*, Nov. 30, 1973, *Proctor 36352*, July 21, 1976. **Trelawny:** Mango Tree Hill, along road between Burnt Hill and Spring Garden, ca. 1800 ft, on *Trichilia reticulata*, *Proctor 35666*, April 1, 1976.

This species is otherwise known from Cuba, Hispaniola, and Puerto Rico. It is distinguished from all but two of the other Jamaican species in having cataphylls (scale sheaths) at the base of all internodes. It differs from *Phoradendron piperoides* (Kunth) Trelease in having the leaves basinerved instead of pinnately nerved, and from *P. flavens* (Sw.) Griseb. in having its flowers in four rows instead of six; it differs from both of these species in its dichotomous branching.

Phoradendron campbellii Krug & Urban, Bot. Jahrb. 24: 40. 1897.

MAP 13.

Adams (1972, p. 243) stated that *Phoradendron campbellii* is "apparently rare and local (St. Andr.). . . . This obscure species has not been seen since

the original collections." However, recent attention paid to mistletoes has revealed that this species is fairly widespread in the interior of the island; it is now known from two more parishes in addition to the original one.

Manchester: Marshalls Pen, ca. 2.25 mi due NW of Mandeville, ca. 2100 ft, on *Nectandra coriacea*, Proctor 28887, July 28, 1968; Top Lincoln, 1.2 mi NNW of Lincoln P.A., ca. 2850 ft, on *Nectandra coriacea*, Proctor 37903, July 20, 1978. **St. Ann:** Cedar Valley distr., ca. 1.5 mi NE of Cave Valley Square, ca. 2000 ft, on *Licaria triandra*, Proctor 37276, Sept. 23, 1977, Proctor 37317, Oct. 7, 1977, on *Guapira fragrans*, Proctor 37391, Nov. 4, 1977; 1.6 mi by road SSE of Stepney, ca. 2300 ft, on *Nectandra anullana*, Proctor 36322, July 3, 1976.

Phoradendron crenulatum Urban, Symb. Antill. 5: 332. 1907. MAP 14.

Adams (1972) cited this species only from the parish of Clarendon, having overlooked the fact that the type was collected in St. Andrew. Numerous collections in recent years have revealed its occurrence in at least seven parishes—St. Thomas, St. Andrew, St. Catherine, Clarendon, St. Ann, Manchester, and St. Elizabeth. In some districts it is very common and conspicuous. MAP 14 shows its present known distribution.

Phoradendron crenulatum is most often found as a parasite on members of the Simaroubaceae, especially *Picrasma excelsa* (Sw.) Planchon and *Simarouba glauca* DC. The only other hosts known to me are *Cordia alliodora* L. and *C. gerascanthus* L. (Boraginaceae). I have twice found *P. crenulatum* parasitized by other mistletoes, once by *P. tetrapterum* Krug & Urban and once by *Oryctanthus occidentalis* (L.) Eichler.

Phoradendron solandrae Proctor, sp. nov.

FIGURE 3, MAP 14.

Frutex monoecius glaber parasitatur in *Solandra grandiflora*, a *Phoradendron albivaginato* in foliis grandioribus 6–15 × 1.5–5 cm (versus 3.5–5 × 1.5–2.5 cm), spicis carnosioribus longioribusve 2–4.5 cm (versus circa 2 cm) longis usque ad 6 simul ex axillis (versus spicibus solitariis), et fructibus grandioribus 4.5 mm (versus 2 mm) in diametro, differt.

Monoecious, glabrous shrub parasitic on *Solandra grandiflora* Sw. Plant bushy, robust, up to 1.5 m tall; young stems somewhat compressed and 2-edged, not broadened below nodes, becoming terete and woody with age, up to 1 cm thick or more toward base of plant. Cataphylls basal only, tubular, 2-lipped, white margined. Petioles 5–10 mm long; leaf blades subcoriaceous, lanceolate to broadly lanceolate, inequilateral, sometimes curved, 6–15 by 1.5–5 cm, blunt at apex, cuneate-attenuate at base, decurrent, up to 7-nerved from near base. Spikes solitary or up to 6 together in axils, 2–4.5 cm long, 3- or 4-jointed, fleshy, androgynous, terminal joint staminate and deciduous after flowers have fallen, others pistillate; flowers in 4 rows; staminate flowers usually 10 (4 rows of 2 each, plus 2 single ones between and beyond each of 2 rows at distal end), 1.4–1.8 mm in diameter; pistillate flowers 4



FIGURE 3. *Phoradendron solandrae*, portion of fruiting branch.

to 10 per joint, ca. 2 mm in diameter, deeply sunken in pits in fleshy rachis. Fruits globose, exserted, pale orange, ca. 4.5 mm in diameter.

Clarendon: Knox Woodland, ca. 1.3 mi due SE of Spaldings P.O., 2800–3000 ft, *Proctor* 37430, Nov. 19, 1977 (flowering) (holotype), *Proctor* 37474, Dec. 4, 1977; Glenwood Springs, along road between Balcarres and Sunbury, ca. 3100 ft, *Proctor* 38165, May 24, 1979; 1.7 mi due SSE of Cumberland, ca. 3000 ft, *Proctor* 37603, Jan. 18, 1978, *Proctor* 37802, April 30, 1978, ripe fruits from same plant coll. July 9, 1978. **Manchester:** 0.5 mi due NNE of Banana Ground, ca. 3100 ft, *Proctor* 37592, Jan. 18, 1978.

When compared with the Jamaican species listed by Adams (1972), the cited plants seem to key out to *Phoradendron albovaginatum* Urban, but few of the descriptive details of that species tally with the present one. In fact, examination of an isotype of *P. albovaginatum* (Harris 6703, NY) shows a very different plant, parasitic on *Simarouba glauca* DC. (Simaroubaceae). Although the specimen is in fragments, it obviously differs from *P. solandrae* in its smaller leaves, its more slender, solitary spikes, and its smaller flowers and fruits, the latter not so deeply sunken in pits.

Phoradendron solandrae is the only Jamaican mistletoe to have been found as a parasite of *Solandra*, and the numerous plants seen over its very limited range were only on *Solandra*. Such narrow host specificity is unusual although not unique among the Viscaceae. Because of the chaotic state of *Phoradendron* taxonomy, no precise relationship can be suggested for this

species. It is entirely unlike any other known in the West Indies, and search in several large herbaria has failed to turn up anything very similar among the continental species.

RAFFLESIACEAE

Pilostyles Guillaumin

Pilostyles globosa (S. Watson) Hemsley, Jour. Linn. Soc. Bot. **31**: 311. 1896. FIGURE 4, MAP 14.

Apodanthes globosa S. Watson ex Robinson in Coulter, Bot. Gaz. **16**: 83, pl. 9. 1891.

Family, genus, and species new to Jamaica. **Clarendon**: hill S of Broom Hall, 1.2 mi due SW of Cave Valley Square, 1800–2000 ft, *Goodfriend s.n. (IJ 64441)*, Dec. 6, 1976 (flowers), *Proctor 36693*, Dec. 14, 1976 (flowers), *Proctor 36715*, Jan. 8, 1977 (fruits), *Proctor 37505*, Dec. 16, 1977 (fruits).

All of the above specimens were found on *Bauhinia divaricata* L. The species was previously known only from Mexico, where it likewise occurs as a parasite only on species of *Bauhinia*. This is the first discovery of the family Rafflesiaceae in the West Indies.



FIGURE 4. *Pilostyles globosa* in fruit on stems of *Bauhinia divaricata*.

POLYGONACEAE³*Coccoloba* P. Browne

Coccoloba priorii Fawcett & Rendle, Jour. Bot. London **51**: 124, 1913; Fl. Jamaica **3**: 120, 1914. MAP 15.

In an earlier treatment of *Coccoloba* in Jamaica (Howard, 1957), I had placed *C. priorii* in the synonymy of *C. zebra* Griseb. and noted that the latter species "is not adequately known and additional material is needed." The locality at which the type of *C. zebra* (Wilson 168, K) was collected is not known but presumably must have been somewhere toward the eastern end of the island. The loose fruits associated with the type specimen are distinctive, and truly comparable material has not been collected again.

Recent collections of George R. Proctor from several locations in Clarendon and St. Ann parishes first appeared to be a new taxon, but after reexamination of my treatment of *Coccoloba zebra* and especially the single collection representing *C. priorii*, it appears that Fawcett and Rendle were correct in recognizing that species. Material now assigned to *C. priorii* consists of staminate and pistillate flowering specimens, mature fruits, and adventitious shoots. One noteworthy characteristic is in the ocreae, where the base of the petiole is above the middle of the ocrea; in addition, each inflorescence is normally branched above the base ("racemes . . . geminate," according to Fawcett & Rendle), and the rachis is puberulous, as is the perianth both in flower and in fruit. Both the staminate and pistillate flowers are predominantly single at the nodes of the inflorescence; the staminate buds are obovate-oblong in outline.

Clarendon: Quaco Rock, near Ritchies, ca. 3000 ft, *Proctor 34944*, March 30, 1975 (A, U), *Proctor 35245*, Aug. 31, 1975, *Morley & Whiteford 942* (A); Glenwood Springs, along road between Balcarres and Sunbury, 3000–3100 ft, *Proctor 35642*, March 31, 1976, *Proctor 35659*, March 31, 1976. **St. Ann:** James Webster Patent, along new road between Mason River and Alexandria, 2200–2300 ft, *Proctor 31668*, March 27, 1971; Douglas Castle distr., 2200–2400 ft, *Proctor 36253*, May 21, 1976 (GH, U).

Coccoloba priorii would be placed with the key couplet of *C. longifolia* Fischer ex Lindau and *C. tenuifolia* L. in the publications of Howard (1957) and Adams (1972), as follows:

- A. Tree generally with scrambling branches; leaves usually lanceolate-ovate, apex obtusely acuminate. *C. longifolia*.
- A. Shrub or tree without scrambling branches; leaves usually elliptic, apex shortly acute.
 - B. Inflorescence single, tenuous, thin, curved; staminate flowers in clusters of 2 or 3 at each node of inflorescence; fruits glabrous, ovoid, obtuse at

³By Richard A. Howard.

- apex. *C. tenuifolia*.
 B. Inflorescence usually branched near base, erect, straight; staminate flowers borne singly; fruits puberulous, ovoid but subcoronate at apex. . . *C. priorii*.

***Coccoloba longifolia* Fischer ex Lindau × *C. tenuifolia* L. MAP 15.**

I have also reexamined several collections from the parish of Trelawny that were previously assigned to either *Coccoloba longifolia* or *C. tenuifolia* (Howard, 1957). These appear to be intermediate between the two species in leaf shape and size but have the copious hirsute pubescence of golden brown, usually retrorse hairs on the internodes that is characteristic of *C. longifolia*, and the tenuous curved inflorescence of *C. tenuifolia*. Regrettably, only staminate or sterile material is available. A hybrid status is suggested for the following specimens:

Trelawny: Ramgoat Cave, 1500 ft, *R. A. Howard 14143*, Sept. 26, 1954 (A), *R. A. Howard & Proctor 14393*, July 4, 1955 (A), *R. A. Howard & Proctor 14420*, July 4, 1955 (A); Burnt Hill, 1640 ft, *Barkley 22J241*, April 29, 1952.

***Coccoloba uvifera* (L.) L. × *C. longifolia* Fischer ex Lindau MAP 15.**

A collection from Prospect Estate, east of the White River, parish of St. Mary (*Proctor 36330*) appears to be a hybrid between *Coccoloba uvifera* and *C. longifolia*. The single specimen (on two sheets) has large, broadly ovate, coriaceous leaves to 24 by 20 cm, cordate at the base and tapering to an acute apex. A single inflorescence 25 cm long with multiple pedicels at each node but without flowers represents the staminate condition.

Earlier (Howard, 1957), the hybrid status of *Coccoloba* × *jamaicensis* Lindau was suggested, with the parentage *C. uvifera* × *C. tenuifolia*. On Hispaniola suggested hybrids of *C. uvifera* with *C. krugii* Lindau and *C. pubescens* L. are known. In all cases only a single or very few plants were found, and these were primarily staminate.

CHENOPODIACEAE

***Salicornia* L.**

***Salicornia virginica* L. Sp. Pl. 1: 4. 1753.**

I am unable to distinguish the Jamaican population of *Salicornia* from this widespread North American species. Therefore, the name *S. perennis* Miller (1768), as used by Adams (1972), must be replaced by the earlier Linnaean epithet. In any case, I believe that the name *perennis* was based on a European type and represents a different species.

***Suaeda* Forskål**

***Suaeda linearis* (Ell.) Moq. Chenopod. Monogr. Enum. 130. 1840.**

MAP 16.

Genus and species new to Jamaica. **Clarendon:** Rocky Point, 0.8 mi W of Jackson Bay, sea level, *Proctor* 32972, Oct. 24, 1972 (det. C. O. Hopkins).

The known range of *Suaeda linearis* includes the eastern coast of the United States, Yucatan, the Bahamas, Cuba, and Haiti; therefore, its discovery in Jamaica is not surprising. The nearly terete leaves easily distinguish *Suaeda* from other genera of Chenopodiaceae in Jamaica. In *Chenopodium* and *Atriplex* the leaves are flat; in *Salicornia* they are reduced to rudimentary scales or ridges, so the terete stems appear to be leafless unless examined closely.

AMARANTHACEAE

Amaranthus L.

The genus *Acnida* was long distinguished from *Amaranthus* on the basis of being dioecious instead of monoecious, and in lacking a perianth on the pistillate flowers. Adams (1972) listed *Acnida cuspidata* Bert. ex Sprengel for Jamaica. However, Sauer (1955, p. 7) had previously submerged *Acnida* in *Amaranthus* because of what he termed "the absence of a clear-cut morphological discontinuity . . . accompanied by the absence of an absolute reproductive barrier." This required the generic description of *Amaranthus* to be modified as follows: first, plants monoecious or dioecious (instead of monoecious only); and second, ♀ tepals 0 to 5 (instead of 1 to 5). The sole Jamaican dioecious amaranth should be known as:

Amaranthus australis (A. Gray) J. D. Sauer, *Madroño* **13**: 15. 1955.

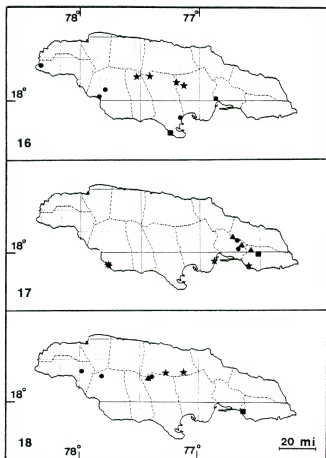
MAP 16.

Sauer cited no localized Jamaican specimens, yet his distribution map of this species showed two dots on Jamaica! In fact, there are now records of *Amaranthus australis* from at least four parishes—Westmoreland, St. Elizabeth, Clarendon, and the border of St. Catherine and St. Andrew. It is very common in some marshy localities, and under favorable conditions it may reach at least 3.5 m in height, with stems as much as 15 cm in diameter.

NYCTAGINACEAE

Guapira Aublet

The genus *Guapira* is distinguished from *Pisonia* L. especially by its drupelike, nonglandular anthocarps, and also by the fact that none of its species is either scandent or armed with thorns. However, difficulties arise in distinguishing sterile or immature material of arborescent species. This problem has led to some confusion in the treatment of these genera by Adams (1972) and has resulted in the delayed recognition of an anomalous Jamaican species of *Guapira*.



MAPS 16-18. Distributions: 16, *Suaeda linearis* (square), *Amaranthus australis* (dots), *Guapira rotundifolia* (stars); 17, *Phytolacca icosandra* var. *anomala* (square), *Portulaca aurantiaca* (stars), *P. umbraticola* (asterisk), *Cerastium glomeratum* (dots), *C. triviale* (triangles); 18, *Opuntia sanguinea* (square), *Ocotea exaltata* (dots), *O. harrisii* (triangle), *O. staminoides* (stars).

In a sense the problem is a legacy inherited from Heimerl (1912), who described a species he called *Neea* (*Pisonia*?) *rotundifolia* on the basis of immature material from Peckham Woods, parish of Clarendon (Harris 1985). Fawcett and Rendle (1914) included this species under *Neea* without comment. In 1968 I drew Dr. C. D. Adams's attention to certain material from the interior of Jamaica that matched *Pisonia subcordata* Sw., previously known from Puerto Rico and the Lesser Antilles, and Adams subsequently decided that Heimerl's *N. rotundifolia* was the same. This conclusion was published in *Flowering Plants of Jamaica* (1972). Unfortunately, he also included within his concept of *P. subcordata* certain specimens resembling this species that are now known—with more adequate material available—to represent a *Guapira*. A further complication arises from the fact that *P. subcordata* and the mysterious *Guapira* are very nearly sympatric and occur in the same kind of habitat. Since the flowering season of both species is brief and erratic, the trees are in sterile condition most of the time. Fortunately, there are leaf characters that seem to be reasonably distinctive. In addition, *P. subcordata* is deciduous and drops its leaves just before flowering, the flowers emerging with the new leaves; the *Guapira* is evergreen, producing inflorescences at the apex of mature leafy shoots.

It has recently become possible to examine some of the Harris specimens from Peckham Woods, Jamaica, on which Heimerl based his *Neea rotundifolia*. Surprisingly, this is not *Pisonia subcordata* with which Adams identified it, but instead belongs to the large-leaved evergreen *Guapira*. The anomalous persistence of perianth lobes on developing anthocarps does indeed suggest a *Neea*, but the ample flowering material now available from this and other localities has the exerted stamens and pistil of *Guapira* or *Pisonia*. The complete absence of glandularity on the anthocarps (if this is really a sufficient generic criterion!) points to *Guapira* rather than *Pisonia*, and the texture and venation of the leaves suggest a relationship to *G. obtusata* (Jacq.) Little, although the size of the leaves in the species under consideration is much larger.

Closer examination of all available material indicates possible clinal variation in the size of the staminate perianths. Much more surprising is the fact that in this species many of the staminate flowers have a well-developed, exerted pistil and are thus apparently bisexual or "perfect." The species is nevertheless essentially dioecious because some trees bear strictly unisexual pistillate flowers. Since all members of the *Neea-Pisonia-Guapira* complex are supposed to be strictly dioecious with unisexual flowers, the reproductive biology of the present species deserves closer investigation.

Neea rotundifolia was transferred to *Guapira* many years ago by Lundell, but without comment. There is a strong possibility that *Guapira* should be considered only subgenerically distinct from *Pisonia*. Whatever its ultimate generic disposition, the species *rotundifolia* must be reinstated as a member of Jamaica's endemic flora.

***Guapira rotundifolia* (Heimerl) Lundell, Wrightia 4: 83. 1968. MAP 16.**

Neea rotundifolia Heimerl in Urban, Symb. Antill. 7: 218. 1912.

Pisonia subcordata of Adams, Fl. Pl. Jamaica, 262. 1972, in part, as to the citations A 12610 and P 27530.

This species differs from *Guapira obtusata* (apparently its closest Jamaican congener) in its greater stature (tree to at least 15 m tall vs. shrub or small tree 2.5–8 m tall), its larger leaves (up to 15×8 cm vs. $3.5\text{--}10 \times 2.5\text{--}6$ cm), its larger panicles (often 10 cm or more long vs. 4–6 cm), and its larger (3.6–6 mm long vs. 2.5–4 mm) staminate perianths that are often apparently bisexual. *Guapira rotundifolia* is endemic to Jamaica, whereas *G. obtusata* also occurs widely in the Bahamas, Turks and Caicos Islands, and Cuba, as well as Jamaica.

St. Catherine: Roaring River distr., 1.5 mi due SE of Lluidas Vale, ca. 1650 ft, *Proctor 31524* (sterile), Nov. 21, 1970, *Proctor 32481*, July 10, 1971 (δ); hill 1.5 mi W of Lluidas Vale, 1200–1400 ft, *Proctor 28432*, Aug. 4, 1967 (dry infl.); 2–3 mi by road W of Lluidas Vale, ca. 1750 ft, *Proctor 27530*, July 7, 1966 (\varnothing), *Proctor 37971*, Jan. 21, 1979 (\varnothing , young fruits). **Clarendon:** Peckham Woods, 2300–2500 ft, *Harris 10958*, July 6, 1911 (young fruits) (us), *Harris 10985*, July 7, 1911 (\varnothing , immature) (ny, us, isotypes of *Neea rotundifolia*), *Harris 11183*, Sept. 27, 1912 (fruits) (us), *Crosby & Anderson 1263* (= *Adams 12610*), Aug. 19, 1963 (δ) (cat), *Proctor 34371*, Nov. 28, 1974 (δ ?—buds only). **Manchester:** Gourie Forest, ca. 1 mi due SW of Coleyville, 2700–2900 ft, *Proctor 35602*, Jan. 16, 1976 (δ).

PHYTOLACCACEAE

Phytolacca L.

Phytolacca icosandra L. var. *anomala* Proctor, var. nov. MAP 17.

A var. *icosandra* in floribus parvioribus, segmentis perianthii lanceolatis vel oblongo-lanceolatis 3–4 mm longis et 1–1.5 mm latis apicibus acuminatis vel subattenuatis et antheris circa 0.5 (haud circa 1) mm longis, differt.

Robust herb 1.5 m tall, forming thickets, differing from typical *Phytolacca icosandra* in its smaller flowers with lanceolate or oblong-lanceolate perianth segments 3–4 by 1–1.5 mm, acuminate to subattenuate at apex and narrowed at base, and in having smaller anthers (0.5 mm long vs. ca. 1 mm) devoid of pollen.

St. Thomas: along forestry road N of Union Hill, 3000–3500 ft, *Proctor 37371*, Oct. 19, 1977 (holotype).

Despite the apparent lack of pollen, this variant produces normal-appearing fruits and seeds. The perianth segments of var. *icosandra* are broadly elliptic or roundish-ovate, 3.5–4.5 by 2.5–3.5 mm, and blunt to somewhat acute at the apex.

PORTULACACEAE

Portulaca L.

The species listed by Adams (1972) as *Portulaca phaeosperma* Urban should properly be known as **Portulaca rubricaulis** Kunth in H.B.K. Nova Gen. Sp. Pl. 6: 73. 1820. Adams (p. 267) also mentioned a "larger variant with reddish petals." In fact, this variant comprises a rather distinctive population, differing not only in size and flower color but also in number of petals and in color and surface sculpture of the seeds. Somewhat similar plants also occur in Puerto Rico and the Virgin Islands (and perhaps elsewhere). I have been unable to find reference to such material in the literature, and although loath to describe a new species on the basis of incomplete evidence, have decided to do so in order to provide an epithet and a starting point for further studies.

Portulaca aurantiaca Proctor, sp. nov.

MAP 17.

Herba subsucculenta perennis a *Portulaca rubricaulis* in statura grandiore, foliis longioribus, floribus aurantiacis petalis 5 (haud flavis, petalis 6), capsulis acuminatis grandioribus, et seminis rufo-brunneis minute papillois, differt.

Erect perennial herb with long fleshy roots; stems up to 25 cm tall and 4 mm in diameter toward base, glabrous except for tufts of soft, white hairs in leaf axils. Leaves flattened-cylindrical, linear, 7–18 mm long, mostly 0.5–1.5 mm wide, sharply long-acuminate at apex, glabrous. Peduncles 1–2.5 cm long, glabrous, enlarged distally to 2–3.5 mm in diameter at apex; flower cluster subtended by whorl of few bracts similar to leaves, stem apex within this whorl bearing dense tuft of soft, white hairs mostly 6–8 mm long. Sepals not observed, petals 5, orange, 8–10 mm long. Capsules ovoid-acuminate, 4.5–5 mm in diameter, circumscissile below middle; seeds reddish brown, 0.5–0.7 mm in diameter, minutely and densely papillose.

St. Thomas: W side of Yallahs R. below coastal highway crossing, near sea level, Proctor 36519, Nov. 10, 1976 (holotype). (Presumably Adams's specimens from "beaches around Kingston" (1972, p. 267) are the same; not seen in conjunction with present study.) **St. Catherine:** Fort Clarence, 50–150 ft, Proctor 32626, Sept. 12, 1971.

At the latter locality, there appears to be a "hybrid swarm" of varying intermediates between *Portulaca aurantiaca* and *P. rubricaulis*.

Portulaca umbraticola Kunth in H.B.K. Nova Gen. Sp. Pl. 6: 72. 1820.

MAP 17.

Confirmed for Jamaica. **St. Elizabeth:** vic. of Billy Bay, 0.9 mi due WNW of Treasure Beach Hotel, ca. 50 ft, Proctor 35441, Nov. 8, 1975.

Adams (1972, p. 267) listed an unconfirmed report of this species, said to have been collected in "a coastal area of St. Elizabeth by N. L. Britton in 1907." Evidently this report was authentic, as confirmed by the present specimen, which was collected in dry rocky limestone woodland. The present species differs from *Portulaca oleracea* in its erect habit, its thin, widely scattered, narrowly spatulate leaves, and its gray, more prominently tuberculate seeds.

CARYOPHYLLACEAE

Cerastium L.

A critical examination of the *Cerastium* specimens at the Institute of Jamaica by Mr. David Good, formerly of Michigan State University, has shown the presence of two species in Jamaica, although in published floras (Fawcett & Rendle, 1914; Adams, 1972) only one is listed. These species can be distinguished as follows:

- A. Hairs of inflorescence glandular; upper bracts with green margins; pedicels much shorter than sepals. *C. glomeratum*.
- A. Hairs of inflorescence not glandular; upper bracts with broad, scarious margins; pedicels often equaling sepals in length or nearly so. *C. triviale*.

Cerastium glomeratum Thuill. Fl. Paris, ed. 2. 226. 1799. MAP 17.

St. Andrew: Silver Hill Gap, ca. 3500 ft, *Proctor* 24610, Feb. 11, 1964; along track between Guava Ridge and Bellevue, Port Royal Mts., 3000–3500 ft, *Proctor* 24638, Feb. 16, 1964.

This is the only species of *Cerastium* heretofore recorded from Jamaica.

Cerastium triviale Link, Enum. Hort. Berol. I: 433. 1821. MAP 17.

New to Jamaica. **St. Andrew:** Clydesdale, ca. 3500 ft, *Barry s.n.* (IJ 252), Aug. 24–31, 1943. **Portland:** near Green Hills, ca. 3600 ft, *von der Porten* (née Barry) s.n. (IJ 3072), May 24, 1950. **St. Thomas:** Arntully, ca. 3000 ft, *Proctor* 24570, Feb. 2, 1964.

This species is very widespread in North Temperate regions. In *Flora Europaea* (I: 142. 1964) it is listed as a subspecies of *Cerastium fontanum* Baumg.

CACTACEAE

The Jamaican representatives of this family pose a number of unsolved taxonomic problems, most of which cannot be discussed at the present time. These problems occur especially in the genera *Hylocereus*, *Mammillaria*, *Selenicereus*, and *Opuntia*. In *Opuntia*, variation in *O. tuna* (L.) Miller needs

investigation, particularly with reference to populations occurring in southern Clarendon and Manchester parishes. Although this species was attributed to the Cayman Islands by Adams (1972), all the Cayman records pertain to *O. dillenii* (Ker-Gawl.) Haw.

Opuntia Miller

Opuntia sanguinea Proctor, sp. nov.

MAP 18.

Frutex multo ramosus *Opuntia tuna* et affines in habitu simile, sed in statura grandiore et floribus sanguineis staminibus pistillisque perianthiis in longitudine subaequalibus, differt.

Plants bushy, much branched, ascending to erect, up to 2 or 3 m high, forming dense thickets. Joints broadly oblanceolate, oblong-oblanceolate, or elliptic, not easily detached, 14–19 cm long, 5.5–8 cm broad chiefly above middle, rounded at apex, tapering toward base; areoles 2–2.5 cm apart, each bearing tuft of yellow glochids 3–4.5 mm long, dense tuft of grayish woolly hairs much shorter than glochids, and single long, terete, brownish, retrorse spine mostly 2–3.5 cm long, or few areoles with 1 long spine and 1 usually 0.8–1 cm long. Flowers often 7 or more per joint, oxblood red, ca. 3–5 cm broad when fully open; ovary narrowly obconic, 2–2.5 cm long, 0.9–1.3 cm thick at apex, bearing numerous areoles each with tuft of glochids surrounded by much shorter mass of whitish, woolly hairs; petals obovate, up to 2.5 cm long, notched at broadly rounded apex; stamens almost equaling perianth in length, the filaments distally same color as petals, the anthers pale yellow, linear-oblong, 1–1.5 mm long; pistil about same length as stamens, stigma 6-rayed. Ripe fruits not seen.

St. Thomas: along road SE of Eleven Mile, ca. 300 ft, *Proctor 38043*, Feb. 24, 1979 (holotype).

The flowering season of this large species is very short, ranging from mid-February to a varying extent into March.

The species is unusual not only for its blood-red flowers, but also for the fact that the stamens and pistil approximately equal the perianth in length. In all other indigenous West Indian species these structures are much shorter than the perianth, whereas in the Mexican and Central American group of *Opuntia cochenillifera* (L.) Miller (*Nopalea* Salm-Dyck), they are much longer.

LAURACEAE

Ocotea Aublet

Few plant families have given rise to as much confusion as the Lauraceae, and few lauraceous genera are as confusing as *Nectandra* Rolander ex Rottb. In fact, there is a growing body of opinion that this genus is not really sep-

arable from *Ocotea*; I concur with this opinion. In the present paper the nomenclature of the four species of *Nectandra* recognized by Adams (1972) will not be considered because there exist unsolved problems of species delimitation. However, Adams's treatment of *N. coriacea* included two elements that should probably be considered separate species, as shown by the following discussion.

Fawcett and Rendle (1914) recognized six species of *Nectandra* and distinguished two (*N. sanguinea* "Roland ex Rottb." and *N. coriacea* (Sw.) Griseb.) that were separated by the following key characters:

- A. "Leaves membranous or chartaceous, axils of nerves beneath generally hairy. Inflorescence white-strigose-tomentellous, subequalling the leaves or shorter." *N. sanguinea*.
- B. "Leaves leathery, glabrous. Inflorescence glabrescent, evidently shorter than the leaves." *N. coriacea*.

The foliage characters used in this key are clear-cut, but the inflorescence distinction does not hold up; however, there are differences in the fruits not seen by Fawcett and Rendle. It should be noted in passing that Fawcett and Rendle's *Nectandra sanguinea* is equivalent to *N. exaltata* of Grisebach (1860) with regard to citations from Jamaica; Grisebach's *N. sanguinea* was what we now understand to be *N. coriacea*.

Nectandra sanguinea was cited by Fawcett and Rendle as a rare species not collected since about 1879, while *N. coriacea* was credited with numerous more modern collections. The range of *N. sanguinea* was given (p. 217) as "Mexico, Nicaragua, British Guiana, Surinam, Colombia," while that of *N. coriacea* was given (p. 218) as "West Indies, Yucatan."

Allen (1945), in discussing the two corresponding populations in Central America, pointed out that the type of true *Nectandra sanguinea* came from Suriname and represents a species different from the Central American material passing under this name. To the latter she applied the name *N. salicifolia* Kunth.

Adams (1972) did not separate or distinguish these two taxa and listed (p. 284) "[*Nectandra*] *sanguinea* of F. & R. (1914), not Roland ex Rottb. (1778)" as a synonym of *N. coriacea*.

My own attention was drawn to this problem in 1977 by Mr. G. Goodfriend, a student of land-snail ecology. In attempting a total listing of the flora in his study quadrat at Broom Hall, parish of Clarendon, Jamaica, he noticed several trees of a presumed *Nectandra* that seemed unlike typical *N. coriacea*; these turned out to show the differentiating characters of "*N. sanguinea*" as described by Fawcett and Rendle. After careful study of this population, I became convinced that it could not reasonably be included within the circumscription of *N. coriacea* and should probably be associated taxonomically with the Central American population called *Nectandra salicifolia* by Allen. However, if this is the case, then the oldest name applicable to the group as a whole is in fact the epithet *exaltata* as used by Grisebach, based on a Swartz collection from Jamaica. The nomenclature thus can be summarized as follows:

Ocotea exaltata (Sw.) Proctor, comb. nov.

MAP 18.

Laurus exaltata Sw. Prodr. 65. 1788.

Ocotea salicifolia Kunth in H.B.K. Nova Gen. Sp. Pl. 2: 132. 1817.

Nectandra salicifolia (Kunth) Nees, Syst. Laurin. 302. 1836.

N. exaltata (Sw.) Griseb. Fl. Brit. W. Indian Is. 281. 1860, in part.

N. sanguinea of Fawcett & Rendle, Fl. Jamaica 3: 217. 1914, not Rolander ex Rottb., 1778.

In addition to the old, unlocalized collections of this entity cited by Fawcett and Rendle, several modern Jamaican collections (including those of Goodfriend) have been seen. These are:

Clarendon: Broom Hall Hills, 1.2 mi due SW of Cave Valley Square, 1800–2000 ft, Goodfriend s.n. (IJ 66656), July 6, 1977, Goodfriend s.n. (IJ 66277, 69793), July 27, 1977, Proctor 37385, Oct. 22, 1977. **St. Elizabeth:** near Ipswich, 200–300 m, Maxon & Killip 1503, April 1, 1920 (A, GH, US). **Westmoreland:** 0.5 mi due W of Darliston, 1300–1400 ft, Proctor 37632, Feb. 5, 1978.

Ocotea harrisii Proctor, sp. nov.

MAP 18.

Arbor glabra parva foliis coriaceis, a *Ocotea* staminea in foliis parvioribus laevibus, venatione laterali obscura haud manifeste reticulata, et fructibus parvioribus, differt.

Glabrous tree 12 m tall. Petioles 3–5 mm long; leaf blades coriaceous, elliptic, (3–)4–7 by 1.5–3 cm, obtuse at apex, cuneate at base, margins slightly reflexed, both surfaces smooth, lateral venation obscure and not visibly reticulate. Inflorescences axillary racemes 5–8 cm long. Flowers not seen. Fruiting cupules single margined, ca. 6 mm across; fruits ellipsoid, 1.3–1.5 cm long.

Clarendon: Peckham Woods, 2500–2800 ft, Harris 10872 (holotype, UCW).

This is the entity described as "Sp. A" by Adams (1972, p. 282). Although there is no further information about this plant, it seems appropriate to provide it with a name.

Ocotea staminoides Proctor, sp. nov.

MAP 18.

Arbor dioecia *Ocotea* staminea affinis, sed in foliis grandioribus reti venularum multo remotiore, et floribus unisexualibus cum inflorescentiis staminatis paniculatis et inflorescentiis pistillatis racemosis, differt.

Dioecious tree to 15 m tall with glabrous foliage; youngest branchlets glabrate, 5–8 mm thick, often with small, corky lenticels. Petioles stout, 2-edged, 1–2 cm long; leaf blades thickly coriaceous, elliptic or oblong-elliptic, 11–19 by 5.5–11.5 cm, blunt to somewhat acute at apex, abruptly cuneate at base; venation prominently and coarsely reticulate, especially beneath, the

areoles to 2 mm or more across. Staminate inflorescences paniculate, minutely puberulous, 4–6 cm long and wide; flowers subsessile, cream colored, ca. 7 mm across when expanded; perianth segments broadly ovate, up to ca. 5 mm long, somewhat acute at apex, densely and minutely puberulous on outer side, glandular-ciliolate on margins, densely and minutely glandular-puberulous within; outer anthers subsessile, lance-oblong, ca. 2 mm long, acute, with both pairs of cells near margins, the lower pair not directly beneath the upper; inner anthers somewhat flattened-oblong, quadrangular, cells on opposite narrow sides; staminodes ovoid, ca. 1 mm long. Pistillate inflorescences racemose, 5–6 cm long, 7- or 8-flowered, lowermost flowers on pedicels 7–9 mm long; flowers white, very fragrant. Fruiting cupules fleshy, 2-margined, ca. 1.5 cm across, bearing persistent, reflexed, thickened perianth lobes in ring ca. 1–2 mm below and outside inner margin; fruits cylindrical, green, 2–2.3 by ca. 1 cm.

St. Ann: Douglas Castle distr., 2200–2400 ft, *Proctor 26413*, May 23, 1965 (♀) (holotype), *Proctor 36272*, June 11, 1976 (♂), *Proctor 37327*, Oct. 8, 1977 (young fruits), *Proctor 37405*, Nov. 12, 1977 (nearly mature fruits); Schwallenburgh, 2300 ft, *Harris 7169*, Jan. 27, 1898 (old fruiting cupules) (cat).

This species resembles *Ocotea staminea* (Griseb.) Mez, particularly in the size and structure of the fruits (2-margined cupules and accrescent persistent perianth segments). It clearly differs in its larger leaves with much coarser vein reticulation, and in the details of floral structure. *Ocotea staminea* has bisexual flowers; in *O. staminoides* the flowers are unisexual and the plants are dioecious.

NYMPHAEACEAE

Nymphaea L.

Fawcett and Rendle (1914) reported three species of *Nymphaea* from Jamaica, but Adams (1972) accepted only one of these (*N. ampla*) as a valid record. Adams (p. 290) stated his opinion that *N. amazonum* and *N. rudgeana* should be excluded because "they have not been confirmed by recent collections and may have been cultivated plants." Since the publication of Adams's book, however, field study of aquatic plants in Jamaica by Dr. Richard M. Lowden has demonstrated that three indigenous species of *Nymphaea* are indeed present in Jamaica. The presence of *N. amazonum* has been reconfirmed, and a species not previously suspected to occur here, *N. jamaisoniana*, has been discovered. I have found no further information on *N. rudgeana*. The known Jamaican species of *Nymphaea* can be distinguished as follows:

- A. Flowers diurnal; carpels free from one another at sides; styles short, stiff, fleshy, not enlarged at tip. *N. ampla*.
- A. Flowers nocturnal; carpels united by their sides; styles slender, with enlarged, club-shaped tips.

- B. Petioles with ring of long hairs at top; stamens usually 100 to 188.
 *N. amazonum*.
 B. Petioles glabrous, lacking ring of hairs at top; stamens 52 to 65.
 *N. jamesoniana*.

Field data on the last two can be summarized as follows:

Nymphaea amazonum Martius & Zucc. Abh. Bayer. Akad. Math.-Phys.
 Cl. 1: 363. 1832. MAP 19.

St. Elizabeth: Frenchman, sea level, *Proctor 38188* (coll. Lowden), June 16, 1979. **Westmoreland:** 2.5 mi WNW of Hopewell, ca. 1500 ft, *Proctor 11218* (det. Lowden), Nov. 21, 1955. **Hanover:** in the Great Morass ca. 1.9 mi due SW of Logwood, sea level, *Proctor 37518*, Dec. 20, 1977.

Fawcett and Rendle recorded this species from the parishes of St. Catherine and St. Thomas. It is otherwise known from Cuba, Hispaniola, Puerto Rico, the Lesser Antilles, Tobago, Trinidad, and South America.

Nymphaea jamesoniana Planchon, Revue Hort. IV. 2: 66. 1853. MAP 19.

New to Jamaica. **St. Elizabeth:** Frenchman, sea level, *Proctor 38190* (coll. Lowden), June 16, 1979.

This species was recorded from Cuba, Hispaniola, Puerto Rico, and Ecuador by Britton and Wilson (1924). The flowers of both *Nymphaea jamesoniana* and *N. amazonum* open only at night, which may explain why these species have usually been overlooked by collectors.

CERATOPHYLLACEAE

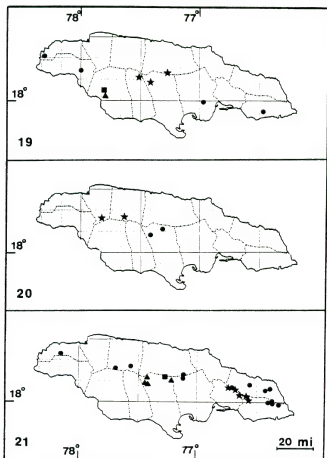
Ceratophyllum L.

The genus *Ceratophyllum* was credited with but one species by Adams (1972)—the cosmopolitan *C. demersum* L. However, field work carried out early in 1978 revealed that a second species occurs in a limited area of southwestern Jamaica. Despite the difficulty of identification, this population appears to represent the plant now correctly known as *C. muricatum*.

Ceratophyllum muricatum Cham. Linnaea 4: 504. 1829. MAP 19.

New to Jamaica. **St. Elizabeth:** Salt Spring distr., sea level, *Proctor 37683*, Feb. 20, 1978, *Proctor 37708*, March 5, 1978.

Ceratophyllum muricatum has a wide distribution in eastern North America but is reported to be much less common than *C. demersum*. The two species can usually be distinguished, at least in Jamaica, by the following key:



MAPS 19-21. Distributions: 19, *Nymphaea amazonum* (dots), *N. amazonum* and *N. jamesoniana* together (square), *Ceratophyllum muricatum* (triangle), *Laplacea glabrata* (stars); 20, *Ternstroemia bullata* (dots), *T. glomerata* (stars); 21, *Clusia havetioides* var. *havetioides* (stars), *C. havetioides* var. *pauciflora* (triangles), *C. havetioides* var. *stenocarpa* (dots), *Dionaea muscipula*, *Sarracenia minor*, and *S. rubra* (location of Mason River Field Station; square).

- A. Plants of somewhat stiff, harsh texture; leaves forked 1 or 2 times (rarely unforked), with divisions of nearly uniform width up to tapered apices; fruits un-winged, with 1 long spine at distal end and 2 divergent spines from basal end. *C. demersum*.
- A. Plants of soft, slippery texture; leaves forked 2 to 4 times, with basal division inflated above narrowed base; fruits narrowly winged, with 1 apical spine and 0 to 2 or more relatively short spines along margins. *C. muricatum*.

THEACEAE

Laplacea Kunth**Laplacea glabrata** Proctor, sp. nov.

MAP 19.

Frutex vel arbor parva usque ad 8 m alta, a speciebus aliis Laplaceae Jamaicae in indumento fere nullo et floribus parvioribus subsessilibus differt, a Laplacea haematoxylon in forma laminae et fructibus seminisque grandioribus differt, et a *L. villosa* in sepalis multo parvioribus et filamentis brevioribus differt.

Shrub or small tree to 8 m tall. Terminal buds glabrous or minutely and sparsely puberulous; young branchlets glabrous. Leaves coriaceous, glabrous throughout, glossy deep green adaxially, paler abaxially, elliptic to narrowly obovate, 6–12 by 2.5–4.5 cm, obtuse and minutely emarginate at apex, subsessile at base or narrowed to petiole 1–2 mm long, the margins obscurely crenate-serrulate chiefly along distal half, the veins obscure, in 12 to 20 pairs, minutely prominulous on both sides when dry. Flowers solitary in upper axils, creamy white, 2.5–3 cm in diameter when open, nearly sessile, the stout glabrous peduncle nearly obsolete or scarcely 1 mm long; bracteoles 2, sepaloid, caducous; sepals 5, unequal, imbricate, rounded, concave, glabrous except for ciliolate margins, 4–6 mm long and wide; petals 5 or 6, white, oblanceolate to narrowly obovate, unequal, ranging from 1.2 to 1.5 cm long and from 0.5 to 1.1 cm wide on same flower (wider petals deeply and broadly emarginate), glabrous or sparsely ciliate near apex; filaments glabrous, subequal, more or less adnate to each other at base, 2–3 mm long, anthers ca. 0.2 mm in diameter, ovary globose, appressed-puberulous, 5-locular, bearing cluster of minute, sessile stigmas at apex. Capsules woody, narrowly obovoid, 2.2–2.5 cm long, ca. 1 cm in diameter above middle, minutely and sparsely appressed-puberulous; seeds ca. 3 in each locule, 15–17 mm long including wing.

St. Ann: Mason River distr., ca. 3 mi due NW of Kellits P.O., ca. 2100 ft, *Proctor 28611*, April 12, 1968 (holotype). **Clarendon:** Glenwood Springs, along road between Balcarres and Sunbury, ca. 3100 ft, *Proctor 33486*, Aug. 18, 1973, *Proctor 37470*, Dec. 4, 1977. **Manchester:** 0.5 mi NW of Christiana, ca. 3000 ft, *Proctor 18293*, Oct. 25–26, 1958.

This species differs from both its Jamaican congeners in being nearly gla-

brous and in having smaller, nearly sessile flowers. In addition, it differs from *Laplacea haematoxylon* in leaf shape and texture and in its larger fruits and seeds, and from *L. villosa* in its much smaller sepals and shorter filaments. From *L. wrightii* Griseb. of Cuba (the only other species of *Laplacea* with glabrous terminal leaf buds), *L. glabrata* differs in its much larger leaves, nearly sessile flowers, and smaller and glabrous sepals, as well as in other details.

Laplacea glabrata is one of a large number of rare relict species representing many families that survive precariously in threatened habitats around the fringes of the region known to geologists as the Central Inlier. The following species, *Ternstroemia bullata*, is another of these.

***Ternstroemia* Mutis ex L. f.**

***Ternstroemia bullata* Proctor, sp. nov.**

MAP 20.

Arbor glabra 10–18 m alta ramis verticillatis foliis bullatis revolutisque, a *Ternstroemia howardiana* in petiolis multo brevioribus, pedicellis crassioribus, sepalis angustioribus, filamentis brevioribus haud dilatatis, et antheris brevioribus, differt.

Glabrous tree 10–18 m tall with verticillate branches. Petioles 2–5 mm long; leaf blades coriaceous, dark green adaxially, paler abaxially, broadly elliptic to obovate or subrotund, 3–7 by 1–4.5 cm, the margins broadly and deeply recurved-revolute (revolute portion up to 7 mm wide), entire, the apex rounded, subemarginate, the base abruptly cuneate, the midvein narrowly grooved adaxially, prominent abaxially, the veins obscure, 6 to 9 pairs. Flowers solitary; pedicels 10–17 mm long, flattened and 2-edged toward ca. 1.5-mm-wide distal end; bracteoles 2, opposite, subequal, narrowly oblong-deltate, ca. 2.5 mm long, margins glandular-denticulate; sepals 5, subequal, oblong to ovate, with glandular-denticulate margins, the outer ones 4.5–5 by ca. 2.5 mm, with apex acute or apiculate, the inner similar but slightly longer and broader; petals white, subequal, slightly exceeding sepals, connate at base; filaments glabrous, 1.5–2 mm long, adnate to base of corolla, anthers ca. 1.5 mm long, calcarate at apex; ovary conical, glabrous, ca. 4 mm long and 1.8 mm in diameter at base, 2-loculate; stigma entire. Fruits not seen.

Clarendon: Glenwood Springs, along road between Balcarres and Sunbury, ca. 3100 ft, *Proctor 34103*, June 29, 1974 (holotype), *Proctor 33632*, Nov. 30, 1973, *Proctor 33825*, April 24, 1974; stream gully 0.9 mi by road E of Reckford, ca. 2000 ft, *Proctor 38109*, March 29, 1979, *Proctor 38134*, April 29, 1979.

Ternstroemia bullata is unique in its bullate-revolute leaves; in other respects it most resembles *T. howardiana* Kobuski of the John Crow Mountains among Jamaican congeners, differing from that species in its much shorter petioles, thicker pedicels, narrower sepals, shorter and nondilated filaments, and shorter anthers.

***Ternstroemia glomerata* Proctor, sp. nov.**

MAP 20.

Arbor 10–15 m alta foliis planis late ellipticis et floribus terminalibus glomeratis subsessilibus.

Tree 10–15 m tall. Petioles 7–15 mm long; leaf blades coriaceous, broadly elliptic, 8–14 by 4–8 cm, the margins flat, entire, the apex blunt to broadly rounded, minutely emarginate, the base abruptly cuneate, the midvein grooved in lower 2/3 adaxially, prominent abaxially, the veins 8 to 10 pairs, minutely prominulous on both sides when dried. Flowers 3 to 6 aggregated in glomerate terminal clusters; pedicels 2–5 mm long, terete, ca. 2 mm thick; bracteoles 2, opposite, nearly equal, broadly ovate, ca. 3 mm long and wide, margins glandular-denticulate; sepals 5, subequal, broadly ovate, 4.5–5.5 mm long and wide, margins glandular-denticulate, apex blunt or subacute; petals white, subequal, 2–3 mm longer than sepals, rounded at apex, shortly connate at base; filaments glabrous, 2–3 mm long, adnate to base of corolla, the anthers 1.1–1.3 mm long, calcarate at apex; ovary conical, glabrous, 4–4.5 mm long, ca. 3 mm in diameter at base, 2-locular, stigma entire. Fruits (immature?) ovoid, ca. 10 by 7 mm, acuminate beaked.

St. James: White Rock Hill, 1 mi S of Sweet Water, ca. 2100 ft, *Proctor 34509*, Dec. 22, 1974 (holotype), *Proctor 34459*, Dec. 13, 1974. **Trelawny:** near Crown Lands road extension 4.5–5 mi NW of Troy, ca. 2000 ft, *Proctor 34715*, Jan. 26, 1975.

Ternstroemia glomerata is perhaps unique in the genus for its tightly clustered flowers, always borne at the apex of a leafy stem. It is also unusual in having very short, thick pedicels, which cause the flowers to appear nearly sessile. Among the West Indian species of this genus, only *T. subsessilis* Britton of Puerto Rico has shorter pedicels, but it is a shrub with solitary flowers and eglandular sepals.

GUTTIFERAE

***Clusia* L.**

The Jamaican species of this genus, especially the complex of endemic forms included under *Clusia havetioides* (Griseb.) Planchon & Triana by Adams (1972), appear to require further study and taxonomic evaluation. In the case of *C. havetioides* it is here proposed that three varieties be recognized, rather than having all variants submerged under a single name.

- A. Ripe fruits 1 to 9 per inflorescence, 15–20 mm long; petals of staminate flowers 6 mm long.
- B. Leaves 7–18 cm long (rarely less); staminate flowers numerous per inflorescence. var. *havetioides*.
- B. Leaves 3–6 cm long (rarely more); staminate flowers 1 to 3 per inflorescence. var. *pauciflora*.

- A. Ripe fruits 9 to 50 per inflorescence, 10–14 mm long (rarely more); petals of staminate flowers 3–4 mm long. var. *stenocarpa*.

Clusia havetioides (Griseb.) Planchon & Triana, Ann. Sci. Nat. Bot. IV. 13: 368. 1860.

Clusia havetioides var. **havetioides**

MAP 21.

This variety is confined to the higher slopes of the Blue and Port Royal mountains at elevations of 4200–5200 ft or more.

Clusia havetioides var. **pauciflora** Proctor, var. nov.

MAP 21.

A vars. *havetioides* et *stenocarpa* in ramulis ascenduntibus, foliis parvulis chartaceis, et inflorescentibus 1–3 floris differt.

Glabrous tree 10–12 m tall, d.b.h. to 25 cm; branches noticeably ascending. Leaves thin, papery, narrowly obovate to obovate, mostly 3–6 cm long, 1.5–3.5 cm broad above middle, at base narrowed to broad petiole 5–10 mm long. Inflorescences 1- to 3-flowered. Staminate flowers pale yellow; petals 6 mm long; stamens numerous, free, filaments 3.5–4 mm long. Pistillate flowers not seen. Fruits ovoid, ca. 15 mm long.

Clarendon: upper W slope of Crofts Mt., 2250–2500 ft, *Proctor* 29239, Oct. 4, 1968 (♂)(holotype, ♀); near S end of Crofts Mt., 2250–2500 ft, *Proctor* 31185, Jan. 10, 1970 (♀—fruits). These trees growing on steep, densely wooded hillside over limestone; numerous individuals seen. Other collections probably belonging here: **Clarendon:** Peckham Woods, ca. 2500 ft, *Proctor* 34369, Nov. 28, 1974; along road between Ritchies and Balcarres, ca. 3000 ft, *Proctor* 34378, Nov. 28, 1974.

Clusia havetioides var. **stenocarpa** (Urban) Proctor, comb. et stat. nov.

MAP 21.

Clusia stenocarpa Urban, Symb. Antill. 5: 433. 1908.

This is the commonest variety of the *havetioides* complex and has a wide distribution throughout Jamaica, chiefly at medium elevations.

DROSERACEAE

Dionaea Ellis

Dionaea muscipula Ellis ex L. Mant. Pl. 2: 238. 1771.

MAP 21.

Genus and species new to Jamaica. **Clarendon:** Mason River Field Station, ca. 2300 ft, *Proctor* 36282, June 11, 1976.

This well-known insectivorous plant was introduced at the above locality

from North Carolina in 1968; the population derives from a single live plant sent in a letter by the late Mrs. Marie Wurdack. The species has flourished and spread at Mason River and can now be considered naturalized. It flowers and fruits regularly in May and June every year, and numerous seedlings have become established and have grown to maturity.

SARRACENIACEAE

Sarracenia L.

Genus new to Jamaica. Two species have been introduced into Jamaica and have seemingly become established. They can be distinguished as follows:

- A. Pitcher orifice covered by hood, the hood with translucent spots; petals pale yellow. *S. minor*.
 A. Pitcher orifice exposed, the hood without translucent spots; petals dark red. *S. rubra*.

Sarracenia minor Walter, Fl. Carolin. 153. 1788.

MAP 21.

New to Jamaica. **Clarendon:** Mason River Field Station, ca. 2300 ft, *Proctor* 36301, June 10, 1976, *Proctor* 37223, Sept. 9, 1977.

I introduced this plant from Gilchrist County, Florida, in July, 1975. It has been producing flowers every year since its introduction, but no seedlings have thus far been observed.

Sarracenia rubra Walter, Fl. Carolin. 152. 1788.

MAP 21.

New to Jamaica. **Clarendon:** Mason River Field Station, ca. 2300 ft, *Proctor* 36302, June 10, 1976.

Introduced from North Carolina in 1968. This species has been flourishing vegetatively at Mason River but so far has not flowered there.

LEGUMINOSAE SUBFAMILY CAESALPINIOIDEAE⁴**Caesalpinia** L.

The prickly-fruited vines called "nickal" in Jamaica were placed in two species by Adams (1972): *Caesalpinia bonduc* (L.) Roxb., with gray seeds; and *C. major* (Medicus) Dandy & Exell, with yellow seeds. He pointed out, however, that the latter name might not be correct for the Jamaican yellow-

⁴Adams (1972) recognized three legume families: Caesalpiniaceae, Mimosaceae, and Papilionaceae (Fabaceae). I prefer to treat these as subfamilies of Leguminosae.

seeded plants, which would more likely show a relationship with similar Cuban species. Shortly before his untimely death, Dr. W. T. Gillis and I were investigating this problem and studied the types of the relevant Cuban taxa. Our conclusion—never published—was that Jamaica had two yellow-seeded species, both originally described by Urban from Cuba. These can be distinguished as follows:

- A. Leaflets mostly 4–6 cm long; pods ca. 4 cm broad, abruptly rounded or subtruncate at base. *C. intermedia*.
- A. Leaflets mostly 2–3.5 cm long; pods less than 3.5 cm broad, often narrowed toward base. *C. wrightiana*.

Caesalpinia intermedia Urban, Symb. Antill. 2: 274. 1900.

C. major of Adams, Fl. Pl. Jamaica, 320. 1972, not (Medicus) Dandy & Exell, 1938.

This species is quite common on the interior limestone hills of Jamaica, reaching an elevation of at least 2700 ft. It has been recorded from the parishes of St. Catherine, Clarendon, Manchester, St. Elizabeth, and Trelawny.

Caesalpinia wrightiana Urban, Symb. Antill. 2: 274. 1900.

New to Jamaica. **Manchester:** Gut R., sea level, *Proctor* 38194, June 17, 1979 (?). **St. Elizabeth:** below Lovers Leap, ca. 1 mi due SSE of Southfield P.O., 500–1500 ft, *Proctor* 32990, Nov. 11, 1972 (fruits).

LEGUMINOSAE SUBFAMILY FARBOIDEAE

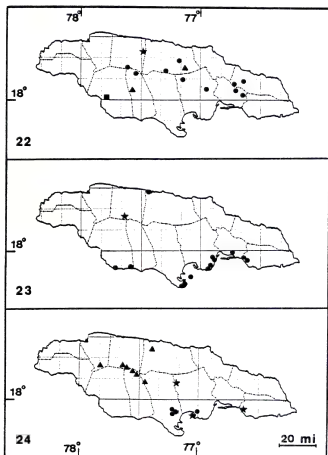
Rhynchosia Lour.

Adams (1972) listed four Jamaican species of this genus, but a recent monographic study by Grear (1978) has shown that the Jamaican material included by Adams under the name *Rhynchosia phaseoloides* in reality represents three species, among which the monographer found "absolutely no intermediates" (p. 49). These can be distinguished as follows:

- A. Pods inflated and deeply constricted, glabrous or becoming so, brown to blackish and shiny with age; each seed not equally red and black.
 - B. Seeds red with small black spot. *R. pyramidalis*.
 - B. Seeds black with small red spot. *R. erythrinoides*.
- A. Pods subinflated and only slightly constricted, permanently rusty-pubescent; each seed equally red and black. *R. phaseoloides*.

Rhynchosia pyramidalis (Lam.) Urban, Repert. Sp. Nov. 15: 318. 1918, in part. MAP 22.

For this and the following species, the specimens cited include those re-



MAPS 22-24. Distributions: 22, *Rhynchosia erythrinoides* (dots), *R. pyramidalis* (triangles), *R. erythrinoides* and *R. pyramidalis* together (star), *Sesbania emerus* (square); 23, *Spathelia coccinea* (star), *Bursera lunanii* (dots); 24, *Malpighia adamsii* (triangles), *M. cauliflora* (stars), *M. proctorii* (dots).

ported by Grear (1978) and the material at U, none of which was studied by Grear.

Manchester: Somerset distr., ca. 5 mi NW of Mandeville, ca. 2300 ft, *Proctor 16032*, Dec. 29–30, 1956 (flowers), *Proctor 11589*, Feb. 25, 1956 (young fruits). **Trelawny:** Westwood School, 1 mi NW of Stewart Town, 1000 ft, *Chevannes s.n. (IJ 4067)*. **St. Ann:** Moneague, *Alexander (Prior) 8*, 1850 (K). **St. Andrew?**: "vic. Kingston,"⁵ *Crawford 618-a*, April 22–24, 1910 (PH).

Rhynchosia erythrinoides Schlecht. & Cham. *Linnaea* 5: 587. 1830.

MAP 22.

St. Andrew: Clydesdale, 3500 ft, *von der Porten s.n. (IJ 2394)*, Aug. 28, 1948 (fruits); near Newcastle, 3937 ft, *Barkeley & Rishbeth 1119*, June 20, 1952 (fruits). **St. Catherine:** 1.5 mi due SE of Sligoville, 1800–1900 ft, *Proctor 31726*, April 16, 1971 (flowers); along road between Ewarton and Worthy Park, ca. 1700 ft, *Proctor et al. 24075*, Feb. 21, 1964 (flowers). **Manchester:** summit of Mt. Denham, 3236 ft, *Proctor 34883*, March 7, 1975 (flowers); 1.5 mi due SE of Mandeville, ca. 2100 ft, *Proctor 33755*, March 30, 1974 (flowers); vic. Mandeville, *Brown 118*, Feb. 15–26, 1910 (SY, PH). **Trelawny:** near Troy, *Harris 8775*, Aug., 1904 (BM, F, NY); vic. of Westwood High School, Stewart Town, ca. 1150 ft, *Powell 827*, March 10–12, 1960 (flowers). **St. Ann:** Douglas Castle distr., ca. 2300 ft, *Proctor 32867*, March 31, 1972 (flowers); near Lydford P.O., 1500 ft, *Proctor 8645*, April 22, 1954 (flowers), *R. A. Howard & Proctor 14100*, Sept. 23, 1954 (fruits). **Portland:** near Green Hill P.O., ca. 2600 ft, *Proctor 23411*, March 30, 1963 (flowers) (U, MICH, NY, U. US); ca. 1 mi SW of Shirley Castle, 1600–1900 ft, *Proctor 30026*, April 9, 1969 (flowers). **St. Thomas:** above Farm Hill Works, ca. 3800 ft, *Barry s.n. (IJ 933)*, July 29, 1946.

Other Jamaican specimens were seen and annotated by Grear at various herbaria but were not cited in his monograph. This species appears to be the most common of the three now being reported; it has the widest range in Jamaica.

Rhynchosia phaseoloides (Sw.) DC. *Prodr.* 2: 385. 1825, in part.

Known in Jamaica only from the unlocalized type collected by Swartz in 1784–86. Some of Swartz's material at Stockholm is mixed with specimens of *Rhynchosia pyramidalis*. This suggests that the two species may have been collected at the same time and locality (unfortunately still unknown, but most likely in the Cockpit Country area).

Sesbania Scop.

Sesbania emerus (Aublet) Urban, *Repert. Sp. Nov.* 16: 149. 1919.

MAP 22.

New to Jamaica. **St. Elizabeth:** 0.5 mi NE of Salt Spring Junction, near sea level, *Proctor 32755*, Dec. 13, 1971.

⁵This locality may be incorrect.

Occurs elsewhere in Florida, the Bahamas, the Greater Antilles, and through most of Central America, chiefly at low elevations.

Among the recorded Jamaican species, *Sesbania emerus* could be confused only with *S. exasperata* Kunth. From the latter it is distinguished by having fewer leaflets (up to 25, vs. 30 to 50), longer calyx teeth (ca. 2 vs. ca. 1 mm long), and slightly smaller flowers that are more or less densely maroon dotted (vs. nearly without such dots). It should be noted that the occurrence of *S. exasperata* in Jamaica at the present time is doubtful, the sole record being an unlocalized collection of Purdie dating from the 1840's.

RUTACEAE

Spathelia L.

This genus is represented in Jamaica by three endemic species, one of them described here for the first time. These can be distinguished as follows:

- A. Leaflets all sessile or subsessile; filaments with hairy, winglike appendages. *S. sorbifolia*.
- A. Leaflets all (or at least lower ones) distinctly stalked; filaments lacking winglike appendages.
 - B. Leaves 30–55 cm long; pedicels hispidulous with straight hairs; flowers crimson, sepals and petals bearing minute, capitate-glandular hairs; fruits acuminate at both ends. *S. coccinea*.
 - B. Leaves up to 110 cm or more long; pedicels puberulous with curved hairs; flowers pink, sepals and petals glabrous; fruits blunt at both ends. *S. glabrescens*.

***Spathelia coccinea* Proctor, sp. nov.**

MAP 23.

Arbor gracilis haud ramosa *Spathelia glabrescenti* affine, sed in statura parvior, pedicellis hispidulis, floribus sanguineis sepalis petalisque glandibus minutis capitatis munitis, et fructibus acuminatis, differt.

Slender, unbranched tree to 5 m tall, glabrous throughout except flowers. Leaves glossy, 30–55 cm long; leaflets 14 to 18 pairs, the petiolules 1–5 mm long, the blades oblong, 3–10 by 1–2.3 cm, apiculate at apex, often inequilateral at broadly cuneate base, margins entire or crenulate. Inflorescences with branches glabrous or nearly so; pedicels densely hispidulous. Flowers crimson, both calyx and corolla bearing numerous minute, capitate-glandular hairs; sepals narrowly oblong-elliptic, 2.5–3 mm long, acute and with sessile resinous gland at apex; petals narrowly oblong-elliptic, 4–6 by ca. 2 mm, acute and with sessile resinous gland at apex; filaments without winglike appendages, glabrous or sparsely hairy toward base, 3–3.5 mm long; fertile pistil not seen. Fruits 1–1.9 by 1–1.4 cm, acuminate at both ends, apex pointed.

Trelawny: near Crown Lands road extension 4.5–5 mi NW of Troy, ca. 2000 ft,

Proctor 34571, Jan. 4, 1975 (mounted on 3 sheets bearing, respectively, leaves, flowers, and fruits) (holotype), *C. D. Adams 12844*, May 8, 1966.

This species was mentioned by Adams (1972, p. 383) as "almost certainly a distinct species"; he also stated that the flowers are scarlet, although his specimen label gives the color as crimson. Actually, "oxblood red" might be a closer approximation among these subtle shades of color, but "crimson" is a more felicitous term.

BURSERACEAE

***Bursera* Jacq. ex L.**

***Bursera lunanii* (Sprengel) C. D. Adams & Dandy ex Proctor, comb. nov. MAP 23.**

Amyris lunanii Sprengel in L. Syst. Veg. ed. 16. 2: 217. 1825 (Jan.-May).
Bursera simplicifolia DC. Prodr. 2: 78. 1825 (mid-Nov.).

Urban (Symb. Antill. 6: 102. 1909) placed *Amyris lunani* (*sic*) into the synonymy of *Bursera simplicifolia* after comparing the original specimens of these species, without at the time being aware that Sprengel's name antedated that of de Candolle. Adams (1972) mentioned the necessary new combination, *Bursera lunanii* (with corrected spelling of the specific epithet), without formally validating it.

MALPIGHIACEAE

***Malpighia* L.**

In his 1979 Ph.D. thesis at Cornell University, José Vivaldi significantly revised and augmented our knowledge of this genus. Three new Jamaican species were described. Because these have not hitherto been formally published, Dr. Vivaldi has generously given permission for them to be included in this paper. He has asked that William J. Dress's aid with the Latin descriptions be acknowledged.

***Malpighia adamsii* Vivaldi, sp. nov.**

Malpighia ficata sensu Adams, Fl. Pl. Jamaica, 398. 1972, not Ker-Gawl. Bot. Register 3: t. 180. 1817.

Ab *Malpighia harrisii* differt in ramis novellis strigosis, setis malpighiaceis 1.5–2 mm longis rectis vel parum undulatis aliquantulum rigidis pungentibusque in basibus tuberculatis prominentibus longe-persistentibus praeditis, ramis vetustioribus plerumque nigris, tuberculatis; folia (6.5–)10–17(–22) cm

longa, 3–5(–9.5) cm lata, lanceolata vel ovato-lanceolata; inflorescentia strigilosa.

Shrub or small tree 1–3(–5) m tall, the young branches densely strigose, with bristles 1.5–2 mm long, straight or slightly undulate, somewhat persistent, borne on prominently raised, long-persistent, tuberclelike bases, the older branches usually black and tuberculate. Petioles (3–)5–12 mm long, green and strigose like young branches (but bristles sessile and deciduous), usually becoming black and rough, with prominent, long, transverse lenticels; stipules ca. 1.5 mm long, subulate or linear-lanceolate, black, strigillose when young; leaf blades chartaceous to subcoriaceous, lanceolate or sometimes ovate-lanceolate, (6.5–)10–17(–22) by 3–5(–9.5) cm, (2–)2.5–5 times longer than wide, the apex acute, very rarely obtuse or retuse, the base obtuse; young leaves strigose on both sides, the bristles sessile, 5–8 mm long, the adaxial surface becoming glabrous; dry leaves green, with clearly marked or sometimes prominent reticulate venation, the abaxial surface sometimes becoming glabrous, only midvein prominent. Inflorescences corymbose or umbellate panicles or racemes composed of (1 to) 3 long-stalked, 4- to 10-flowered umbels arising from common short stalk, 1.5–3.5 cm long, densely strigillose; peduncle (3–)4–9(–11) mm long; bracts 1(–1.5) mm long; pedicel with the lower part (2–)3–5 mm long, the upper part 10–20 mm long, (2–)3–7 times longer than lower part; bracteoles 1 mm long. Flower buds ca. 4 mm in diameter, corolla at anthesis ca. 15 mm in diameter; sepals (2–)2.5–3.5(–4) mm long, somewhat strigillose, the glands 6 (to 8), 1.5–2(–2.5) mm long, all about equal in size; petals slightly winged, with wings up to 0.5 mm wide and decurrent at apex, the posterior petal 7–10 mm long, with claw (2.5–)3.5–4 mm long and limb 4–6.5 mm in diameter; filaments (2.5–)3.5–4(–4.5) mm long, lateral anthers 1.5–1.7 mm long, others 0.8–1 mm long; styles uncinate at apex, lateral ones 4–5 mm long with pollination gap ca. 1 mm long, anterior one 3–4 mm long, the ovary 1.5–2 mm in diameter, usually 3-lobed. Fruits ca. 1 cm in diameter, pyramidal-globose; pyrenes 6–9 by 4–7 mm, the dorsal wing entire, 1–1.5 mm wide, the lateral wings small, blunt, crenate.

Trelawny: Troy, ca. 1550 ft, *Proctor* 9908, March 13, 1955 (holotype, λ ; isotypes, u , ny); Crown Lands area, ca. 5 mi NW of Troy, 1750–2000 ft, *Proctor* 35234, June 10, 1975. **Manchester:** slopes of Mt. Denham, 3000–3100 ft, *Proctor* 34890, March 7, 1975; $\frac{1}{2}$ mi NW of Christiana, 3000 ft, *R. A. Howard & Proctor* 14326, July 3, 1955 (λ , u). **Clarendon:** Ritchies to Banana Ground, 2 mi S of White Shop, ca. 2000 ft (*sic*), *Vivaldi* 366 and 367, Nov. 28, 1974 (nh , u , su). **St. Ann:** Browns Town, ca. 2000 ft, *Adams* 12744, Nov. 13, 1965 (mo). **St. James:** White Rock Hill, 1 mi S of Sweet Water, ca. 2100 ft, *Proctor* 34508, Dec. 22, 1974.

Named for Dr. C. Dennis Adams, author of *Flowering Plants of Jamaica* (1972), who first recognized this taxon as distinct from *Malpighia harrisii* Small.

Malpighia cauliflora Proctor & Vivaldi, sp. nov.

Frutex vel arbor parva usque ad 6 m. Folia (3.5)–4.5–6(–8) cm longa, (2)–2.5–4.5(–5) cm lata, plana, subcoriacea, elliptica vel elliptico-ovata, utrinque glabra, apice acuta, rarissime obtusa, base acuta, margine integra, petiolo (2)–3–4(–6) mm longo, glabro. Umbellae 2- ad 10-florae, sessiles, cauliflorae, pedunculo nullo, parte inferiore pedicelli 1.5–3 mm longa, pilis malpighiaceis tenuibus, minutis, rufis, sparsis, parte superiore pedicelli 9–12 mm longa, glabra. Flores rosei, 12–15 mm diametro, sepalis 2–2.5 mm longis, ovatis, glabris, apice acutis, raro obtusis, glandulis 6, 1.5–2 mm longis, oblongis, staminibus duobus petalis lateralibus oppositis quam ceteris manifeste longioribus crassioribusque, curvatis, stylis 2 posticis quam antico manifeste longioribus crassioribusque, curvatis, apice uncinatis.

Shrub or small tree up to 6 m tall, the young branches green, smooth, the older branches usually with prominent lenticels. Petioles (2)–3–4(–6) mm long, slender, glabrous; stipules 0.3–0.5(–0.7) mm long, early deciduous; leaf blades subcoriaceous, elliptic to elliptic-ovate, (3.5)–4.5–6(–8) by (2)–2.5–4.5(–5) cm, apex acute (rarely obtuse), base acute, glabrous on both surfaces; glands located near base. Inflorescences sessile, cauliferous, 2- to 10-flowered, umbel-like, contracted panicles or racemes, 1.5 cm long, sparsely covered with reddish, minute hairs except for glabrous upper part of pedicel; bracts 0.5–1 mm long; pedicel with lower part 1.5–3 mm long, upper part 9–12 mm long; bracteoles 0.5 mm long, usually 0.5–1 mm below articulation of lower and upper parts of pedicel. Flower buds up to 4 mm in diameter, corolla at anthesis 12–15 mm in diameter; sepals 2–2.5 mm long, glabrous, the glands 6, 1.5–2 mm long; petals not winged, the posterior petal 5.5–7.5 mm long, with claw 2.5–3 mm long and limb 3–4.5 by 4–6 mm; filaments 2–2.5 mm long, lateral anthers 1.3–1.5 mm long, others 0.7–1 mm long; lateral styles 2–2.5 mm long, apex uncinuate with pollination gap 0.5–1 mm long, the anterior style ca. 1.5 mm long, apex obtuse or truncate, the ovary 1.5 mm in diameter, unlobed. Fruits 5–8 mm in diameter; pyrenes ca. 5 mm long, the lateral wings coarse, blunt, ca. 3 mm wide, the dorsal wing poorly developed.

St. Catherine: hilltop 1.5 mi W of Lluïdas Vale, 1200–1400 ft, *Proctor 34120*, July 12, 1974 (holotype, *u*; isotype, *sn*), *Vivaldi 376*, Nov. 30, 1974 (*sn*); Great Goat Is., near sea level, *Scott 296*, Sept. 9, 1970 (*UCW, u*). **St. Thomas:** Eleven Mile, 300 ft, *Lewis s.n.*, May 14, 1952 (*u, us*).

The leaves of this species usually suffer from corky spots and blistered areas on the underside, a condition known as "edema"; this is believed to be caused by a physiological upset in the water balance of affected plants that occurs when the roots take in water faster than it can be transpired. The excess water builds up pressure in the mesophyll cells of the leaf, causing them to enlarge and burst. Within the genus *Malpighia*, the condition seems to occur only in *M. cauliflora*.

***Malpighia proctorii* Vivaldi, sp. nov.**

Frutex vel arbor parva usque ad 4 m, ramis novellis rubellis, strigillosis. Folia (1.5-)2-3.5(-5) cm longa, 1-2.3(-3.5) cm lata, plana vel undulata, coriacea, elliptico-oblonga, interdum obovata, apice obtusa, interdum retusa, plerumque mucronulata, base obtusa, raro cuneata, margine integra vel crenata, supra atroviridi, nitida, fere vel omnino glabra, infra olivacea, dense strigillosa, pilis malpighiaceis flavescentibus, translucentibus, rigidis, rectis, 0.5-0.7(-1) mm longis, petiolo (1-)1.5-2 mm longo, strigillosa. Umbellae 2- ad 4- (ad 6-)florae, axillares, pedunculo strigilloso, 2-8(-12) mm longo, parte inferiori pedicelli strigillosa, (2.5-)3.5-5.5(-6.5) mm longa, parte superiori pedicelli (7-)10-12 mm longa, glabra. Flores rosei, albescentes, ca. 20 cm in diametro, sepalis (2.5-)3-3.5 mm longis, ovato-lanceolatis, apice obtusis, ciliatis, glandulis 10, 1.5-2 mm longis, oblongis, staminibus aequalibus, eis petalis lateralibus oppositis quam ceteris manifeste crassioribus, curvatis, antheris 0.8-1.2 mm longis, ovatis, connectivo ovato, apice valde acuto, atrorubro vel nigro, stylis 2 posticis quam antico manifeste longioribus crassioribusque, curvatis, apice uncinatis. Fructus 0.8-1 cm in diametro, subglobosus.

Shrub or small tree up to 4 m tall, the young branches reddish, strigillose, with hairs 0.5-1 mm long, sessile, undulate or v-shaped, both arms about same in length. Petioles (1-)1.5-2 mm long, densely strigillose, with hairs like those on young branches; stipules 0.7-1.2(-1.5) mm long; leaf blades coriaceous, elliptic-oblong or sometimes obovate, (1.5-)2-3.5(-5) by 1-2.3(-3.5) cm, flat or somewhat undulate, the apex obtuse, sometimes retuse, the base obtuse, rarely somewhat cuneate, the margin entire or slightly crenate, usually unarmed, the adaxial surface shiny dark green, glabrous or sometimes sparsely strigillose but becoming glabrous, the abaxial surface pale green, usually very densely strigillose, with hairs 0.5-0.7(-1) mm long, somewhat stiff, sessile, 2-armed, the arms about equal in length. Inflorescences 2- to 4- (to 6-)flowered, 2-2.5 cm long, equal to or shorter than leaves, strigillose except for the glabrous upper part of pedicels; peduncle 2-8(-12) mm long; bracts 1-1.5 mm long; pedicel with the lower part (2.5-)3.5-5.5(-6.5) mm long, the upper part (7-)10-12 mm long, 1.5-3 times longer than lower part, usually with collar of stiff hairs just below calyx; bracteoles 0.5-1 mm long. Corolla at anthesis ca. 20 mm in diameter; sepals (2.5-)3-3.5 mm long, glabrous but with apex usually ciliate, the glands 10, 1.5-2 mm long, $\frac{1}{2}$ to $\frac{2}{3}$ as long as sepals; posterior petal 9-12.5 mm long, the claw 4-6 mm long, the limb 5-6.5 mm long, usually sharply reflexed backward; filaments 2-3.5 mm long, the anthers 0.8-1.2 mm long, the connective dark red to black, usually sharply pointed at apex; styles uncinuate at apex, the lateral ones 3-4.4 mm long with pollination gap 1-1.5 mm long, the anterior one 0.5-1 mm shorter than others, with pollination gap ca. 0.5 mm long, the ovary ca. 1.5 mm in diameter. Fruits 8-10 mm in diameter; pyrenes 5-7 by 4.5-5.5 mm, dorsal wing ca. 1 mm wide, lateral wings small, thick.

Clarendon: along road from Free People S toward Harris Savanna, 300-400 ft, Proctor 34236, Oct. 31, 1974 (holotype); Harris Savanna, 300-400 ft, Proctor

34203, Oct. 1, 1974, *Proctor* 34307, Nov. 13, 1974, *Vivaldi* 349 and 351, Nov. 26, 1974 (BH, U, SIU); along road 1–1.5 mi SSW of Inverness, toward Breadnut Gully, 200–300 ft, *Proctor* 34194, Oct. 1, 1974, **St. Catherine**: Hellshire Hills, area W of Salt Island Lagoon, 10–100 ft, *Proctor* 28785, June 23, 1968.

Named for Dr. George R. Proctor, who first collected it and recognized it as new.

Malpighia proctorii is closely related to *M. nummulariifolia* Niedz. of Cuba, but differs in its much larger leaves and its pedunculate inflorescences. It is also closely related to *M. micropetala* Urban of Hispaniola, but differs from that species in having densely strigillose leaves. With both of these species it shares the black to dark red anther connectives that are usually pointed at the apex, as well as the very thickly coriaceous, flat leaves.

POLYGALACEAE

Polygala L.

Polygala leptocaulis Torrey & Gray, Fl. N. Am. 1: 130. 1838. MAP 25.

New to Jamaica. **St. Elizabeth**: Slipe distr., in savannalike pasture along edge of swamp, near sea level, *Proctor* 33389, July 1, 1973.

This species has also been found in Cuba and ranges on the continent from the southern United States to South America. It somewhat resembles *Polygala paniculata* L. (a common Jamaican weed) but differs in having glabrous instead of glandular-puberulous stems; narrower, more widely scattered leaves; smaller, more numerous flowers with shorter pedicels; and smaller seeds.

Polygala spathulata Griseb. Catal. Pl. Cubens. 13. 1866. MAP 25.

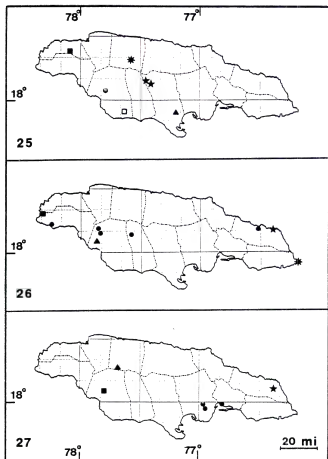
New to Jamaica. **Clarendon**: along road S from Free People toward Harris Savanna, 300–400 ft, *Proctor* 34248, Oct. 31, 1974.

This is a very small species differing markedly in growth habit from the other herbaceous Jamaican congeners. The plants form small, flat rosettes not more than ca. 10 cm across, the several short stems lying flat on the ground, radiating out from a central woody taproot. The spatulate leaves, in whorls of four, are usually 4–7 mm long and nearly as wide. The racemes are short, sessile, and few flowered, with the greenish white flowers ca. 2.5 mm long. The species is otherwise known only from the Bahamas and Cuba.

EUPHORBACEAE

Sebastiana Sprengel

The number of known species of *Sebastiana* in Jamaica has been increased from three to six, of which one occurs in two varieties. Despite certain dif-



MAPS 25-27. Distributions: 25, *Polygala leptocaulis* (dot), *P. spathulata* (triangle), *Sebastiana crenulata* (solid square), *S. lesteri* (stars), *S. lesteri* var. *glabrata* (hollow square), *S. howardiana* (asterisk); 26, *Cuerveia hawkesii* (star), *C. jamaicensis* (dots), *C. kappleriana* (triangle), *Elachyptera floribunda* (square), *Hippocratea volubilis* (asterisk); 27, *Huerteia cubensis* (triangle), *Abutilon indicum* (dots), *Hibiscus striatus* subsp. *lambertianus* (square), *Wercklea flavovirens* (star).

faculties inherent in keying out dioecious plants, these taxa can usually be distinguished as follows:

- A. Uppermost leaves opposite or in whorls of 3, sessile or nearly so. *S. fasciculata*.
- A. Leaves alternate or subopposite, distinctly petiolate.
 - B. Leaves with distinctly crenulate margins; staminate floral glands rudimentary; anthers subsessile. *S. crenulata*.
 - B. Leaves entire or minutely toothed; staminate floral glands well developed; anthers terminating distinct filaments.
 - C. Inflorescences terminal; staminate flowers sessile. *S. spicata*.
 - C. Inflorescences chiefly axillary (or few terminal); staminate flowers pedicellate.
 - D. Stems and leaves puberulous. *S. lesteri*.
 - D. Stems and leaves glabrous.
 - E. Leaves emarginate; sepals lance-linear. *S. howardiana*.
 - E. Leaves not emarginate; sepals ovate or broadly deltate.
 - F. Leaf blades somewhat narrowed at both ends, the apex obtuse, not apiculate. *S. alpina*.
 - F. Leaf blades rounded at both ends, the apex minutely apiculate. *S. lesteri* var. *glabrata*.

***Sebastiania crenulata* Proctor, sp. nov.**

MAP 25.

Frutex glaber circa 2 m altus, ab speciebus aliis Jamaicensibus in foliis crenulatis et floribus staminatis glandulis rudimentariis sepalis obsoletis et antheris subsessilibus, differt.

Glabrous shrub ca. 2 m tall; youngest branchlets terete or slightly angulate. Leaves alternate; petioles 4–11 mm long; blades chartaceous, elliptic or oblong-elliptic, 5–10 by 2.5–4.5 cm, rounded and sometimes slightly emarginate at apex, obtuse at base, the margins somewhat unevenly crenulate, the midrib prominent adaxially, prominent abaxially, the veins prominent on both sides. Staminate inflorescences axillary, subracemose, racemes 1.5–3.5 cm long; floral bracts deltate, fimbriolate, 0.3 mm long; glands rudimentary, lingulate; pedicels 0.2–0.5 mm long; flowers ca. 0.8–1 mm across; sepals obsolete; anthers subsessile, filaments 0.2 mm or less long. Pistillate inflorescences, capsules, and seeds not seen.

Hanover: summit of Bubby Hill, ca. 1 mi SW of Hillsbrook, ca. 1450 ft, Proctor 31314, May 31, 1970 (♂) (holotype).

This rare shrub was collected at the type (and only known) locality of *Reynosa jamaicensis* M. C. Johnston (Rhamnaceae). It is unique among the Jamaican species of *Sebastiania* not only in its crenulate leaves, but also in its reduced staminate flowers with rudimentary glands, obsolete sepals, and subsessile anthers, the filaments being 0.2 mm or less long. Unfortunately, the pistillate flowers and fruits have not yet been seen. With incomplete material, it is not possible to suggest the affinities of this plant in *Sebastiania*.

Sebastiana lesteri Proctor, sp. nov.

MAP 25.

Frutex a speciebus aliis Jamaicensibus in indumento puberulo differt; *Sebastiana alpina* affine, sed in foliis brevioribus rotundatis apicibus emarginatis, floribus parvioribus, et bracteis ciliatis sepalisve parvioribus, differt.

Shrub ca. 2 m tall; youngest branches shallowly sulcate or terete, densely puberulous with short pluricellular hairs. Leaves alternate or sometimes subopposite; petioles 2–4 mm long; blades stiffly chartaceous, broadly elliptic to rotund, 1–4 by 1–3 cm, rounded and emarginate at apex, rounded or very broadly cuneate at base; midrib prominulous adaxially, prominent abaxially, nerves more or less prominulous on both sides; adaxial surface glabrous to sparsely puberulous, petiole and abaxial surface densely puberulous, or at least puberulous on midrib. Staminate inflorescences terminal and axillary, puberulous, racemose; racemes 1–2(–4.5) cm long; pedicels 0.3–0.6 mm long; flowers ca. 1 mm across; floral bracts and sepals deltate, ciliate; glands cylindrical with minute, cup-shaped apex. Pistillate inflorescences terminal, puberulous; sepals lanceolate, ciliate, ca. 2 mm long; ovary puberulous, styles puberulous on lower side. Capsules puberulous, 6–7 mm in diameter; seeds brown, smooth, ca. 3.5 mm long.

Clarendon: summit of Quaco Rock, near Ritchies, ca. 3000 ft, *Proctor 34940*, March 30, 1975 (♂) (holotype), *Proctor 34941*, March 30, 1975 (♀), *Proctor 33821*, April 24, 1974 (♂); Glenwood Springs, along road between Balcarres and Sunbury, ca. 3100 ft, *Proctor 33649*, Nov. 30, 1973 (♂), *Proctor 33706*, Jan. 4, 1974 (♀).

Named for Mr. Lester Dinnall, of Glenwood Springs, who originally discovered this plant and brought it to my attention, insisting (despite my initial doubts) that it was new and "different." It is, in fact, a very distinct species, especially in its pubescence, its small, rotund, emarginate leaves, and its very small, pedicellate staminate flowers. The staminate flowers of *Sebastiana alpina* (Fawcett & Rendle) Pax & K. Hoffman (apparently the most closely related species) are about twice as large.

Sebastiana lesteri var. **glabrata** Proctor, var. nov.

MAP 25.

A var. *lesteri* in foliis glabris lucidis ellipticis apicibus apiculatis et floribus pistillatis sepalis late ellipticis marginibus glabris glandulosisque, differt.

Shrub resembling var. *lesteri* but differing in its glabrous, elliptic to broadly elliptic leaves minutely apiculate at the apex, and in its broadly deltate pistillate sepals, these glabrous and glandular on the margins.

St. Elizabeth: 2 mi NNE of Top Hill P.O., 1700 ft, *R. A. Howard & Proctor 13925*, Sept. 16, 1954 (♀) (holotype).

It is possible that this plant represents a species distinct from *Sebastiana lesteri*, but the material available is not sufficient to establish this fact.

Sebastiana howardiana Proctor, sp. nov.

MAP 25.

Frutex *Sebastiana lesteri* affine sed in trichomatibus carentibus, foliis multo grandioribus, floribus pistillatis pedicellis longioribus, et seminis nigriscentinereis, differt.

Glabrous shrub 2–3 m tall; youngest branchlets longitudinally sulcate and striate. Leaves alternate; petioles 4–6 mm long, minutely glandular along adaxial groove; blades coriaceous, broadly elliptic to rotund, 4–9 by 2.5–6 cm, rounded and shallowly to deeply emarginate at apex, rounded or very broadly cuneate at base, margins narrowly and tightly revolute; midrib prominent adaxially, prominent abaxially, the venation strongly reticulate-prominulous on both sides, the tissue dark green adaxially, noticeably paler abaxially. Staminate inflorescences axillary, yellow, 0.6–3 cm long; floral bracts deltate, acute, fimbriolate, 0.2–0.3 mm long; glands cylindrical with minute, cup-shaped apex; pedicels 0.2–0.5 mm long; flowers ca. 0.8–1 mm across; sepals dark brown, lance-linear, fimbriolate, ca. 0.3 mm long; filaments 0.2–0.4 mm long. Pistillate inflorescences terminal and axillary, 2- or 3-flowered; bracts broadly deltate, minutely fimbriolate, the glands simple or sometimes bifurcate, abruptly expanded and cup-shaped at apex; pedicels 2–2.5 mm long; sepals not seen. Capsules glabrous, 6–8 mm in diameter; seeds blackish gray, smooth, ca. 3.5 mm long.

Trelawny: Ramgoat Cave area, ca. 1500 ft, *R. A. Howard & Proctor 14396*, July 4, 1955 (fruits) (holotype), *R. A. Howard & Proctor 14135*, Sept. 26, 1954 (fruits), *R. A. Howard & Proctor 14421*, July 4, 1955 (♂).

The affinity of this species seems to be with *Sebastiana lesteri*, but *S. howardiana* is a much more robust plant with larger, glabrous leaves of thicker texture, longer pistillate pedicels, and blackish gray instead of light brown seeds.

CELASTRACEAE SUBFAMILY HIPPOCRATEOIDEAE

This subdivision of the Celastraceae has often been treated as an independent family (Hippocrateaceae) even though it was always recognized that the two taxa are closely allied. However, it was conclusively shown by Ding Hou (1964) that all the characters used to differentiate the two groups break down at one point or another. It is necessary to emphasize this fact because in Jamaica the two groups are sharply distinct, and on a local basis it is tempting to treat them as separate families. This distinctiveness can be summarized in the following key, which in the present context applies only to Jamaica:

- A. Woody vines; leaves opposite; stamens 3, attached at base of ovary within disc, anthers dehiscing extrorsely near apex; fruits consisting of 3 capsular carpels attached only at base; seeds without endosperm. . . . subfam. Hippocrateoideae.
- A. Shrubs or trees; leaves alternate, opposite, or whorled; stamens 4 or 5, attached outside disc or fused with it, anthers dehiscing introrsely; fruits drupes or capsules

(if capsules, carpels fused and not winglike); seeds with endosperm.
 subfam. Celastraceae.

The treatment of the Celastraceae by Adams (1972) included the Hippocrateoideae, thought at that time to be represented in Jamaica by but a single species, *Cuervea kappleriana* (Miq.) A. C. Sm. However, recent field studies have revealed that not only does the genus *Cuervea* have more than one representative in Jamaica, but also that two other related genera are present as well. Observations of these plants have shown that the subfamily is a much more important element in the flora than was previously supposed. In the classification of the Jamaican species, the generic concepts of Smith (1940) have been followed. The three genera represented can be keyed as follows:

- A. Inflorescence branches glabrous; petals glabrous within; disc cup shaped, membranous.
- B. Inflorescence branches terete, nonglandular; flowers few, loosely arranged; petals 4–9 mm long; fruiting carpels broadly obovate or suborbicular in outline. *Cuervea*.
- B. Inflorescence branches quadrangular, minutely and densely granulose-glandular; flowers numerous, densely arranged; petals less than 1 mm long; fruiting carpels elliptic or ovate-elliptic in outline. *Elachyptera*.
- A. Inflorescence branches minutely and densely puberulous with pluricellular hairs; petals bearded within; disc thickly fleshy, annular-pulvinate. *Hippocratea*.

***Cuervea* Triana ex Miers**

It has been very difficult to decide just how many species of this genus are really represented in Jamaica. The chief reason for this is the extraordinary infrequency of flowering and fruiting in a taxon whose vegetative parts fail to provide much in the way of differentiating features. Yet considerable populations of these plants occur at many widely scattered localities; in fact, in certain areas these high-climbing woody lianas are quite an important element in the flora. I am convinced that several species can be distinguished in Jamaica, despite the fact that Smith (1940) attributed only three species to the whole genus, and but one of these to Jamaica.

The following key will serve to differentiate the three Jamaican species of *Cuervea* now being recognized:

- A. Flowers pink; fruiting carpels longer than wide, diverging from each other by narrowed, stipitate bases. *C. hawkesii*.
- A. Flowers cream or pale yellow; fruiting carpels mostly wider than long, closely contiguous from about middle to short-stipitate or nearly truncate base.
- B. Petals 4.5–5 mm long; fruiting carpels 3–4 cm broad. *C. jamaicensis*.
- B. Petals 5.5–9 mm long; fruiting carpels mostly 7–9 cm broad.
 *C. kappleriana*.

***Cuervea hawkesii* Proctor, sp. nov.**

MAP 26.

Liana lignosa glabra floribus roseis et carpellis fructificantibus longioribus quam latis per bases angustatae stipitatae divergentibus.

Glabrous liana or scrambling shrub; branchlets opposite, cinereous to brownish, with numerous small lenticels. Petioles 9–12 mm long; leaf blades chartaceous, lance- or elliptic-oblong, 13–20 by 5–7 cm, gradually acuminate at apex, rounded at base, the margins entire, the costa somewhat prominent on both surfaces, the secondary nerves about 7 or 8 per side, prominulous on both surfaces, the veinlets reticulate and prominulous, the adaxial surface glossy. Inflorescences 2–3 cm long, few flowered; peduncle terete or faintly angled, 2–10 mm long, together with the few branches dark purple-brown; bracts irregularly ovate-deltate, 0.5–0.9 mm long, fimbriate, fimbriae gland tipped. Pedicels slender, 1.5–2.5 mm long; flowers fragrant, 10–12 mm across at anthesis; sepals imbricate, unequal, broadly rounded-deltate, 1–1.5 mm long and as broad or broader, margins fimbriate-ciliate; petals "peach-pink," very broadly elliptic with narrowly inflexed entire margins, 6–6.5 by 3.5–5 mm, rounded at apex; disc membranous, ca. 1.5 mm in diameter and 0.3–0.4 mm high; filaments flat, ca. 0.5–0.7 mm long, the anthers roundish in outline, 0.4–0.6 mm in diameter; style 0.5–0.7 mm long, apex irregularly lobulate, stigmas minute and inconspicuous. Fruiting carpels (capsules) elliptic to obovate in outline, noticeably longer than broad, 5.5–6 by 3.5–4 cm, rounded at apex, tapering to stipelike base ca. 5 mm long; seeds 2 per carpel, main body of each ca. 2.5 cm long, wing ca. 6 mm long with maximum width of 2 mm.

Portland: Turtle Cove, Drapers P.A., 0–50 ft, *Hawkes s.n.* (J 48280), May 2, 1970 (holotype) (specimen from cultivated plant originally collected wild in adjacent coastal woodland).

This species is named to commemorate the late Alex D. Hawkes, who discovered it.

Cuervea jamaicensis Proctor, sp. nov.

MAP 26.

Liana lignosa glabra floribus luteolis, a *Cuervea kappleriana* in petalis brevioribus 4.5–5 mm (versus 5.5–9 mm) longis et carpellis fructificantibus parvioribus 3–4 cm (versus 7–9 cm) latis, differt.

Glabrous, high-climbing, woody liana; branchlets opposite, the younger ones green, smooth, the older ones brownish-cinereous, finely roughened by numerous narrowly elliptic lenticels. Petioles 5–10 mm long; leaf blades chartaceous or somewhat coriaceous, ovate, ovate-oblong, or elliptic, 6–19 by 3–9 cm, short-acuminate at apex, rounded to broadly cuneate and slightly inequilateral at base, the margins entire, the costa prominent on both surfaces, the secondary nerves 5 to 9 per side, prominent on both surfaces, the veinlets reticulate and strongly prominulous. Inflorescences 3–12 cm long, many flowered, peduncle 0–2.5 cm long, together with the several branches

green and subangulate; bracts variable in shape, tips acute and colorless. Pedicels 1.5–2 mm long; flowers fragrant, 9–10 mm across at anthesis; sepals imbricate, unequal, 1–1.5 by up to 2 mm, the margins rounded, minutely erose-denticulate; petals pale yellow, oblong or elliptic-oblong with inflexed entire margins, 4.5–5 by 2–2.5 mm, subacute at apex; disc subcarinose, ca. 1 mm in diameter and 0.3 mm high; filaments ca. 0.5 mm long, the anthers obcordate in outline, ca. 0.4 mm in diameter; style 0.3–0.4 mm long, roughened-truncate at apex. Fruiting carpels (capsules) oblate in outline, 3–4 by 3.5–4.5 cm, broadly rounded at apex, similarly rounded at base except for abruptly stipelike point of attachment 1–1.5 by 3 mm; seeds 2 or 3 per carpel, main body of each 2–2.5 cm long, wing 7–10 mm long with maximum width of 4 mm.

Portland: near mouth of Rio Grande, on wooded brink of vertical cliff overlooking E end of highway bridge, ca. 100 ft, *Proctor 37458*, Nov. 30, 1977 (holotype), *Proctor 25653*, Nov. 19, 1964, **Manchester:** 0.3 mi SE of Comfort Hall Halt, ca. 1100 ft, *Proctor 38356*, Nov. 7, 1979. **St. Elizabeth:** between mileposts 4 and 5, Redgate to Ipswich road, ca. 500 ft, *Proctor 36762*, April 20, 1977; Y.S. Falls, 150–250 ft, *Proctor 37567*, Jan. 8, 1978. **Westmoreland:** Negril Hills 0.5 mi E of Little Bay, ca. 100 ft, *Proctor 11153*, Nov. 18, 1955.

A plant cultivated at Mountainside, St. Elizabeth, grown from a seed said to have been obtained in the parish of Westmoreland, may possibly represent still another species, but the available material (*Proctor 38100*, March 26, 1979; *Proctor 38172*, May 31, 1979) is too incomplete for determination.

Elachyptera A. C. Sm.

Elachyptera floribunda (Bentham) A. C. Sm. *Brittonia* 3: 387. 1940.
MAP 26.

Genus and species new to Jamaica. **Westmoreland:** inland from milepost 23, 2.5 mi NE of Negril, wooded swamp with peat substrate, sea level, *Proctor 35347*, Oct. 7, 1975, *Proctor 35535*, Dec. 13, 1975, *Proctor 37128* (flowers) and *Proctor 37129* (fruits), July 18, 1977.

Previously known from Belize and eastern Guatemala to Guyana and Amazonian Brazil at widely scattered localities; this new Jamaican record is the first for its genus and species in the West Indies.

Hippocratea L.

Hippocratea volubilis L. *Sp. Pl.* 2: 1191. 1753. MAP 26.

Genus and species new to Jamaica. **St. Thomas:** Morant Point, coastal thickets over limestone, near sea level, *Proctor 34368*, Nov. 27, 1974, *Proctor 37495*, Dec. 9, 1977, *Proctor 38583*, Feb. 16, 1980.

It is rather surprising that this common and widespread species had not previously been found in Jamaica, particularly since it grows at a locality that has been repeatedly visited by botanists. However, it flowers very seldom there, and numerous observations have thus far failed to reveal any fruits.

The range of *Hippocratea volubilis* extends throughout tropical America from Florida to Argentina; in the West Indies this species has been recorded from Cuba, Hispaniola, Puerto Rico, and the Lesser Antilles.

STAPHYLEACEAE

Huetea Ruiz & Pavon

Huetea cubensis Griseb. Catal. Pl. Cubens. 66. 1866.

MAP 27.

Genus and species new to Jamaica. **Trelawny:** Cockpit Country, dense woods on limestone hills beyond Belmore Castle, ca. 1–2 mi NW of Quick Step, alt. ca. 1500 ft, G. L. Webster 5262, August 11, 1954 (A).

The small family Staphyleaceae was previously thought to be represented in Jamaica only by the genus *Turpinia*, with a single rather common species. *Huetea cubensis* is otherwise known from Cuba and Hispaniola. *Huetea* and *Turpinia* can be distinguished by the following key:

- A. Leaves opposite, leaflets 3 to 11; styles 3, free; fruits 3-locular. *Turpinia*.
 A. Leaves alternate, leaflets 17 to 21; style single, short, with 2-lobed stigma; fruits 1- or 2-locular. *Huetea*.

MALVACEAE

Abutilon Miller

Abutilon indicum (L.) Sweet, Hortus Brit. 54. 1826.

MAP 27.

According to Adams (1972, p. 463), this species is "very rare and known only from two unlocalized early collections" (*Distin s.n.*, 1830–40; and *March s.n.*, 1857–58). Material recently gathered, however, suggests that *Abutilon indicum* is in fact not uncommon in a limited area between Kingston and Spanish Town. The following specimens can be cited:

Kingston: Newport East, near sea level, *Proctor* 34253, Nov. 4, 1974, **St. Catherine:** along bypass highway S of Spanish Town, ca. 50 ft, *Proctor* 34208, Oct. 1, 1974; 1.5 mi WSW of Bernard Lodge Factory, ca. 50 ft, *Proctor* 32653, Sept. 23, 1971.

Hibiscus L.

Hibiscus striatus Cav. Monad. Cl. Diss. Decem **3**: 146. *t.* 54, *fig.* 1. 1787.

Hibiscus striatus subsp. **lambertianus** (Kunth) Blanch., comb. et stat. nov.⁶ MAP 27.

Hibiscus lambertianus Kunth in H.B.K. Nova Gen. Sp. Pl. **5**: 226. *t.* 478. 1822.

Hibiscus cubensis A. Rich. Essai Fl. Cuba, 140. 1845.

New to Jamaica. **St. Elizabeth**: Frenchman, sea level, *Proctor* 38095, March 26, 1979, *Proctor* 38186, June 16, 1979 (both det. P. A. Fryxell).

In addition to its occurrence in Cuba, this entity has a wide continental range from the Gulf coast of Texas and Mexico south to northern Bolivia. The type of Kunth's *Hibiscus lambertianus* was found in Venezuela. This plant resembles *H. trilobus* Aublet but has leaves undivided or only slightly lobed at the base, and larger flowers with pink petals up to 12 cm long.

Pavonia Cav.

Pavonia schiedeana Steudel, Nomencl. Bot. ed. 2. **2**: 279. 1841.

Pavonia rosea Schlecht. Linnaea **11**: 355. 1837, not Moris, 1833, or Adams, 1972.

Dr. Paul Fryxell (pers. comm.) has pointed out this necessary change of name. The Moris publication, including a full description and a plate, was based on a plant from Calcutta presumably collected by Wallich, but Moris did not mention Wallich by name; therefore, the specific epithet must be attributed to Moris alone.

Wercklea Pittier & Standley

Wercklea flavovirens Proctor in Fryxell, Jour. Arnold Arb. **62**: 475. 1981. MAP 27.

Genus and species new to Jamaica. **Portland**: McRobert Patent, in John Crow Mts. ca. 6 mi by road S of Sherwood Forest, ca. 1150 ft, *Watts, Podzorski, & Kelly JCM* 1548 (*IJ* 69960), March 27, 1979 (flower) (holotype), *Proctor* 36707, Dec. 20, 1976 (juvenile), *Proctor* 37837, May 12, 1978 (fruit).

THYMELAEACEAE

Daphnopsis Martius & Zucc.

Daphnopsis occidentalis (Sw.) Krug & Urban, Bot. Jahrb. **15**: 349. 1892.

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This species, usually listed as endemic to Jamaica, also occurs on Grand Cayman (*Proctor 31041*) and Cayman Brac (*Proctor 29020*).

FLACOURTIACEAE

Xylosma Forster f.

Xylosma proctorii Sleumer, Fl. Neotrop. **22**: 142. 1980. MAP 28.

This plant is listed as "sp. A" by Adams (1972). In publishing it as a new species, Sleumer had but two collections available. Additional material includes:

Trelawny: Belmore Castle area, N of Quick Step, ca. 1500 ft, *Proctor 36290*, June 12, 1976, *Proctor 38057*, March 3, 1979; Tyre distr., N of Troy, ca. 1750 ft, *Proctor 9948*, March 14, 1955, *Proctor 15736*, Aug. 28, 1956; Burnt Hill, 1700–1800 ft, *Proctor 34335*, Nov. 23, 1974. **Manchester**: Glasgow distr., ca. 1250 ft, *Proctor 31533*, Dec. 1, 1970 (holotype, v; isotype, v). **St. Ann**: 2 mi W of Albion, ca. 2500 ft, *Proctor 33144*, Feb. 3, 1973.

TURNERACEAE

Piriqueta Aublet

Piriqueta viscosa Griseb. Catal. Pl. Cubens. 114. 1866. MAP 28.

New to Jamaica. **Clarendon**: Harris Savanna, ca. 350 ft, *Proctor 34296*, Nov. 13, 1974.

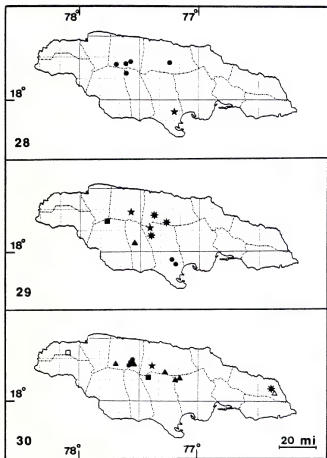
Originally described from Cuba, this species is also known to occur at scattered South American localities as far south as Paraguay. As an ephemeral annual, it is easily overlooked by collectors unless they happen to be in the right locality at just the right time.

Piriqueta viscosa is easily distinguished from *P. cistoides*, the only other Jamaican species, by its dense covering of viscid glandular hairs and its pink flowers. The flowers of *P. cistoides* are yellow.

Turnera L.

Turnera pumilea L. Syst. Nat. ed. 10. 2: 965. 1759. MAP 28.

Until recently, this rare, short-lived annual had been gathered in Jamaica but a few times, notably by the pre-Linnaean collectors Sloane (1686–87) and Browne (1746–55), and later by Swartz (1784–86). In modern times it had only been found by William Harris (12066), who collected it at "Two mile Wood, St. Catherine" on June 8, 1915. It is now possible to record a more recent collection.



MAPS 28-30. Distributions: 28, *Xylosma proctorii* (dots), *Piriqueta viscosa* and *Turnera pumilea* together (star); 29, *Passiflora callicola* (stars), *Begonia guaduensis* (triangle), *Ammannia auriculata* (dots), *Calyptanthes capitata* (asterisks), *C. uniflora* (square); 30, *Eugenia aboukirensis* (star), *E. crassicaulis* (hollow triangle), *E. hanoverensis* (hollow square), *E. kellyana* (asterisk), *E. laurae* (dots), *E. websteri* (solid triangles), *E. laurae* and *E. websteri* together (solid square).

Clarendon: Harris Savanna, ca. 350 ft, *Proctor 34297*, Nov. 13, 1974.

Numerous plants were observed when this collection was made, but none has been seen at this locality again during many subsequent visits.

PASSIFLORACEAE

***Passiflora* L.**

***Passiflora calcicola* Proctor, sp. nov.**

MAP 29.

Planta glabra scandens *Passiflora cubense* affine, sed in lamina transversaliter oblonga vel late obdeltoidea basi cordata, pedunculis infra medium articulatis, bracteis parvioribus, floribus pallide purpureis, tubo calycis longiore et angustiore base cuneato, sepalis petalisve angustioribus, operculo angustiore integro, fructibus parvioribus ellipsoideis, et seminis grandioribus alatis transversaliter rugulosis, differt.

Trailing, glabrous vine; stems pale green, flattened-angulate, striate; stipules linear-subulate, 1–4 mm long, persistent. Petioles 6–11 mm long, glandless; leaf blades transversely oblong to very broadly obdelate, 3-nerved, entire and truncate or very slightly 2- or 3-lobed, 4–12 cm in greatest width, the midrib 1.5–4.5 cm long, together with principal side nerve on each side terminating in a mucro, the base shallowly cordate, the tissue rigidly coriaceous, lustrous, ocellate, the venation prominulous on both sides. Peduncles solitary or in pairs, 2–3 cm long, articulated below middle (0.9–1.1 cm above base); bracts setaceous, 0.5–1 mm long, borne at and below point of articulation; flowers light purple, the calyx tube narrowly cup shaped, ca. 10 mm long, 6–7 mm wide at top, cuneate at base, the sepals and petals narrowly linear-oblong, 2–2.5 cm by 2–3 mm, the corona filamentose, with filaments in single series, narrowly linear, ca. 4 mm long, pale green, the operculum incurved, 0.3 mm wide, entire, the ovary ellipsoid, smooth. Fruits ellipsoid, 1.7–1.9 cm long; seeds broadly fusiform, ca. 4 by 2 mm, transversely rugulose, winged along 1 side.

Trelawny: 0.6 mi N of Spring Garden, crevices of exposed vertical limestone cliff, ca. 1800 ft, *Proctor 34499*, Dec. 18, 1974 (holotype), *Proctor 35318*, Sept. 20, 1975. **Clarendon:** Peckham Woods, in crevices of limestone crags, ca. 2500 ft, *Proctor 35677*, April 4, 1976.

Among the Jamaican species, *Passiflora calcicola* is most nearly related to *P. perfoliata* but differs markedly in the petiolate and differently shaped leaves and in the shape and color of the fruits.

BEGONIACEAE

Begonia L.

Begonia fischeri Schrank, Pl. Rar. t. 59. 1820.

This is believed to be the correct name of the species listed by Adams (1972) as *Begonia patula* Haw. He attributed it only to the parish of Westmoreland, but it is now also known from St. Elizabeth.

Begonia guaduensis Kunth in H.B.K. Nova Gen. Sp. Pl. 7: 178. 1825.
MAP 29.

New to Jamaica. **Manchester:** Mike Town distr., ca. 2.5 mi NW of Mandeville, ca. 2200 ft, *Proctor 37590*, Jan. 17, 1978 (det. L. B. Smith).

Smith and Schubert (1946) gave the known distribution of *Begonia guaduensis* as Panama, Colombia, and Venezuela. In Jamaica the species may be an escape from cultivation, yet it was found growing under wholly natural conditions on a wooded, rocky, limestone hillside. If not indigenous, it should nevertheless be considered fully naturalized.

This species somewhat resembles *Begonia glabra* Aublet in technical characters; the latter, however, is a high-climbing vine rooting at the nodes, with the roots serving as holdfasts. *Begonia guaduensis* is said to become somewhat scandent, but the Jamaican plants are upright herbs. It also differs from *B. glabra* in its oblong or lance-oblong leaves; these are strongly asymmetric and have petioles 2–8 mm long. Leaves of *B. glabra* are broadly ovate and symmetrical, and they have much longer petioles. In Adams's (1972) key to the Jamaican species of *Begonia*, *B. guaduensis* would seem to come out to *B. acutifolia* or possibly *B. purpurea*. From both of these species it differs in having completely glabrous leaves.

LYTHRACEAE

Ammannia L.

Ammannia auriculata Willd. Hortus Berol. 1: 7. t. 7. 1803. MAP 29.

New to Jamaica. **Clarendon:** Harris Savanna, ca. 350 ft, *Proctor 34313*, Nov. 15, 1974, *Proctor 38028*, Feb. 10, 1979; Mineral Heights, ca. 1.3 mi due S of May Pen, ca. 250 ft, *Proctor 37199*, Aug. 25, 1977.

This pantropical species is rare in the West Indies, being known previously in this area only from Cuba. It is widespread in central and southern United States, Mexico, and parts of Central America.

Ammannia auriculata can be distinguished from other Jamaican species of

this genus (all of which have sessile flowers) by its pedicellate flowers in small axillary cymes. It differs from all but *A. coccinea* in having flowers with petals.

MYRTACEAE

The proliferation of this family in Jamaica is emphasized by the rather numerous new discoveries made in recent years.

***Calyptranthes* Sw.**

***Calyptranthes capitata* Proctor, sp. nov.**

MAP 29.

Arbor glabra, gracilis, usque ad 6 m alta, a speciebus aliis *Calyptranthes* in Jamaica in inflorescentiis haud ramosis capitatis, capitulo 6–8 mm in diametro e floribus circa 18 ad 25 sessilibus composito pedunculo 2–2.5 cm longo terminanti, a speciebus in Cuba in inflorescentiis congruentibus sed in petiolis 3–6 mm longis et lamina ovato-lanceolatis acuminibus longis, differt.

Slender, dense-crowned tree to 6 m tall; youngest branchlets cinereous, terete, glabrous, ca. 0.8 mm in diameter. Leaves glabrous; petioles 3–6 mm long; blades coriaceous, opaque, glandular-punctate (dots not pellucid), ovate-lanceolate, 3–4.5 by 1–1.8 cm, sharply long-acuminate at apex, rounded at base, midrib lightly impressed adaxially and somewhat prominent abaxially, secondary venation obscure. Inflorescence an apparently unbranched pedunculate capitulum, solitary or paired from axils of penultimate pair of leaves; peduncles 2–2.5 cm long, compressed, minutely brownish-tomentose; flower buds obovoid or ellipsoid, bluntly apiculate, minutely tomentellous, 1.5–1.7 mm long; flowers white, fragrant, sessile, ca. 18 to 25 together in dense head 6–8 mm in diameter at anthesis, each flower ca. 1 mm in diameter at apex of hypanthium. Fruits dark red, globose, glabrous, 1- or 2-seeded, 3–4 mm in diameter.

St. Ann: Douglas Castle distr., ca. 2300 ft, *Proctor 36274*, June 11, 1976 (flowers) (holotype), *Proctor 37329*, Oct. 8, 1977 (fruits); vic. of Aboukir, ca. 2200 ft, *Proctor 37445*, Nov. 26, 1977 (fruits). **Clarendon:** Glenwood Springs, along road between Balcarres and Sunbury, 3000–3100 ft, *Proctor 35645*, March 31, 1976, *Proctor 36359*, July 21, 1976.

Among Jamaican species of *Calyptranthes*, this species is unique in its apparently simple, headlike inflorescence with the minute flowers crowded together in a dense capitulum. Actually, the heads are not strictly simple; if dissected, they are seen to be minutely 3-branched, the branches each approximately 1 mm long and completely hidden by the crowded sessile flowers.

***Calyptranthes uniflora* Proctor, sp. nov.**

MAP 29.

Frutex foliis petiolatis ovatis vel oblongo-ovatis apicibus acuminatis, e speciebus aliis Antillanae Calyptanthus in floribus solitariis terminalibus pedunculis 4.5–6.5 cm longis, differt.

Shrub 2.5 m tall; youngest branchlets terete, deciduously covered with appressed, flattened, whitish, dibrachiate hairs and with few thin, irregular, subarachnoid scales; older branchlets glabrous. Petioles glabrous, 5–9 mm long, deeply grooved adaxially; leaf blades coriaceous, opaque, at first with scattered whitish arachnoid tomentum, soon becoming glabrous, ovate to oblong-ovate or elliptic, 3.5–7.5 by 2–3.8 cm, acuminate at both ends, the midrib narrowly grooved in lower half adaxially, prominent abaxially, the side nerves obscurely prominulous on both sides. Inflorescences 2 or 3, terminal, 1-flowered, the peduncles soon glabrous, compressed, 4.5–6.5 cm long; flower buds ovoid, acuminate, ca. 10 mm long, deciduously covered with appressed dibrachiate hairs like those of youngest branchlets. Flowers and fruits unknown.

St. Elizabeth: Cooks Bottom, E of Elderslie, 1600–1700 ft, *Proctor* 20862, May 13, 1960 (holotype).

This plant was listed as "sp. B" in Adams (1972).

***Eugenia* L.**

***Eugenia aboukirensis* Proctor, sp. nov.**

MAP 30.

Arbor tenui ad 6 m alta *Eugenia clarendonense* affine, sed petiolis brevioribus, laminis longioribus tenuioribusve, et floribus pluribus parvioribusve, differt.

Slender tree to 6 m tall; youngest branchlets slightly compressed, glabrous; older ones terete, cinereous. Leaves glabrous; petioles 3–4 mm long; blades chartaceous, lanceolate to narrowly elliptic, 3–5.5 by 0.8–1.7 cm, acuminate at apex, cuneate at base, the midrib slightly grooved toward base adaxially, prominent abaxially, the veins slightly prominulous on both sides, the tissue with scattered very minute pellucid dots. Flowers up to 8 in subumbellate clusters in leaf axils; rachis 0–1 mm long; bracts brown, deltate-acuminate, 0.5 mm long, ciliate; bracteoles similar to bracts; pedicels glabrous, 2–3 mm long; calyx minute, the lobes broadly rounded, 0.5–0.6 mm long after anthesis, glabrous; petals light pink, ca. 2.5 mm long, ciliate at apex; hypanthium apex puberulous within calyx; filaments pink, ca. 2.5 mm long; style ca. 3 mm long. Fruits not seen.

St. Ann: vic. of Aboukir, ca. 2200 ft, *Proctor* 37484, Dec. 4, 1977 (holotype), *Proctor* 37444, Nov. 26, 1977, *Proctor* 37493, Dec. 4, 1977.

This species keys out to the group of species that includes *Eugenia rhom-*

bea (O. Berg) Krug & Urban, *E. clarendonensis* Urban, and *E. brownei* Urban, but it differs from all of these in leaf shape and in having much smaller flowers. Its flowers are even smaller than those of *E. axillaris* (Sw.) Willd., but they are borne on longer pedicels and are pink, with glabrous instead of ciliate sepals.

***Eugenia crassicaulis* Proctor, sp. nov.**

MAP 30.

Frutex, ramulis juvenilissimis crassis 3–4 mm in diametro, floribus subsessilibus solitariis vel binatis ad nodos defoliatos instructis, pedicellis glabris 1–3 mm longis, sepalis fructificantibus circa 3.5 mm longis, et fructis late ovoideo-ellipticis 1.3–1.5 mm longis.

Shrub of stiff texture; youngest branchlets somewhat compressed, glabrous, 3–4 mm thick; older ones with rough, gray, corky bark. Leaves glabrous; petioles thick, 2–5 mm long; blades thick, coriaceous, broadly ovate-elliptic, 5–7.5 by 4–5.5 cm, blunt to very bluntly short-acuminate at apex, rounded or subcordate at base, the midrib grooved adaxially, prominent abaxially, the venation prominulous on both sides, the tissue opaque. Flowers solitary or paired at leafless nodes along stems, subsessile; bracts not seen; bracteoles broadly deltate, ca. 2 mm long, ciliolate at apex; pedicels glabrous, 1–3 mm long; petals, stamens, and style not seen; hypanthium black when dried; fruiting sepals ca. 3.5 mm long, rounded at apex. Fruits broadly ovoid-ellipsoid, 1.3–1.5 by 1–1.2 cm; seeds ca. 9 mm long.

Portland: E slope of John Crow Mts. 2.5 mi SE of Ecclesdown, 2000–3000 ft, Proctor 5733, April 4, 1951 (holotype).

This species, known only from the unicate type specimen, seems related to a group of species (*Eugenia lamprophylla* Urban, *E. marchiana* Griseb., and *E. amplifolia* Urban) characterized by leaves 9–30 cm long and flowers clustered at leafless nodes of older stems. It differs from all of them in its much smaller leaves, its mostly solitary or paired flowers, its much shorter pedicels, and its shorter sepals.

***Eugenia hanoverensis* Proctor, sp. nov.**

MAP 30.

Arbor *Eugenia jamaicense* affine, sed in ramulo glabro, foliis angustioribus et longioribus, inflorescentiis pubescentia brunneola praeditis, et sepalis longioribus, differt.

Tree 10 m tall; youngest branchlets somewhat compressed, glabrous. Petioles 5–8 mm long, appressed-puberulous; leaf blades chartaceous, glabrous or nearly so, lanceolate, 6–10.5 by 1.5–2.3 cm, sharply acuminate-attenuate at apex, cuneate at base; midrib narrowly grooved its entire length adaxially, prominent abaxially, the veins slightly prominulous beneath only, the tissue dark green adaxially, paler abaxially, with scattered minute pellucid dots.

Flowers white, fragrant, in densely brown-puberulous axillary racemes; rhachis up to 1.5 cm long (often less); bracts deltate, ca. 1 mm long, puberulous; bracteoles similar but smaller; pedicels puberulous, 5–7 mm long; sepals puberulous, broadly rounded, 1.5–1.8 mm long; petals ca. 6 mm long, ciliate at apex; filaments and style white, slightly exceeding petals. Fruits not seen.

Hanover: 0.7 mi due W of Hillsbrook, 700–800 ft, *Proctor 26665*, Aug. 29, 1965 (holotype).

This species is near to *Eugenia jamaicensis* O. Berg but differs in its glabrous branchlets, narrower and longer leaves, light brown instead of white pubescence on the inflorescence, and slightly longer sepals. Comparison of the fruits has not been possible.

***Eugenia kellyana* Proctor, sp. nov.**

MAP 30.

Arbor tenui *Eugenia virgultosa* affine, sed in foliis tenuioribus, indumento breviori non strigoso, pedicellis longioribus, sepalis apicibus rotundato-apiculatis (haud acuminatis) et filamentis longioribus, differt.

Slender tree 10 m tall; youngest branchlets compressed and shallowly bisulcate, densely puberulous. Petioles puberulous, 2–3 mm long; leaf blades thinly chartaceous, finely appressed-pubescent adaxially, glabrate abaxially except along midrib, lanceolate to ovate, 1.8–6 by 1–2.3 cm, sharply acuminate at apex, cuneate at base, the midrib narrowly grooved adaxially, prominent abaxially, the veins scarcely evident adaxially, finely prominulous abaxially. Flowers white, in puberulous axillary racemes; rhachis 4–8 mm long; bracts deltate, sharply acute, 0.8 mm long; bracteoles similar but smaller; pedicels filiform, puberulous, 5–8 mm long; sepals minutely puberulous, rounded-apiculate, 1.5–2 mm long; petals ca. 4 mm long, ciliate; stamens and style white, glabrous, ca. 6 mm long. Fruits not seen.

Portland: John Crow Mts. ca. 6 mi by road S of Sherwood Forest, 1200–1500 ft, *Proctor 37189*, Aug. 18, 1977 (holotype).

With its pointed sepals, this plant seems to key out to *Eugenia virgultosa* (Sw.) DC., from which it differs in its thinner leaves, shorter and nonstrigose pubescence, longer pedicels, rounded-apiculate (vs. acuminate) sepals, and longer filaments. *Eugenia kellyana* is named for Dr. Daniel Kelly, in recognition of his ecological studies at the locality where this tree was found.

***Eugenia lauræ* Proctor, sp. nov.**

MAP 30.

Frutex vel arbor tenui ad 5 m alta, *Eugenia alexandri* affine, sed in indumento strigilloso, foliis parvioribus aliter formatis, pedicellis sepalisque brevioribus, et filamentis pubescentibus, differt.

Shrub or slender tree to 5 m tall; youngest branchlets somewhat compressed, strigillose-puberulous. Petioles 5–8 mm long; leaf blades rigidly coriaceous, finely and sparsely pubescent adaxially at first, becoming glabrous, broadly lanceolate to broadly ovate, 3–6.5 by 1.5–3.4 cm, bluntly short-acuminate at apex, rounded or broadly cuneate at base, the midrib narrowly grooved adaxially, prominent abaxially, the veins scarcely evident or faintly prominulous on both sides. Flowers in densely strigillose axillary racemes; rachis up to 1.4 cm long; bracts deltate, 0.5 mm long; bracteoles similar but carinate; pedicels flattened, densely strigillose, 2.5–4(–6) mm long; sepals densely strigillose, rounded and often minutely apiculate, ca. 1.5 mm long; petals white with central pink spot, ca. 2.5 mm long; filaments pubescent, 2–3 mm long, anthers lightly pubescent. Fruits globose or obovoid, ca. 7 mm in diameter, sparsely strigillose.

Trelawny: Miss Laura's Hill, Wilson Valley distr., ca. 1 mi N of Warsop, 2000–2200 ft, *Proctor 24841*, May 17, 1964 (holotype); Island View Hill, ca. 1.5 mi N of Warsop, 2000–2200 ft, *Proctor 21343*, June 26, 1960; Ramgoat Cave distr., ca. 1500 ft, *R. A. Howard & Proctor 14413*, July 4, 1955 (A). **Clarendon:** Peckham Woods, ca. 2500 ft, *Proctor 10223*, May 26, 1955 (GH. D).

This material long remained unidentified or else was tentatively associated with *Eugenia alexandri* Krug & Urban. *Eugenia lauræ* can be distinguished from *E. alexandri* by its strigillose pubescence, smaller leaves, shorter pedicels and sepals, and pubescent filaments. The last character is unusual if not unique among the Jamaican species of *Eugenia*.

Eugenia mandevillensis Urban, *Symb. Antill.* 7: 306. 1912.

Eugenia mandevillensis* var. *perratonii (Proctor) Proctor, *comb. et stat. nov.*

Eugenia perratonii Proctor, *Rhodora* 59: 305. 1958.

This and the following new combination were listed but not formally published in *Flowering Plants of Jamaica* (Adams, 1972). Their validation is long overdue.

Eugenia virgultosa (Sw.) DC. *Prodr.* 3: 280. 1828, in part.

Eugenia virgultosa* var. *jamaicensis (O. Berg) Proctor, *comb. nov.*

Eugenia modesta DC. β *jamaicensis* O. Berg in Martius, *Fl. Brasil.* 14(1): 314. 1857. (Type from Jamaica, ex Hooker, w, not seen.)

Eugenia websteri Proctor, *sp. nov.*

MAP 30.

Frutex vel arbor tenui e *Eugenia clarendonense* et *E. brownei* in foliis lucidis grandioribus crassioribusve apicibus rotundatis, pedicellis multo bre-

vioribus vel obsoletis, et floribus grandioribus saepe solitariis ad nodos defoliatos instructis, differt.

Glabrous shrub or slender tree to 6 m tall; youngest branchlets longitudinally striate. Petioles 1–3 mm long; leaf blades lustrous, rigidly coriaceous, elliptic or broadly oblong to broadly obovate or rotund, 3–6(–7) by 1.5–4(–5) cm, usually broadly rounded at apex and sometimes slightly emarginate, broadly cuneate or rounded at base, the midrib channeled adaxially in lower half, prominent abaxially, the veins prominent on both sides, the tissue opaque. Flowers solitary and sessile or in small umbellate clusters on older leafless or leafy stems; bracts dark brown, deltate, 0.5 mm long; bracteoles rotund, apiculate, minutely ciliolate, ca. 1.5 mm long; pedicels 0–6 mm long; sepals (on fruits) broadly rounded, 3–4 mm long; petals, filaments, and style not seen. Ripe fruits crimson, with juicy, astringent but edible flesh, irregularly globose, ca. 1 cm or more in diameter; seeds 7 mm in diameter.

St. Catherine: 3.6 mi N of Worthy Park, ca. 1500 ft, *G. L. Webster 13644*, July 4, 1965 (holotype); Forest Reserve area E of Crofts Mt., 1650–1850 ft, *Proctor 22737*, Sept. 6, 1962. **Clarendon:** Peckham Woods, ca. 2500 ft, *Proctor 10224*, May 26, 1955. **Trelawny:** 5.3 mi by road N of Quick Step, ca. 1250 ft, *Proctor 36332*, July 14, 1976; Burnt Hill, 1800–1900 ft, *Proctor 26690*, Sept. 3, 1965. **St. Ann:** Douglas Castle distr., 2100–2300 ft, *Proctor 28451*, Aug. 25, 1967.

This very distinctive species keys out to the group represented in Jamaica by *Eugenia clarendonensis* Urban and *E. brownei* Urban and characterized by flowers borne in sessile umbels. It differs markedly from these, however, in its larger, thicker, more lustrous leaves rounded at the apex, in the much shorter or obsolete pedicels, and in the apparently larger flowers often solitary at leafless nodes. It is named for Dr. Grady L. Webster, collector of the holotype, in recognition of his contributions to Jamaican botany.

Mitranthes Berg

The presence of this genus in Jamaica has been known since the studies of McVaugh (1968) and was reported in Adams (1972). Until now, however, the species have not been worked out or—in the case of published taxa—transferred to *Mitranthes* from *Calypttranthes*. The group is still imperfectly known, but it seems advisable at this time to present a preliminary treatment on which further studies can be based. According to McVaugh, *Mitranthes* is similar to *Calypttranthes* in its inflorescence and calyx but differs in having a multilocular, multiovulate ovary and a myrcioid type of embryo. The type species is *M. ottonis* Berg of Cuba. So far as can now be determined, there are at least five Jamaican species belonging to *Mitranthes*. All of these differ from the Cuban type species in having sessile, cordate or subcordate leaves. They can be distinguished from each other as follows:

- A. Youngest branchlets compressed, more or less keeled or narrowly winged distally.
 - B. Leaves less than 2.5 cm long; inflorescence 3-branched, with a total of up to 12 flowers in 3 capitate clusters. *M. maxonii*.
 - B. Leaves 4–7 cm long; inflorescence unbranched, flowers solitary or sometimes in single capitate cluster of 3. *M. nivea*.
- A. Youngest branchlets terete, grooved, or quadrangular, not compressed or keeled.
 - C. Leaves glabrous on both sides. *M. glabra*.
 - C. Leaves tomentellous abaxially, at least when young.
 - D. Leaves 2.5–5 cm long. *M. clarendonensis*.
 - D. Leaves 6–10 cm long. *M. macrophylla*.

Mitranthes maxonii (Britton & Urban) Proctor, comb. nov. MAP 31.

Calyptranthes maxonii Britton & Urban in Urban, Symb. Antill. 7: 296. 1912.

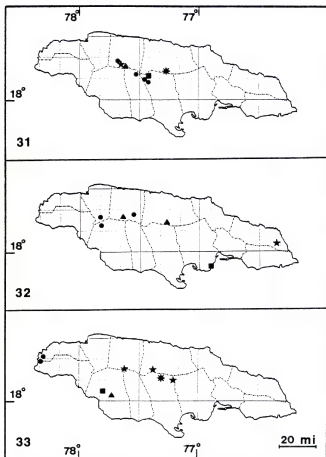
TYPE: Jamaica, parish of Trelawny, near Troy, *Maxon* 2896. Because the holotype at Berlin was presumably destroyed in the second World War, a duplicate at NY or US should be selected as lectotype.

Mitranthes nivea Proctor, sp. nov. MAP 31.

Arbor parva ramulis juvenibus glabris complanatis bicarinatis 2–3 mm in diametro, a *Mitranthes maxonii* in foliis multo grandioribus et inflorescentiis haud ramosis, floribus solitariis vel 3 simul in fasciculis sessilibus dispositis, differt.

Small tree to 8 m tall; youngest branchlets somewhat compressed and keeled or narrowly winged distally, glabrous, cinereous, 2–3 mm in diameter. Leaves sessile, glabrous, oblong-ovate or broadly oblong-elliptic, 4–7 by 3–5 cm, rounded at apex, subcordate at semiclasping base, the midrib channeled adaxially, prominent abaxially, enlarged at base, the secondary venation evident and prominulous on adaxial side, less so abaxially. Inflorescences terminal or subterminal, 1 or often 2 per axil; peduncles simple, mostly 5–10 cm long, angulate, minutely appressed-puberulous with dibrachiate hairs. Buds oblong-obovoid, 12–15 mm long, 5–7 mm thick above middle, acute to abruptly acuminate (acumen 1–3 mm long), minutely sericeous with dibrachiate hairs. Flowers white; hypanthium projecting beyond top of ovary; calyx splitting irregularly into several unequal lobes, the largest calyptrate, the others concave, 5–11 mm long, all deciduous; petals absent; stamens very numerous, 6–12 mm long, slightly exceeded by slender style. Fruits black, globose, 10–12 mm in diameter, crowned with irregularly split free portion of hypanthium; seeds several, light brown, smooth, ca. 5 mm in diameter.

St. Ann: Mason River distr., ca. 3 mi due NW of Kellits P.O., ca. 2300 ft, *Proctor* 26480, June 30, 1965 (flowers) (holotype), *Proctor* 15973, Dec. 21–22, 1956 (sterile), *Proctor* 26471, June 22, 1965 (buds), *Proctor* 26659, Aug. 19, 1965 (young fruits); Douglas Castle distr., 2200–2400 ft, *Proctor* 26546, July 15, 1965 (flowers), *Proctor* 26726, Dec. 13, 1965 (fruits); James Webster Patent, along road #144 between Mason River and Stepney, ca. 2100 ft, *Proctor* 32860, March 31, 1972 (fruits).



MAPS 31-33. Distributions: 31, *Mitranthes clarendonensis* (square), *M. glabra* (dots), *M. glabra* and *M. nivea* together (asterisk), *M. macrophylla* (star), *M. maxonii* (triangle); 32, *Myrcia calcicola* (star), *Pimenta obscura* (dots), *P. richardii* (triangles), *Psidium longipes* var. *orbiculare* (square); 33, *Ludwigia alata* (dots), *L. inclinata* (square), *Myriophyllum pinnatum* (triangle), *Anagallis pumila* (asterisk), *Mastichodendron floribundum* (stars).

The specific name of this species alludes to its likeness, when in full bloom, to a snowdrift. This is the species discussed by McVaugh (1968); it was described as "sp. A" under *Calyptanthus* in Adams (1972).

Mitranthes glabra Proctor, sp. nov.

MAP 31.

Arbor parva ramulis juvenibus glabris teretibus 1–1.3 mm in diametro, a *Mitranthes clarendonensis* in foliis parvioribus glabris basi rotundatis (haud cordatis et amplexantibus), pedunculis glabris, et fructibus glabris leviter grandioribus, differt.

Glabrous tree to 10 m tall, or sometimes shrub; youngest branchlets terete or slightly grooved, 1–1.3 mm in diameter. Leaves sessile, obovate to broadly elliptic or rotund, 2–3.5 by 1.3–2.8 cm, blunt to shortly subacuminate at apex, rounded to subcordate at base, the midrib channeled toward base adaxially, prominent abaxially, enlarged at base, the secondary venation faintly prominulous on both sides. Inflorescences solitary, arising from either ultimate or penultimate leaf axils; peduncles glabrous, 2.5–5 cm long, simple or shortly 3-branched at apex, the flowers solitary, in capitate cluster of 3, or apparently solitary at apex of peduncle branches. Flowers not seen; hypanthium in fruit slightly projecting beyond ovary, entire, with flaring apex; ovules 3 to 12. Fruits black at maturity, asymmetric and very unequal in size, 10–17 mm in diameter, 3- to 12-seeded.

St. Ann: Douglas Castle distr., 2100–2300 ft, *Proctor* 26833, Jan. 22, 1966 (holotype, u; isotype, GH). **Clarendon:** Glenwood Springs, along road between Balcarres and Sunbury, 3000–3100 ft, *Proctor* 35657, March 31, 1976; Knox Woodland, ca. 1.3 mi due SE of Spaldings P.O., 2800–3000 ft, *Proctor* 37424, Nov. 19, 1977. **Manchester:** 1 mi SE of Pike, ca. 3000 ft, *Proctor* 18306, Oct. 25, 1958. **Trelawny:** 5.3 mi by road N of Quick Step P.A., 1250–1500 ft, *Proctor* 35327, Sept. 26, 1975.

Of the Jamaican species of *Mitranthes*, *M. glabra* evidently has the widest distribution.

Mitranthes clarendonensis (Proctor) Proctor, comb. nov.

MAP 31.

Calyptanthus clarendonensis Proctor, *Rhodora* 60: 323. 1958. TYPE: Jamaica, parish of Clarendon, Peckham Woods, *Proctor* 11399.

Mitranthes macrophylla Proctor, sp. nov.

MAP 31.

Frutex vel arbor parva ramulis juvenibus tomentosis, subteretibus vel sulcatis 1.8–2.5 mm in diametro, a *Mitranthes clarendonensis* in foliis multo grandioribus, floribus grandioribus, et fructibus seminibusque parvioribus, differt.

Shrub or slender tree to 7 m tall; youngest branchlets nearly terete to deeply grooved, 1.8–2.5 mm in diameter, deciduously tomentose with pale brown,

crispate hairs. Leaves sessile, deciduously brownish tomentellous abaxially, oblong-ovate to very broadly ovate, 6–10 by 4–8 cm, blunt at apex, cordate-clasping at base, the midrib broadly channeled toward base adaxially, prominent abaxially, enlarged at base, the secondary venation prominulous on both sides. Inflorescences paired in penultimate leaf axils; peduncles tomentose, simple, the flowers sessile in cluster of 3 at apex. Buds tomentose, acuminate, 6–7 mm long. Flowers white; filaments 3–4 mm long; ovary 4-locular. Fruits globose, tomentellous, 8–10 mm in diameter, usually 4-seeded; seeds light brown, smooth, 4–6 mm in diameter.

Trelawny: near Crown Lands road extension 4.5–5 mi NW of Troy, ca. 2000 ft, *Proctor 34573*, Jan. 4, 1975 (flowers and fruits) (holotype), *Proctor 34140*, Aug. 20, 1974 (sterile).

This is the largest-leaved species of *Mitranthes* so far discovered.

***Myrcia* DC. ex Guillemain**

***Myrcia calcicola* Proctor, sp. nov.**

MAP 32.

Frutex glaber foliis ovatis 4.5–8 cm longis et 2–4.5 cm latis rigidis coriaceis apicibus acuminatis, calyce 4-lobato lobis deltatis acutis, baccis globosis 4–5 mm in diametro.

Glabrous shrub 2 m tall; youngest branchlets terete. Petioles 2–4 mm long; leaf blades stiffly coriaceous, opaque, ovate to broadly ovate, 4.5–8(–9) by 2–4.5 cm, acuminate at apex, broadly cuneate at base, the midrib shallowly channeled adaxially, prominent abaxially, the venation closely reticulate-prominulous on both sides. Panicles terminal or arising from penultimate leaf axils, many flowered, 5–8 cm long, basal stalk 3–5 cm long, ultimate branches mostly ending in 3-flowered dichasia. Flowers not seen; fruiting hypanthium produced beyond ovary; fruiting calyx 4-lobed, the lobes deltate, acute, ca. 1 mm long. Berries globose, 4–5 mm in diameter.

Portland: E slope of John Crow Mts. 1.5–2.5 mi SW of Ecclesdown, 1500–2500 ft, *Proctor 23871*, July 27, 1963 (holotype, A).

This species was listed in Adams (1972) as "sp. A." Although it has not yet been found again, it should be provided with a specific epithet. Its glabrous, stiffly coriaceous, ovate-acuminate leaves, four-lobed calyx, and small berries are distinctive among the Jamaican and other West Indian species.

***Pimenta* Lindley**

***Pimenta obscura* Proctor, sp. nov.**

MAP 32.

Frutex vel arbor aromatica ad 10 m alta a *Pimenta dioica* in foliis obovatis vel rotundatis, compositione olei essentialis, paniculis parvioribus, lobis calycium brevioribus acutioribusve, stylis pubescentibus, et fructibus cylindraceis vel ovoideis costatis vel angulatis, differt.

Aromatic shrub or tree to 10 m tall; youngest branchlets slightly compressed, glabrous or sometimes puberulous, or at least terminal leaf buds strigillose-puberulous. Petioles 5–10 mm long; leaf blades obovate to rotund, 2.5–9 by 1.5–5(–9) cm, obtuse or rounded at apex, cuneate at base, glabrous or sometimes minutely and deciduously appressed-puberulous beneath, the midrib channeled adaxially, prominent abaxially, the lateral nerves prominent especially abaxially. Inflorescences glabrous to puberulous, few-flowered, axillary panicles usually shorter than leaves; stalk 1–3(–4) cm long; bracts puberulous, narrowly deltate, 0.2–0.3 mm long, soon deciduous; bracteoles similar, to 0.7 mm long. Flowers sessile, solitary or 2 or 3 together on short panicle branches; hypanthium glabrous or puberulous, densely glandular-verrucose, narrowly angular-obconic, 1–1.2 mm long, abruptly expanded at apex into 4 (rarely 5) thick calyx lobes, these dark brown, deltate, acute, 0.6–1 mm long; petals white, somewhat longer than calyx lobes; filaments ca. 1 mm long, glabrous; style ca. 1.5 mm long, pubescent toward base. Fruits cylindrical to ellipsoid or ovoid, 8–10 mm long, up to 7 mm thick, ribbed or angulate, densely verrucose-glandular; ripe seeds not seen.

St. James: White Rock Hill, 1 mi S of Sweet Water, ca. 2100 ft, *Proctor 34507*, Dec. 22, 1974 (holotype), *Proctor 23170*, Jan. 27, 1963, *Proctor 34463*, Dec. 13, 1974, *Proctor 34507-a*, Dec. 22, 1974 (form with especially large, rotund leaves). **St. Elizabeth:** along road between Mulgrave and Elderslie, 1600–1700 ft, *Proctor 20841*, May 13, 1960. **Trelawny:** Burnt Hill, ca. 1800 ft, *Proctor 22536-b*, July 29, 1962, *Proctor 26692*, Sept. 3, 1965.

***Pimenta richardii* Proctor, sp. nov.**

MAP 32.

Arbor ad 15 m alta, a *Pimenta dioica* in compositione olei essentialis et floribus in glomerulis densis puberulis in ramulis panicularum terminalium insertis, differt.

Tree to 15 m tall; youngest branchlets 2.5–3 mm thick, at first dark brown, bisulcate on each side below leaf nodes, becoming terete and somewhat cinereous with age, glabrous but minutely roughened or scurfy, terminal bud densely but very minutely strigillose-puberulous. Petioles 5–11 mm long, dark brown, very minutely stellate-puberulous on one side; leaf blades rigidly coriaceous and often broadly revolute, oblong, oblong-elliptic, or oblong-obovate, 4.5–11 by 2–4.5 cm, obtuse at apex, cuneate or broadly cuneate at base, the midrib narrowly grooved adaxially, prominent and dark brown abaxially, the surface smooth adaxially, the venation prominulous abaxially. Inflorescences terminal, densely but deciduously puberulous, glomerate panicles, the very short panicle branches terminating in dense secondary heads

of tightly packed flowers; main peduncles up to 2.5 cm long; bracts and bracteoles not observed. Flowers sessile, in heads 0.8–1.3 cm in diameter, ca. 30 or more per head; hypanthium densely puberulous, broadly obconical, ca. 1 mm long, slightly wider than long at apex; sepals 4, ovate, densely puberulous on both sides, ca. 1 mm long; petals obovate, ca. 2 mm long, puberulous on inner face; filaments glabrous, ca. 2 mm long; style glabrous except at base, ca. 2.5 mm long, terminated by thickened stigma. Fruiting panicles glabrate; fruits globose, puberulous and minutely glandular-verrucose, 6–7 mm in diameter, with somewhat lemonlike aroma when crushed; ripe seeds not seen.

Trelawny: near Crown Lands road extension 4.5–5 mi NW of Troy, ca. 2000 ft, *Proctor* 34170, Sept. 7, 1974 (fruits) (holotype). **St. Ann:** Douglas Castle distr., 2200–2400 ft, *Proctor* 35686, April 9, 1976 (flower buds), *Proctor* 36252, May 21, 1976 (flowers), *Proctor* 36275 (with R. F. Thorne), June 11, 1976 (flowers).

The major oil constituents of *Pimenta obscura* and *P. richardii* are caryophyllene and limonene, respectively, as contrasted with methyl eugenol for *P. dioica*. I am indebted to Dr. Shirley Thomas, formerly with the Chemistry Department, University of the West Indies, Mona, Jamaica, for analyzing the oils of these plants. *Pimenta richardii* is named for Dr. Richard A. Howard; the type material was collected with the aid of his namesake, Richard A. Proctor.

Psidium L.

Psidium longipes (O. Berg) McVaugh, Jour. Arnold Arb. **54**: 312. 1973.

Psidium longipes var. **orbiculare** (O. Berg) McVaugh, Jour. Arnold Arb. **54**: 314. 1973. MAP 32.

New to Jamaica. **St. Catherine:** Hellshire Hills inland from Half Moon Bay, 50–100 ft, *Proctor* 38392, Nov. 16, 1979, *McKenley* 2, Jan 4, 1980.

This entity is very common in the Bahamas and Turks and Caicos Islands and also occurs in Antigua, Barbuda, Anguilla, and St. Barthélemy. Its discovery in Jamaica constitutes a rather surprising range extension.

ONAGRACEAE

Ludwigia L.

Ludwigia alata Ell. Sketch Bot. S. Carolina Georgia **1**: 213. 1821.

MAP 33.

New to Jamaica. **Westmoreland:** inland from milepost 23, ca. 2.7 mi ENE of Negril Village, sea level, *Proctor* 37733, March 22, 1978. **Hanover:** in the Great

Morass, ca. 1.9 mi due SW of Logwood, sea level, *Proctor 37134*, July 19, 1977.

This species is otherwise known from the Coastal Plain of the southeastern United States from Florida to Virginia.

Ludwigia alata is similar only to *L. simpsonii* Chapman among Jamaican species, having alternate leaves and small, sessile flowers with minute or apparently absent petals; it differs in its much larger size, with leaves (at least the lower ones) up to 5 cm or more long, and in its conspicuously winged stems.

Ludwigia inclinata (L. f.) Gómez de la Maza, *Anal. Hist. Nat.* **23**: 66. 1894. MAP 33.

New to Jamaica. **St. Elizabeth**: Slipe distr., sea level, *Proctor 34212*, Oct. 16, 1974 (det. confirmed by P. Raven), *Proctor 37918*, July 25, 1978.

This species has a chiefly continental range from southern Mexico (Chiapas) to South America; in the West Indies it is otherwise known only from Cuba.

Ludwigia inclinata is an aquatic species with floating stems that often become inflated and spongy; it bears conspicuous yellow flowers. It differs from *L. peploides* (Kunth) Raven, another often floating species, in its quadrangular, obconical capsules (those of *L. peploides* are terete and cylindrical). In addition, the petioles of *L. inclinata* are usually at least as long as the leaf blades, with the relative length much greater than in *L. peploides*. *Ludwigia sedioides* (Humb. & Bonpl.) Hara, another species with floating stems, differs from *L. inclinata* in having all its leaf blades rhombic, floating, and forming a symmetrical rosette on the surface of the water.

HALORHAGIDACEAE

***Myriophyllum* L.**

Myriophyllum pinnatum (Walter) B.S.P. *Prelim. Catal.* 19, 1888.

MAP 33.

Genus and species new to Jamaica. **St. Elizabeth**: upper course of Broad R., ca. 1 mi due W of Burnt Savanna, sea level, *Proctor 36659*, Nov. 28, 1976 (sterile), *Proctor 37925*, July 25, 1978 (fertile).

This species has a wide range in the eastern half of the United States and has also been recorded from Cuba. *Myriophyllum* can be distinguished from *Proserpinaca*, the only other genus of this family known from Jamaica, according to the following key:

- A. All leaves except uppermost (i.e., in inflorescence) divided into capillary segments; calyx 4-lobed, tube 4-grooved; ovary 4-celled. *Myriophyllum*.

- A. Leaves mostly lanceolate with serrate margins; calyx 3-lobed, tube 3-winged; ovary 3-celled. *Proserpinaca*.

PRIMULACEAE

Anagallis L.

Anagallis pumila Sw. Prodr. 40. 1788.

MAP 33.

Until recently, this species, which has a wide general distribution in the tropics, was known in Jamaica only from Swartz's type specimen, collected at an unknown locality during the period 1784-1786. It has now been re-discovered in Jamaica, growing along the base of a steep roadside bank of damp acidic clay, where it was associated with *Drosera capillaris* and other unusual plants.

Clarendon: 1 mi by road W of Rhoden (or Rodon) Hall, ca. 2000 ft, *Proctor* 35488, Nov. 23, 1975.

SAPOTACEAE

Mastichodendron (Engler) Lam

Mastichodendron floribundum (Griseb.) Cronq. *Lloydia* 9: 248. 1946.

FIGURE 5, MAP 33.

This species, well characterized by Cronquist, was placed in the synonymy of *Mastichodendron foetidissimum* (Jacq.) Lam by Adams (1972), without explanation. Late in 1976 I came upon a large mastic tree in moist primary forest near the center of Jamaica. This tree displayed the leaf characters given for *M. floribundum* and grew in a habitat far removed from the rather dry woodland near the seacoast at low elevations characteristic of *M. foetidissimum*. The tree was observed frequently over the following months, and eventually good flowering and fruiting material, together with mature seeds, was obtained. The evidence now available confirms the distinctness of *M. floribundum* and requires it to be removed from the synonymy of *M. foetidissimum*. The two species are distinguished as follows:

- A. Bark gray; leaves broadly elliptic, rounded to somewhat acute at both ends, usually with minute pocket at apex of petiole on adaxial side; flowering period June-July; flowers pale yellow, strongly scented; corolla 3.5-5 mm long, the lobes elliptic-ovate, not or only slightly auriculate at base; filaments shorter than corolla; staminodes nearly as long as filaments, entire or minutely toothed; fruits yellow, ellipsoid, usually more than 2 cm long; seed coat not or scarcely raised around hilum scar. *M. foetidissimum*.
- A. Bark reddish; leaves elliptic or ovate-elliptic, acuminate at apex, without minute pocket at apex of petiole; flowering period March-May; flowers pale green, un-

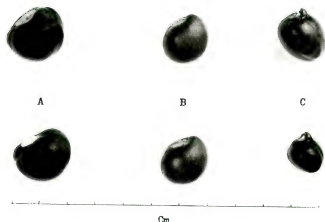


FIGURE 5. Seeds of *Mastichodendron*: A, *M. foetidissimum* from Jamaica; B, *M. foetidissimum* from Florida; C, *M. floribundum*.

scented; corolla ca. 5.5 mm long, the lobes nearly orbicular, conspicuously auriculate at base; filaments equal to or longer than corolla; staminodes much shorter than filaments, 2- or 3-lobed at apex; fruits light green or yellowish green, globose to broadly ellipsoid, 1.5–2 cm long; seed coat raised in conspicuous protuberance on one side of hilum scar. *M. floribundum*.

The relative thickness of the seed coat, a character used by Cronquist to distinguish these two species, does not hold with mature seeds and is not necessary for separating them. Specimens seen of *Mastichodendron floribundum* indicate that it has a distinctive range in the interior of Jamaica.

Trelawny: near Troy, 2000 ft, *J. R. Perkins 1424*, March 23, 1917 (GH). **St. Ann:** Cedar Valley distr., ca. 1.5 mi NE of Cave Valley Square, ca. 2000 ft, *Proctor 36706*, Dec. 18, 1976, *Proctor 36757*, April 8, 1977, *Proctor 36811*, May 4, 1977, *Proctor 36850*, May 13, 1977, *Proctor 37940*, Aug. 18, 1978. **Clarendon:** Crofts Mt., 2500 ft, *Harris 11217*, Sept. 30, 1912 (GH).

OLEACEAE

Forestiera Poiret

Forestiera rhamnifolia Griseb. Catal. Pl. Cubens. 169. 1866.

Forestiera rhamnifolia var. **pilosa** Stearn, Jour. Arnold Arb. 52: 615. 1971. MAP 34.

The recent segregation of two varieties of *Forestiera rhamnifolia* by William T. Stearn associated the Jamaican population of this species with one specimen from Cuba as var. *pilosa*. The glabrous variant of this species (var. *rhamnifolia*) was credited with a wide range throughout the Antilles but was believed to be absent from Jamaica. Recent collections have shown that the situation in Jamaica is more complex. Var. *pilosa* is mostly confined to lower slopes of the Blue Mountains region in the eastern part of the island, but two disjunct records are known. *Forestiera rhamnifolia* var. *rhamnifolia* is now known to occur in the central part of the island, at a higher elevation than any collection of var. *pilosa*.

St. Catherine: 3 mi NW of Old Harbour, 400–500 ft, Proctor 38316, Oct. 3, 1979 (fruits). **St. Elizabeth:** Santa Cruz Mts., Purdie s.n., 1842 (κ, as reported by Stearn).

Forestiera rhamnifolia var. **rhamnifolia** MAP 34.

New to Jamaica. **Clarendon:** Glenwood Springs, along road between Balcarres and Sunbury, ca. 3100 ft, Proctor 34183, Sept. 27, 1974.

GENTIANACEAE

Fagraea Thunb.

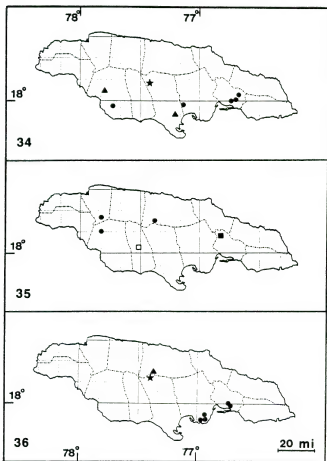
This genus, which was placed by Adams (1972) in the Loganiaceae, has been removed from that family by Fosberg and Sachet (1980) and placed in the Gentianaceae.

Schultesia Martius

Schultesia guianensis (Aublet) Malme, Ark. Bot. 3(12): 9. 1904. MAP 34.

Clarendon: Harris Savanna, ca. 350 ft, Proctor & Adams 34341, Nov. 26, 1974. **St. Elizabeth:** Slipe distr., sea level, Proctor 35445, Nov. 8, 1975.

Only once previously recorded from Jamaica (Macfadyen s.n., as cited by Adams, 1972), this rare species has now been rediscovered at two rather widely separated localities. The second specimen was found in a grassy, savannalike pasture, where it was associated with a number of other rare or unusual species including *Angelonia angustifolia*, *Cheilophyllum jamaicense*, *Curculigo scorzonifolia*, *Pectis linearis*, *Polygala leptocaulis*, *Reynaudia filiformis*, *Sachsia polycephala*, and *Scleria setuloso-ciliata*. A small pond in the same pasture, when full of water, contains the rare *Sagittaria guay-*



MAPS 34–36. Distributions: 34, *Forestiera rhamnifolia* var. *pilosa* (dots), *F. rhamnifolia* var. *rhamnifolia* (star), *Schultesia guianensis* (triangles); 35, *Forsteronia domatiella* (dots), *F. wilsonii* (solid square), report of *F. wilsonii* (which may be *F. domatiella*) (hollow square); 36, *Jacaima costata* var. *costata* (dots), *J. costata* var. *goodfriendii* (triangle), *J. parvifolia* (star).

anensis; when nearly dried out during the dry season it is the only known Jamaican locality of *Heliotropium lagoonense*. Most of the above-listed plants are discussed elsewhere in the present paper.

APOCYNACEAE

Forsteronia G. F. W. Meyer

Forsteronia wilsonii (Griseb.) Woodson, Ann. Missouri Bot. Gard. **22**: 174. 1935. MAP 35.

One of two previously known Jamaican species of *Forsteronia*, *F. wilsonii* is recorded from but a single modern collection, and the fruits have never been collected. The lectotype is an unlocalized specimen gathered by Nathaniel Wilson in the mid-nineteenth century (K). Wilson's specimens were collected in the eastern third of the island, first during his tour of duty (beginning in 1846) as Superintendent of the Bath Botanic Garden in St. Thomas, and later during the establishment of the botanic garden at Castleton, St. Mary, which was officially opened in 1862. In supervising the development of the latter site, he must have visited the valley of the Wag Water River on many occasions, traveling over the Stony Hill watershed from Kingston to Castleton. It was in this locality that I found *F. wilsonii* in 1962 (Proctor 22624), and perhaps this was also where Wilson found it. Unfortunately, the population from which I collected specimens has been obliterated by road reconstruction.

When Grisebach first described this species (1862), he also cited a Purdie specimen from Manchester, which I have not seen. I suspect that this may belong to the smaller-leaved species of this affinity that has been discovered in several localities in mid-western Jamaica, growing in a very different type of habitat from the steep, noncalcareous hillsides of *Forsteronia wilsonii*.

Forsteronia domatiella Proctor, sp. nov.

MAP 35.

Frutex scandens *Forsteronia wilsonii* affine, sed in ramulis 1-1.5 (versus 2-2.5) mm in diametro, foliis parvioribus glandibus conicis nigris 2 ad 5 ad basem costae adaxialis instructis et pagina abaxiali domatiis parvioribus pubescentibus in axillis nervorum instructis, inflorescentiis 1.2-2.5 (versus 3-7) cm longis, et floribus parvioribus, differt.

High climbing, slender, woody vine with latex; youngest stems subquad-rangular, minutely puberulous and glandular; older stems terete and glabrous; ultimate branches 1-1.5 mm in diameter. Petioles puberulous, 1-2 mm long; leaf blades lanceolate to oblong-elliptic, 2-5(-9) by 1-2(-2.5) cm, acuminate to long-acuminate at apex, rounded to subcordate at base, bearing 2 to 5 black, conical glands (mostly paired) toward base of midvein adaxially and very small, more or less hairy domatia in principal nerve axils abaxially.

Inflorescences terminal, dense, puberulous, mostly 1.5–2.5 cm long, branches puberulous and minutely glandular; bracts linear, 3–4.5 mm long, ciliolate. Calyx lobes very narrowly deltate, 2–2.5 mm long, 0.5–0.6 mm wide at base; corolla white, tube ca. 1 mm long, deltate lobes ca. 1.5 mm long. Follicles linear, nearly straight or somewhat curved, 15–18 cm by 4–5 mm; coma pale brown, ca. 2 cm long; seeds not observed.

St. Elizabeth: between mileposts 4 and 5, Redgate to Ipswich road, ca. 500 ft, *Proctor 36763*, April 20, 1977 (flowers) (holotype), *Proctor 36824*, May 5, 1977 (fruit). **St. James:** White Rock Hill, 1 mi S of Sweet Water, ca. 2100 ft, *Proctor 34511*, Dec. 22, 1974 (sterile). Sight record, **St. Ann:** Cedar Valley distr., ca. 1.5 mi NE of Cave Valley Square, ca. 2000 ft, *Proctor*.

All the cited plants were growing on wooded, rocky, limestone hillsides.

ASCLEPIADACEAE

Cynanchum L.

Cynanchum hartii (Schlechter) Proctor, comb. nov.

Metastelma albiflorum Griseb., Fl. Brit. W. Indian Is. 417, 1862.

M. hartii Schlechter in Urban, Symb. Antill. 1: 256, 1899.

Cynanchum albiflorum (Griseb.) Stearn, Phytologia 21: 138, 1971, not Koidz., 1930, or Woodson, 1947.

The epithet *albiflorum*, used by Adams (1972) for this species, is invalid and must be replaced by the next available one.

Jacaima Rendle

Jacaima costata (Urban) Rendle, Jour. Bot. London 74: 340, fig. 1, 1936. MAP 36.

This rare species, representing one of Jamaica's few endemic genera, was until quite recently thought to be confined to arid rocky thickets and woodlands near the south coast of the island. It was known from just two areas (Adams, 1972): St. Andrew Parish, Long Mountain (the type locality, overlooking the city of Kingston); and St. Catherine Parish, Hellshire Hills. It was recorded from near sea level to 800 ft altitude. The recent discovery of *Jacaima costata* growing in damp mesophytic forest at a much higher elevation near the center of the island is therefore most unexpected. The population at this locality, although similar to typical plants from near the south coast, nevertheless differs in several minor characteristics. These, together with geographic disjunction, justify segregation at the varietal level. It is named for its discoverer.

Jacaima costata var. *goodfriendii* Proctor, var. nov.

MAP 36.

A var. *costata* in lamina basi cuneata (haud rotundata vel subcordata), bracteis circa 0.5 mm (haud 1 mm) longis, et lobis calycis oblongis 0.5 mm latis (haud ovatis 1 mm latis), differt.

Differs from typical variety in having leaf blades cuneate (vs. rounded to subcordate) at base, inflorescence bracts ca. 0.5 mm (vs. 1 mm) long, and calyx lobes oblong and 0.5 mm wide (vs. ovate and 1 mm wide). (The single, not quite mature fruit found on var. *goodfriendii* is 7.5 cm long—perhaps not significantly larger than the 6.5 cm average for var. *costata*.)

St. Ann: Cedar Valley distr., ca. 1.5 mi NE of Cave Valley Square, ca. 2000 ft, *Goodfriend s.n.* (IJ 65657), May 17, 1977 (flowers) (holotype), *Goodfriend s.n.* (IJ 66697), July, 1977 (fruit).

Jacaima parvifolia Proctor, sp. nov.

MAP 36.

A *Jacaima costata* in foliis parvioribus, inflorescentibus subsessilibus, floribus paucioribus viridibus purpureo-reticulatis, lobis corollae haud reflexis, et folliculis 3-angulatis parvioribus, differt.

Slender, high-climbing vine with copious latex; stems and leaves puberulous throughout. Petioles 0.3 mm in diameter, mostly 1–1.7 cm long; leaf blades membranous-papery, lance-oblong to ovate-oblong, mostly 2.5–5 by 1–2 cm, mucronate at apex, rounded at base. Inflorescences subsessile, puberulous; peduncle ca. 1 mm long. Flowers about 5 in a small cyme; pedicels 2–4 mm long; bracts narrowly deltate-acuminate, 0.7–0.9 mm long; calyx pilosellous in line along back, the lobes lance-oblong, ca. 2 mm long, acute; corolla campanulate, 5–6 mm across when expanded, greenish with reticulum of maroon lines, glabrous on outside, lightly tomentellous within in ring at base of lobes, the lobes broadly deltate, ca. 2.5 mm long, acute, not reflexed; gynostegium ca. 1 mm high; corona of 5 fleshy lobes adherent to flat top of gynostegium; pollinia horizontal. Follicles narrowly oblong-acuminate, 4.5 cm long, prominently 3-angled, angles narrowly winged.

Clarendon: Broom Hall hills, 1.2 mi due SW of Cave Valley Square, 1800–2000 ft, *Proctor 37887*, July 9, 1978 (holotype).

Although a mature flowering and fruiting plant of this species has been found at but a single site, seedlings are not uncommon on wooded hillsides in the general area. For several years the identity of these young plants was a mystery; they were thought perhaps to represent an unknown species of *Cynanchum*. Discovery of the flowers and fruits revealed the much closer affinity with *Jacaima*. *Jacaima parvifolia* differs from *J. costata* (the only other known species of the genus) in having smaller, more delicate leaves; subsessile inflorescences with fewer flowers, these of a different color and with the corolla lobes not reflexed; and smaller, 3-angled (vs. 5-angled) follicles.

CONVOLVULACEAE

Ipomoea* L.**Ipomoea carmesina* Proctor, sp. nov.**

MAP 37.

Frutex scandens *Ipomoea horsfalliae* affine, sed in foliis trifoliatis, floribus parvioribus lobis calycium inaequalibus, et capsulis parvioribus, differt.

High-climbing, glabrous woody vine; bark of older stems longitudinally ridged. Petioles 2–2.5 cm long; leaflets 3, stalked (petiolules 1–4 mm long), obovate, elliptic, or very broadly elliptic, the middle one 5–8.5 by 3–4.5 cm, short-acuminate at apex, cuneate at base. Inflorescences mostly 8- to 25-flowered, terminating stout peduncles 2.5–7.5 cm long arising from leafless nodes of older stems. Calyx lobes broadly rounded, unequal, the longer ca. 6 mm long; corolla crimson, narrowly tubular with rotate lobes, tube 2.5–3 cm long; stamens exserted; style 3–3.5 cm long, stigma 2-lobed. Capsules 9–10 by 7–8 mm, rounded and abruptly long-pointed at apex due to persistent style base. Ripe seeds not seen.

Trelawny: near Crown Lands road extension 4.5–5 mi NW of Troy, ca. 2000 ft, *Proctor 34169*, Sept. 7, 1974 (holotype); 5.3 mi by road N of Quick Step, 1250–1500 ft, *Proctor 35324*, Sept. 26, 1975.

***Ipomoea mauritiana* Jacq. Collect. 4: 216. 1790.**

MAP 37.

New to Jamaica. **Trelawny:** Dry River distr., ca. 1 mi NNE of Linton Spring, 800–900 ft, *Proctor 29322*, Nov. 4, 1968 (det. D. F. Austin).

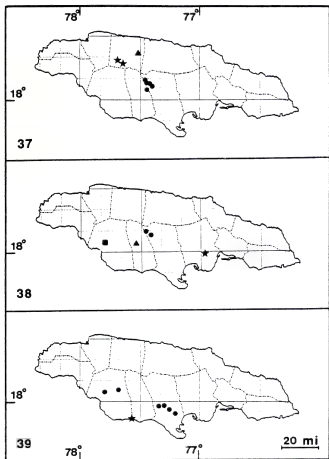
This species was found growing in wet swales and clearings in the bottom of a deep karst valley. It was a "wild trailing or twining herbaceous vine from large underground tuber; corolla light pink with deep pink throat." The leaves are deeply five-lobed, with the lobes oblong or oblanceolate and mostly 4–6 by 1.5–2.5 cm. *Ipomoea mauritiana* is related to *I. batatas* (L.) Lam., the common sweet potato.

***Ipomoea saxicola* Proctor, sp. nov.**

MAP 37.

Frutex scandens foliis trifoliatis, a *Ipomoea ternata* in pubescentia densa, floribus roseis, et capsulis seminibus parvioribus, differt.

High-climbing subwoody vine, densely pubescent throughout with grayish pluricellular hairs mostly 1–1.5 mm long, each arising from pustulate base; older stems shallowly sulcate, remaining covered with persistent hairs. Leaves very variable in size; petioles 2–10 cm long; leaflets 3, stalked (petiolules 2–10 mm long), the middle one obovate or broadly elliptic, 6–24 by 3–13 cm, shortly and sharply acuminate at apex, cuneate at base. Inflores-



MAPS 37-39. Distributions: 37, *Ipomoea carmesina* (stars), *I. mauritiana* (triangle), *I. saxicola* (dots); 38, *Heliotropium lagoense* (square), *Tournefortia smaragdina* (dots), *Nicotiana alata* (triangle), *N. plumbaginifolia* (star); 39, *Angelonia angustifolia* (star marks location of Alligator Pond Savanna).

cences axillary, 5- to 13-flowered, almost sessile or on peduncles up to 13 cm long. Calyx lobes rounded or blunt, slightly unequal, the outer 2 densely pubescent, 8-10 mm long, the inner 3 slightly longer, glabrous; corolla light pink with deep pink throat, oblong-campanulate, ca. 5 cm wide across expanded lobes, the inflated tube 3.5-4.5 cm long, up to 2 cm thick toward distal end, abruptly contracted just above base; stamens included; style ca. 3 cm long, with linear undivided stigma. Capsules globose, 1.2-1.5 cm in diameter, shortly apiculate; seeds 4-4.5 mm in diameter, densely puberulous, with dense fringe of tawny-silky marginal hairs up to 10 mm long.

Clarendon: Glenwood Springs, along road between Balcarres and Sunbury, ca. 3100 ft, *Proctor 34185*, Sept. 27, 1974 (flowers) (holotype), *Proctor 33630*, Nov. 30, 1973 (fruits); 0.6 mi due S of Sunbury Church, ca. 3000 ft, *Proctor 37864*, June 22, 1978 (flowers); along road between Ritchies and Balcarres, ca. 3000 ft, *Proctor 34379*, Nov. 28, 1974 (fruits); vic. of Quaco Rock, near Ritchies, ca. 3000 ft, *Proctor 33715*, Jan. 4, 1974 (sterile). **Manchester:** 0.5 mi due NNE of Banana Ground P.O., ca. 3100 ft, *Proctor 37601*, Jan. 18, 1978 (fruits).

BORAGINACEAE

Argusia

Argusia Amman ex Boehmer in Ludwig, *Defin. Gen. Pl.* ed. 3, 507. 1760; Dandy, *Reg. Veg.* **51**: 28, 121. 1967.

Messerschmidia L. ex Hebenstreit, *Novi Comment. Acad. Sci. Imp. Petrop.* **8**: 315. 1763; I. M. Johnston, *Jour. Arnold Arb.* **16**: 161. 1935.

Mallotonia (Griseb.) Britton, *Ann. Missouri Bot. Gard.* **2**: 47. 1915.

Many years ago, I. M. Johnston (1935) proposed uniting the common West Indian seaside shrub often known as *Mallotonia gnaphalodes* (L.) Britton with two Old World species with which it shares characters of fruit, indument, and habitat. He placed them in the genus *Messerschmidia*, overlooking valid publication of the earlier name *Argusia*, which was based on the same type species. Britton (1915) had already raised Grisebach's sect. *Mallotonia* (of *Tournefortia*) to the generic level for the West Indian plant alone. More recently, Nowicke and Skvarla (1974) have shown that the pollen reveals no features differentiating this group from many species of *Tournefortia*. Although I have a preference for broad, inclusive genera, in the present case maintaining *Mallotonia* alone (or sinking it along with its postulated Old World congeners back into *Tournefortia*) does a disservice to taxonomy by concealing significant facts about apparent relationships and possible phylogeny. At the same time, neither *Mallotonia* by itself nor *Messerschmidia* is a suitable candidate for conservation, since at most but three species are involved, and all have already received combinations in *Argusia*. The West Indian representative of this taxon should therefore be known as follows:

Argusia gnaphalodes (L.) Heine, *Fl. Nouv. Caléd.* **7**: 108. 1976.

Heliotropium gnaphalodes L. Syst. Nat. ed. 10. 2: 913. 1759, Moen. Acad. 5: 394. 1760.

Tournefortia gnaphalodes (L.) R. Br. ex Roemer & Schultes in L. Syst. Veg. 4: 538. 1819.

Mallotonia gnaphalodes (L.) Britton, Ann. Missouri Bot. Gard. 2: 47. 1915.

Messerschmidia gnaphalodes (L.) I. M. Johnston, Jour. Arnold Arb. 16: 165. 1935.

Heliotropium L.

Heliotropium lagoense (Warming) Gürke in Engler & Prantl, Nat. Pflanzenfam. IV. 3a: 97. 1893. MAP 38.

Heliotropium antillanum Urban, Symb. Antill. 4: 528. 1910.

H. trinitense Urban, Symb. Antill. 7: 350. 1912.

New to Jamaica. **St. Elizabeth:** Slike distr., near sea level, *Proctor 33730*, March 3, 1974, *Proctor 35620*, March 13, 1976.

This prostrate, matlike herb grew abundantly in dried mud around the sides of a small pond reduced by seasonal drought. The same species occurs in Cuba, Puerto Rico, Mexico, Guatemala, Panama, Trinidad, and various South American localities. It can be distinguished from other Jamaican members of the genus by the completely prostrate stems and the solitary flowers, these on axillary or supra-axillary peduncles 2–6 mm long. Although plants of this species are said to be “apparently perennial” by Britton and Wilson (1925, p. 136), the Jamaican plants grow as ephemeral annuals at their single known locality, which for most of the year is submerged beneath the waters of a small pond.

Tournefortia L.

Among the Antillean species of this genus is a small group represented by a widespread taxon (*Tournefortia maculata* Jacq.) that also has an extensive continental distribution, and by two others that appear to be locally derived endemics. One of these (*T. laurifolia* Vent.) perhaps occurs only in Puerto Rico, although Urban (1929) reported a single collection (*Abbott 305*) from the Samaná Peninsula in Hispaniola. A somewhat similar population has been discovered in Jamaica; this was initially determined as *T. laurifolia* by E. C. Leonard (about 1953), but this record was overlooked and not mentioned by Adams (1972). A pollen study of this material (under the name *T. laurifolia*) was published by Nowicky and Skvarla (1974). However, in some large herbaria (e.g., the New York Botanical Garden) all specimens of this complex are filed under *T. maculata*, although *T. laurifolia* seems clearly distinct in details of floral and fruit morphology.

In attempting to verify the identity of the Jamaican material, now known from several collections, I noted a number of differences from *Tournefortia laurifolia* as it occurs in Puerto Rico. These, together with a geographic dis-

junction of more than 600 miles, suggest that the Jamaican population should be recognized as a separate species, differing from both *T. maculata* and *T. laurifolia* in leaf shape and many floral details. Unfortunately, the fruits of the Jamaican entity have not yet been seen and therefore cannot be compared. The fruits of *T. laurifolia* are orange and 7–8 mm in diameter; those of *T. maculata* are yellow and 4–5 mm in diameter.

***Tournefortia smaragdina* Proctor, sp. nov.**

MAP 38.

Frutex scandens *Tournefortia laurifolia* affine, sed in foliis angustioribus basibus cuneatis vel anguste acutis, floribus smaragdinis lobis calycibus brevioribus, corolla longiore tubo latiore lobis brevioribus acuminatis (haud attenuato-filiformis), et anthera angustiore apice cum processu gongylodi instructa, differt.

Slender woody vine or vinelike, scrambling, or arching shrub; young stems glabrate to sparsely puberulous except for tuft of yellowish septate hairs in each leaf axil. Petioles 0.6–1.8 cm long; leaf blades membranous, narrowly ovate to elliptic, 5–12.5 by 1.5–5 cm, sharply long-acuminate at apex, cuneate or acuminate at base, entire and sparsely short-ciliate. Inflorescences lax, open, 2- to 4-branched cymes, the branches 2–3 cm long, 5- to 9-flowered, glabrate or sparsely puberulous. Calyx lobes narrowly deltate-acuminate, 1.5 mm long, 0.7–0.8 mm wide at base; corolla deep emerald green, the tube glabrate or sparingly strigillose, 6–7 mm long, inflated at base, 1.2–1.7 mm in diameter near middle, the lobes deltate-acuminate, 1.5–2 mm long, carinate on inner side. Anthers sessile, inserted in corolla tube just below its mouth, lanceolate, 1 mm long, 0.3 mm wide below middle, with

TABLE 1. Comparison of floral details of *Tournefortia laurifolia* and *T. smaragdina*.*

Floral character	<i>T. laurifolia</i>	<i>T. smaragdina</i>
FLOWER COLOR	Greenish yellow, "apricot"	Deep emerald green
CALYX LOBES, LENGTH × WIDTH	2 × 0.8	1.5 × 0.7–0.8
COROLLA TUBE LENGTH	5.5–6.5	6–7
DIAMETER AT NAR- ROWEST POINT	0.7–1.3	1.2–1.7
COROLLA LOBES SHAPE	Attenuate-filiform	Acuminate
LENGTH	4–5	1.5–2
ANTHERS SHAPE	Narrowly deltate, no appendage	Lanceolate, with appendage
WIDTH	0.5 (at base)	0.3 (below middle)

*All measurements are in millimeters.

small, knoblike appendage at apex; stigma minutely hirsutulous. Fruits unknown.

Clarendon: Glenwood Springs, along road between Balcarres & Sunbury, ca. 3100 ft, *Proctor 34863*, March 1, 1975 (holotype), *Proctor 38066*, March 4, 1979; Knox College, Spaldings, 2800 ft, *Proctor 6320* (vs), March 5, 1952.

Although this species resembles *Tournefortia laurifolia* in habit and general appearance, the leaves differ in being proportionately narrower and are always cuneate to acuminate at the base. In addition, the flowers differ strikingly in color as well as in various dimensional details. The fruits cannot be compared because those of *T. smaragdina* have not yet been found. TABLE 1 compares the floral details of *T. laurifolia* and *T. smaragdina*.

SOLANACEAE

Nicotiana L.

Nicotiana alata Link & Otto, Ic. Pl. Rar. Horti Regii Berol. **1:** 63. *t.* 32. 1828. MAP 38.

New to Jamaica. **Manchester:** Marshalls Pen, ca. 2.25 mi due NW of Mandeville, ca. 2100 ft, *Proctor 31108*, Nov. 23, 1969.

An escape from cultivation, this was found growing in chinks of an old stone wall by the roadside. The species is indigenous to southern Brazil, Paraguay, Uruguay, and northern Argentina, but there are many cultivated forms elsewhere.

Nicotiana plumbaginifolia Viv. Elenchus Pl. Horti Bot. **26.** *t.* 5. 1802. MAP 38.

Confirmed for Jamaica. **St. Catherine:** Spanish Town, in open waste ground, 50 ft, *Proctor 27600*, Aug. 16, 1966.

Goodspeed (1954), in giving the range of this species, did not include Jamaica. Alain (1957) did so but gave no source for his information. Adams (1972) mentioned the Alain report but said he had seen no specimen.

The range of *Nicotiana plumbaginifolia* outside Jamaica includes southernmost Florida, Cuba, Trinidad, and various continental localities from Mexico to Paraguay and northern Argentina.

SCROPHULARIACEAE

Angelonia Humb. & Bonpl.

Angelonia angustifolia Benth in DC. Prodr. **10:** 254. 1846. MAP 39.

Although Adams (1972, p. 660) stated that this species is "cultivated and

naturalized locally," its widespread if scattered occurrence in Jamaica at remote marshy and savannalike localities suggests that it may be indigenous after all. Wild plants were collected as long ago as 1853 (only seven years after the species was first described) at "Alligator Pond Savanna," parish of Manchester. I have found it at a number of comparable localities. It is true that cultivars of this species are sometimes grown in Jamaica, but since its natural range includes Cuba, Hispaniola, and Mexico, I can perceive no reason for excluding it from the list of indigenous Jamaican plants.

Clarendon: Harris Savanna, ca. 350 ft, *Proctor 34356*, Nov. 26, 1974; Mineral Heights, ca. 1.3 mi due S of May Pen, ca. 250 ft, *Proctor 37234*, Sept. 9, 1977; Denbigh, 100–200 ft, *Proctor 26796*, Jan. 9, 1966; 0.8 mi by road E of Toll Gate, in low, wet swale, ca. 50 ft, *Proctor 37814*, May 5, 1978. **St. Elizabeth:** Horse Savanna, sea level, *Proctor & Mullings 21840*, Dec. 24, 1960; Slipe distr., sea level, *Proctor 27591*, July 31, 1966, *Proctor 33139*, Jan. 27, 1973.

Cheilophyllum Penn.

Cheilophyllum jamaicense Penn. Bull. Torrey Bot. Club **62**: 256. 1935.

Until recently, this diminutive creeping plant was known only from the type collection, gathered at Ashley Hall Savanna, parish of Clarendon, on December 6, 1917. After a lapse of 56 years, it has been found again in two localities exactly the same as for *Schultesia guianensis* (see MAP 34).

St. Elizabeth: Slipe distr., in a savannalike swale, near sea level, *Proctor 33384*, July 1, 1973. **Clarendon:** Harris Savanna (just N of type locality), ca. 350 ft, *Proctor 34401*, Dec. 7, 1974.

BIGNONIACEAE

Tabebuia DC.

Tabebuia rosea (Bertol.) DC. Prodr. **9**: 215. 1845. MAP 40.

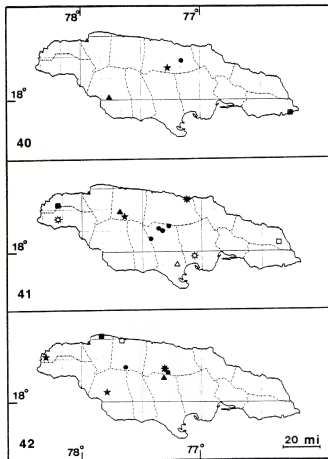
This tree was recorded by Adams (1972) as a cultivated plant only. However, *Tabebuia rosea* has escaped and is becoming naturalized in sandy coastal thickets toward the southeastern end of the island.

St. Thomas: Rocky Point Bay, sea level, *Proctor 36297*, June 15, 1976.

Tabebuia sauvallei Britton(?), Bull. Torrey Bot. Club **42**: 377. 1915. MAP 40.

New to Jamaica, **St. Ann:** Reynolds mine area near Lydford P.O., ca. 1500 ft, *R. A. Howard & Proctor 14209*, June 30, 1955 (A. v).

The cited material was originally identified as *Tabebuia angustata* Britton, from which it differs in its very much smaller leaflets with rounded apices,



MAPS 40-42. Distributions: 40, *Tabebuia rosea* (square), *T. sauuvallei* (dot), *Utricularia purpurea* (triangle), *Justicia mckenleyi* (star); 41, *Antirhea tomentosa* (solid triangle), *Coccocypselum gulanense* (dots), *Diodia teres* (hollow triangle), *Exostema orbiculatum* (star), *Hedyotis callitrichoides* (solid asterisk), *Psychotria bryonicola* (hollow square), *P. hanoverensis* (solid square), *Spermacoce tetraquetra* (hollow asterisk); 42, *Egletes prostrata* (hollow square), *E. prostrata* and *Flaveria trinervia* together (solid square), *Pentacalia inornata* (triangle), *P. subdiscolor* (dots), *P. inornata* and *P. subdiscolor* together at type locality of both (asterisk), *Sachsis polycephala* (stars).

and in its shorter calyx and shorter fruits. The flowers have not been seen. The plant is entirely unlike *T. platyantha* (Griseb.) Britton and differs from *T. riparia* (Raf.) Sandwith (which itself is probably not separable from the widespread Antillean *T. heterophylla* (DC.) Britton) in the totally dissimilar shape and venation of its leaflets. Among the numerous Cuban species of this difficult genus, *T. saauvallei* seems to come closest to matching this collection.

LENTIBULARIACEAE

Utricularia L.

Utricularia purpurea Walter, Fl. Carolin. 64. 1788.

MAP 40.

New to Jamaica. **St. Elizabeth:** upper course of Broad R., sea level, Proctor 37920, July 25, 1978.

The species was first discovered by Mr. Andrew Podzorski while he was investigating the diatoms of this area. Podzorski's specimens are deposited in the herbarium of the University of the West Indies, Mona, Jamaica (UCWI).

Utricularia purpurea is easily distinguished from all other Jamaican species of its genus by its light purple or lilac-colored flowers. Its range elsewhere includes eastern North America from Maine to Florida; it also occurs in the Bahamas and Cuba.

ACANTHACEAE

Justicia L.

Justicia mckenleyi Proctor, sp. nov.

FIGURE 6, MAP 40.

Liana sublignosa tenuis, a *Justicia* anabasa in pilis retrorsis (haud antrorsis) in ramulis praeditis, foliis parvioribus, calyce glanduloso, et corolla luteola haud glandulosa, differt.

Slender, high-climbing subwoody vine; stems subangulate, minutely hirsute to substrigillose, the hairs downwardly curved or retrorse, up to 0.2 mm long, septate, the lower parts of the stem glabrate. Petioles 2–3 mm long, densely hirsutulous with upwardly curved hairs; leaf blades ovate, 2–3.5 by 1–2.3 cm, subacute, narrowed at base, of firm papery texture, the margins entire, slightly revolute, the surfaces glabrous or nearly so except for hirsutulous costa on both sides, the hairs antrorsely curved, the lateral veins about 4 pairs, glabrous, the tissue minutely pellucid-punctate, the cystoliths oblong, obscure. Inflorescences short, axillary and terminal, few-flowered racemes (2 to 4 pairs of flowers), these scattered at intervals along ultimate stem branches, mostly less than 3 cm long; peduncles 3–15 mm long, 0.5–1

mm thick, hirsutulous like stems; rhachis internodes 2–5 mm long, densely puberulous with straight hairs; flowers sessile at tips of pedicellike branches, these 1–4 mm long, puberulous like rhachis, bearing apical pair of deltate-linear, sparingly hirtellous bracts 2 by 0.5 mm at thickened base; bracts subtending flower-bearing branches obovate, 2–4 mm long, lowermost ones leaflike. Calyx ca. 5 mm long, 5-parted, the segments equal, narrowly deltate, ca. 4 mm long, 0.9–1.2 mm wide at base, puberulous and densely capitate-glandular. Corolla 3–3.2 cm long, light yellow, densely puberulous, with hairs 0.1 mm long or less, not glandular; tube 3 mm broad above subsaccate base, widening to 5–6 mm at mouth; lips subequal, ca. 2 cm long, the upper nearly straight and somewhat hooded, ca. 6 mm broad near base, gradually narrowed to 2-lobed tip, the lower lip broadly recurved, ca. 4 mm wide at base, 3-lobed, with lobes oblong, ca. 10 by 1.5–2 mm. Stamens 2, exserted, reaching to within 2 mm of tip of upper lip and partially enfolded by it; filaments puberulous; anther cells straight, 3 by 0.6 mm, glabrous, superposed and attached vertically to connective, lower cell calcarate. Style about equaling lips of corolla, basal half antrorsely hispidulous; stigma subentire; ovary densely puberulous. Capsules narrowly fusiform, 2–2.2 cm long, sparsely puberulous; retinacula oblong, 1.5 mm long, flattened and subscarios at tip; seeds 4, dark brown, papillose-roughened.

St. Ann: James Webster Patent, along road no. 144 between Mason River and Stepney, 2100 ft, *Proctor 38672*, March 24, 1980 (holotype, A).

The plant was a slender, high-climbing vine growing on a wooded, rocky, limestone hillside. From a distance, its flowers resembled those of a *Columnnea* (Gesneriaceae). The species is named for Mr. Clifton G. McKenley, my diligent field assistant (1978–1980), who helped to collect the type material.

From the other Jamaican species of *Justicia*, *J. mckenleyi* is obviously distinct in its climbing habit and its yellow flowers. In fact, very few other congeners anywhere are vines. It differs from the climbing Colombian species *J. anabasa* Leonard in its retrorse (vs. antrorse) hairs on the stems, its smaller, differently shaped leaves, its glandular calyx but nonglandular corolla (just the reverse of *J. anabasa*), its light yellow instead of "burnt orange" corolla, and its densely puberulous ovary. Otherwise, except for minor dimensional differences, the two species show many resemblances. *Justicia mckenleyi* has tetracolporate pollen of a typical *Justicia* type, as shown in FIGURE 6.

RUBIACEAE

Antirhea Comm.

Antirhea tomentosa (Sw.) Fawcett, Provis. List Fl. Pl. Jamaica, 19.
1893. MAP 41.

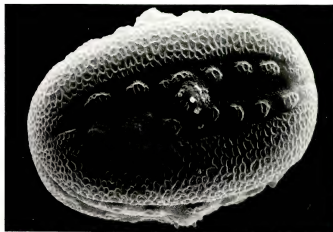


FIGURE 6. *Justicia mckenleyi*, pollen grain, $\times 2000$.

Previously known only from the type, collected by Olof Swartz in 1784–86 at an unknown Jamaican locality, this species has now been rediscovered in the heart of the Cockpit Country. Unfortunately, the area in which it was found is rapidly being cut over and denuded, so the ultimate survival of this and other rare species is in grave jeopardy.

Trelawny: 5.3 mi by road N of Quick Step P.A., 1250–1500 ft, *Proctor* 35328, Sept. 26, 1975.

***Coccocypselum* P. Browne**

Adams (1972) credited this genus with two Jamaican species, *Coccocypselum herbaceum* Aublet and *C. pseudotontanea* Griseb. However, a congeneric population occurring in the central part of Jamaica corresponds to neither of these and in fact represents *C. guianense* (Aublet) Schum., a species not very distinct from *C. herbaceum* but nevertheless separated from it by most authors. The Jamaican species of this genus can be distinguished as follows:

- A. Flower heads sessile or nearly so. *C. herbaceum*.
- A. Flower heads obviously pendunculate.
 - B. Corolla blue or lavender, tube 6 mm or more long; berries 6–10 mm in diameter. *C. guianense*.
 - B. Corolla white, tube 4–5 mm long; berries ca. 4 mm in diameter. *C. pseudotontanea*.

Coccocypselum guianense (Aublet) K. Schum. in Martius, Fl. Brasil. 6(6): 315, 1889. MAP 41.

New to Jamaica. **Clarendon:** Mason River Savanna, ca. 2300 ft, *Proctor 15819*, Nov. 22, 1956, *Proctor 26426-b*, May 23, 1965, *Proctor 34321*, Nov. 17, 1974; Fairburn Savanna, 1 mi SW of Corner Shop, 2000 ft, *Proctor 8474*, March 11, 1954; Carters Hall Savanna, near James Hill, ca. 2000 ft, *Proctor & Harkness 9724*, Jan. 6, 1955; Cabbage Hall distr., 0.5–1 mi SE of Cumberland, ca. 2700 ft, *Proctor 33597*, Nov. 10, 1973.

At the first of the above localities, there is a glabrous variant differing also in habit; this can be designated as follows:

Coccocypselum guianense var. **glabratum** Proctor, var. nov.

Plantae decumbentes vel suberectae, aliquantum fragiles, glabrae, sed foliis ciliato-marginatis.

Decumbent to suberect herb of somewhat brittle texture, glabrous throughout or nearly so except for ciliate margins of leaves.

Clarendon: Mason River Savanna, ca. 2300 ft, *Proctor 15818*, Nov. 22, 1956 (holotype), *Proctor 26426-a*, May 23, 1965.

Diodia L.

Diodia teres Walter, Fl. Carolin. 87, 1788.

MAP 41.

This rare species was cited by Adams (1972) only from the parish of St. Andrew. A large population of it was subsequently discovered at a locality that has also yielded many other rare or unknown species.

Clarendon: along road from Free People S toward Harris Savanna, 300–400 ft, *Proctor 34240*, Oct. 31, 1974; Harris Savanna, ca. 350 ft, *Proctor 34317*, Nov. 15, 1974.

Exostema (Pers.) L. C. Rich. ex Humb. & Bonpl.

Exostema orbiculatum Proctor, sp. nov.

MAP 41.

Frutex glaber arcuatis foliis subsessilibus orbiculato-cordatis 2.5–6 cm longis et 2–6 cm latis rigide coriaceis, floribus terminalibus sessilibus solitariis vel 2–3 simul, hypanthio late obconico circa 5 mm longo laciniis circa 3.5 mm longis, corolla alba tubo 10–13 mm longo intus pilis praedito lobis linearis recurvatis 7–9 mm longis, filamentis tenuissimis versus basem tubi corollae insertis 5 mm longis, antheris linearis 4.5 mm longis. Fructus non visus.

Unarmed, glabrous, arching shrub to 3 m tall; branchlets somewhat compressed and grooved, or flattened and 4-angulate. Leaves sessile, rigidly coriaceous, orbicular or rarely very broadly ovate, 2.5–6 by 2–6 cm, obscurely subacuminate at apex, cordate or subcordate at base, the midvein obscurely grooved adaxially and prominent abaxially, the lateral veins 4 to 6 pairs, prominulous on both sides, the margins narrowly revolute; stipules spinescent from flat deltate base, 4–5 mm long. Flowers terminal, sessile, solitary or 2 or 3 together; hypanthium broadly obconical, ca. 5 mm long, teeth ca. 3.5 mm long; corolla white, the tube 10–13 mm long, hairy within, the recurved linear lobes 7–9 by 1–1.5 mm, sparsely hairy toward base on inner side; filaments inserted near base of corolla tube, filiform, ca. 5 mm long, the anthers linear, 4.5 mm long; style linear, terminated by minutely 2-lobed stigma. Fruits not seen.

Trelawny: Crown Lands area ca. 5 mi NW of Troy, 1750–2000 ft, *Proctor 35236*, June 10, 1975 (holotype).

In the absence of ripe fruits and seeds, the generic affinity of this plant cannot be inferred with certainty. It is assigned to *Exostema* of the Cinchoneae on the basis of the terminal flowers, the linear-recurved corolla lobes, and the attachment and structure of the stamens. It is, however, entirely unlike any other known species of this genus.

Hedyotis L.

I consider the species listed by Adams (1972) under the generic name *Oldenlandia* to belong in *Hedyotis*, following the studies of Lewis (1961) and others. The Jamaican species should therefore be known as follows:

Hedyotis corymbosa Lam. Tabl. Encycl. 1: 272. 1791.

Hedyotis lancifolia Schum. Beskr. Guin. Pl. 72. 1827.

Hedyotis pumila L. f. Suppl. Pl. 119. 1781.

Hedyotis uniflora DC. Prodr. 4: 421. 1830.

To these is to be added another, recently discovered in Jamaica:

Hedyotis callitrichoides (Griseb.) W. H. Lewis, *Rhodora* 63: 222. 1961. MAP 41.

New to Jamaica. **St. Ann:** Ocho Rios, near sea level, *Proctor 37709*, March 7, 1978.

The plants were found growing on soil in a shaded grotto of a limestone sea cliff, associated with *Pilea herniarioides* (Sw.) Wedd.

This species is the smallest and most delicate of its genus in the West

Indies, with filiform stems rooting at nodes and minute, ovate-orbicular leaves. The corolla, although very small, is much longer than the calyx lobes; in the other species, the corolla does not exceed the calyx. *Hedyotis callitrichoides* is also known from the Bahamas, Cuba, Hispaniola, Puerto Rico, St. Croix, St. Barthélemy, Guadeloupe, Dominica, and Trinidad.

Palicourea Aublet

The beautiful endemic species *Palicourea pulchra* Griseb. was stated by Adams (1972, p. 730) to be quite variable in the shape of its corolla. He also mentioned a "striking variant" from Trelawny, noting its "triangular lobes to a broader than usual corolla of deep magenta colour, combined with a leaf with purple abaxial surface." In fact, this variant, which remains distinct in at least one locality where it grows with typical *P. pulchra*, has other differentiating features. The most striking of these is the indument of very short, stiff hairs that covers the inflorescence branches, the calyx, and (to a lesser extent) the upper surface of the leaves. Typical *P. pulchra* is entirely glabrous. Further, the inflorescences of the "variant" are more abruptly deflexed-pendent, have longer peduncles, and are more compact; this compactness is especially noticeable when the plant is fruiting. A case could be made for describing this population as a separate species, were it not for the existence of intermediates. Unless these intermediates can be demonstrated to be of hybrid origin, it is better to name the distinctive local population as a variety.

***Palicourea pulchra* var. *hispidula* Proctor, var. nov.**

Frutex a var. *pulchra* in foliis paginis superioribus ramulis inflorescentiarum et calyce indumento hispidulo praeditis, inflorescentiis compactoribus pedunculis longioribus terminantibus, et corollis atro-magenteis vel purpureis (haud roseis) differt.

Shrub; differing from var. *pulchra* in its hispidulous upper leaf-surfaces, inflorescence branches, and calyx; its more compact inflorescences terminating a longer peduncle; and its deep magenta or purple (vs. pink) corollas.

Trelawny: Mango Tree Hill, ca. 1750 ft, R. W. Read 1904, May 27, 1967 (holotype, us); Ramgoat Cave, ca. 1500 ft, R. A. Howard & Proctor 14389, July 4, 1955, Proctor 10612, Aug. 26, 1955; Windsor Castle, 1200 ft, B. Vuilleumier 53 (s), Aug. 14, 1963. Specimen intermediate between var. *pulchra* and var. *hispidula*: ca. 1-2 mi NW of Quick Step, ca. 1500 ft, G. L. Webster 5269, Aug. 11, 1954.

Both varieties of *Palicourea pulchra* have horticultural potential, but var. *hispidula* is exceptionally beautiful.

Psychotria L.

***Psychotria bryoncola* Proctor, sp. nov.**

MAP 41.

Arbor parva glabra Psychotria clusioides affine, sed in foliis parvioribus rotundatis venulis 5 ad 7 (versus 11 vel 12) paribus, paniculis corymbosis compactioribus, calyce campanulato lobis rotundatis, et fructibus basibus truncatis, differt.

Small tree, glabrous throughout. Petioles stout, 1–2 cm long; leaf blades stiffly leathery, elliptic to rotund, 5–9 by 3–6.5 cm, broadly rounded at apex, abruptly cuneate at base, the margins revolute, the midrib channeled adaxially, prominent toward base abaxially, the lateral veins ca. 5 to 7 pairs, prominulous adaxially, obscure abaxially. Stipules not seen. Panicle terminal, compact-corymbose with ascending branches, stalked, the stalk ca. 3 cm long, the bracts foliaceous, 1.5–2 cm long; bracteoles deciduous, not seen. Flowers not seen; fruiting calyx campanulate, 1.5–2 mm long, broadly 5-lobate, lobes rounded. Fruits oblong-ellipsoid, 6–7 by ca. 4 mm, longitudinally ribbed.

Portland: E slope of John Crow Mts. ca. 2.5 mi SW of Ecclesdown, ca. 2500 ft, *Proctor 22702*, Sept. 1, 1962 (holotype).

This species resembles *Psychotria clusioides* Proctor in general appearance and grows in the same locality, but differs in having smaller, more rotund leaves with fewer veins, more compact corymbose panicles, a campanulate calyx with rounded lobes, and fruits truncate at the base.

***Psychotria hanoverensis* Proctor, sp. nov.**

MAP 41.

Frutex *Psychotria hirsuta* affine, in ramulis glabris, stipulis oblongis vel ovatis persistentibus, foliis grandioribus venulis lateralibus pluribus, calyce pubescente, corollis parvioribus, et fructibus grandioribus, differt.

Shrub 1.5–2 m tall with glabrous branchlets; stipules sheathing, persistent, oblong to ovate, 8–11 mm long, densely rusty-hirsute with septate hairs. Petioles 1–3 cm long, rusty-hirsute; leaf blades broadly elliptic to obovate, 8–19 by 4–9.5 cm, short-acuminate at apex, cuneate at base, usually with 9 to 12 pairs of lateral veins, densely rusty-hirsute especially on midvein and lateral veins abaxially, both surfaces also hirsute, and margin ciliate with septate hairs. Inflorescence rusty-hirsute, shorter than leaves; panicle pentagonal, 4–7 cm long and wide, stalked, stalk 3–5 cm long. Flowers clustered at ends of panicle branches, sessile; calyx densely pubescent and ciliate, the lobes ca. 0.5 mm long, deltate, acute; corolla with glabrous tube ca. 2 mm long, the lobes narrow, recurved, lightly pubescent on outside. Fruits glabrous, longitudinally ribbed, orange, 7–9 mm long.

Hanover: Baulk Pen Mt., ENE of Glasgow, 400–600 ft, *Proctor 36312*, July 2, 1976 (holotype), *Proctor 35525*, Dec. 13, 1975.

Although clearly related to *Psychotria hirsuta* Sw., from the opposite end of Jamaica, this species differs in many details.

Spermacoce L.

Most modern authors have maintained *Borreria* G. F. W. Meyer (nomen conserv.) separate from *Spermacoce* on the basis that both valves of the *Borreria* capsule open instead of only one. Recently, however, the opinion that such a distinction is merely artificial and serves no useful purpose has been gaining support and is beginning to be reflected in scattered literature (e.g., Fosberg, 1976). If the Jamaican species of these taxa are united, the correct names are as follows:

Spermacoce assurgens Ruiz & Pavon, Fl. Peruv. Chil. **1**: 60. *t.* 92, *fig.* C. 1798.

Borreria laevis of modern authors, not *Spermacoce laevis* Lam., 1791.

S. suffrutescens Jacq. Pl. Rar. Horti Caes. Schoenbr. *t.* 322. 1798 (later than *S. assurgens*).

Spermacoce confusa Rendle, Jour. Bot. London **74**: 12, *figs.* D-F. 1936.

Spermacoce repens (DC.) Fosberg & Powell, Smithson. Contr. Bot. **45**: 30. 1980.

Spermacoce and *Borreria ocymoides* of modern authors, not *S. ocymoides* Burman f., 1768.

Spermacoce spinosa Jacq. ex L. Sp. Pl. ed. 2. **1**: 148. 1762.

Spermacoce tenuior L. Sp. Pl. **1**: 102. 1753.

Spermacoce tetraquetra A. Rich. in Sagra, Hist. Fis. Pol. Nat. Cuba **11**: 29. 1850. MAP 41.

New to Jamaica, **Westmoreland**: grounds of Little London Secondary School, ca. 50 ft, *Proctor 37123*, July 18, 1977. **St. Catherine**: 1.25 mi due NE of Spring Village, ca. 75 ft, *Proctor 38168*, May 30, 1979.

Otherwise known from the Bahamas, Cuba, and Cayman Brac.

Spermacoce verticillata L. Sp. Pl. **1**: 102. 1753.

COMPOSITAE

Egletes Cass.

Egletes prostrata (Sw.) Kuntze, Rev. Gen. Pl. **1**: 334. 1891. MAP 42.

Adams (1972, p. 758) cited this species as "very rare (St. Ann); not recently collected." There are, however, two specimens from Jamaica in the

Institute of Jamaica herbarium that show that *Egletes prostrata*, although rare, occurs at widely scattered sites near the north coast of the island.

St. James: Rose Hall, ca. 50 ft, *Proctor 35284*, Sept. 6, 1975. **Trelawny:** Fal-mouth, sea level, *Mr. Curtis s.n. (UCWI 3236)*, March, 1957 (originally submitted for identification by the late Mrs. Edith Robertson, University of the West Indies).

Flaveria Juss.

Flaveria trinervia (Sprengel) C. Mohr, Contr. U. S. Natl. Herb. 6: 810. 1901. MAP 42.

Genus and species new to Jamaica. **St. James:** Rose Hall, ca. 50 ft, *Proctor 35286*, Sept. 6, 1975.

The genus *Flaveria* belongs in the tribe Helenieae; it differs from other Jamaican genera of this group (*Pectis*, *Porophyllum*) in lacking resinous glands in the tissues, and from *Pectis* in lacking ray flowers.

Flaveria trinervia is recorded from the southern United States, Mexico, Venezuela, and a few other South American localities, as well as from the Bahamas, Cuba, and Puerto Rico in the West Indies. Long and Lakela (1971) also cited a report from Hawaii.

Sachsia Griseb.

Sachsia polycephala Griseb. Catal. Pl. Cubens. 150. 1866. MAP 42.

Genus and species new to Jamaica. **St. Elizabeth:** Slipe distr., sea level, *Proctor 33564*, Oct. 26, 1973, *Proctor 33729*, March 3, 1974. **Hanover:** Sambo Clump (Sambo #1) in the Great Morass, ca. 2 mi due SW of Logwood, sea level, *Proctor 37152*, July 19, 1977, *Proctor 37744*, March 23, 1978.

Sachsia, construed in the broad sense as a monotypic genus, has been recorded from Florida, the Bahamas, Cuba, and Hispaniola. Its discovery in Jamaica is therefore not a very surprising extension of its known range.

This genus belongs in the tribe Inuleae, otherwise represented in Jamaica by the genera *Gnaphalium*, *Pterocaulon*, and *Pluchea*. From all of these it differs in habit, being a small rosette-forming herb with a slender, erect flowering scape that bears such inconspicuous leaves as to appear nearly naked. The plants resemble a small *Erigeron* (such as *E. cuneifolius*) but can be distinguished by the tailed anthers and the 4- or 5-angled achenes. The anthers of *Erigeron* lack appendages, and the achenes are flat.

Senecio L.

It has been customary in most floras to treat this genus in a broad sense, and Adams (1972) continued this tradition. If left to my own devices, I would probably do likewise in resistance to the modern tendency toward what seems

to be excessive generic fragmentation. However, the discovery of two new eligulate species related to the endemic Jamaican *Senecio discolor* (Sw.) DC. led to consultation with Dr. Harold Robinson at the Smithsonian Institution regarding generic delimitation among these plants. Dr. Robinson kindly agreed not only to describe the new species, but also to provide a brief review of Jamaican Senecioneae (as follows) according to the systematic treatment that he and some other present-day authors are using.

The various members of the Senecioneae from Jamaica have been subject to extensive revision, mainly at the generic level, since the publication of Adams's flora. Two endemic genera have been described by Nordenstam (1978), *Jacmaia* for the species previously known as *Gynoxys incana* (Sw.) Less., and *Odontocline* for six species previously placed in *Senecio*. More recently, the tropical American genus *Pentacalia* has been resurrected from synonymy under *Senecio* (Robinson & Cuatrecasas, 1978), and that genus now proves to include three species from Jamaica, two of which are previously undescribed. One species mentioned by Adams in his key to *Senecio*, *S. confusus* Britton, is introduced from Mexico and Central America and is properly placed in the genus *Pseudogynoxys* (Greenman) Cabrera (see Robinson & Cuatrecasas, 1977) under the name *P. chenopodioides* (Kunth) Cabrera. At present, therefore, the large north- and south-temperate genus *Senecio* proves to be represented in Jamaica only by its introduced type species, *S. vulgaris* L.

It might be noted that some other Jamaican genera that have previously been placed in the Senecioneae, and which were placed in their traditional positions near *Senecio* by Adams, are now known to belong elsewhere—*Liabum* Adanson in the tribe Liabeae and *Neurolaena* R. Br. in the Heliantheae.

The following is a key to the genera included in *Senecio* by Adams:

- A. Leaves pinnatifid, sessile, mostly in a basal rosette; one introduced annual species. *Senecio*.
- A. Leaves entire to serrate, distinctly petiolate, alternate on elongate stems; indigenous perennial species.
 - B. Style branches and anther appendages with acute tips; flowers reddish orange; endothelial cells with single thickenings on transverse walls; vines. *Pseudogynoxys*.
 - B. Style branches and anther appendages blunt; flowers whitish or yellow; endothelial cells with numerous thickenings on vertical walls; shrubs, small trees, or woody vines.
 - C. Flowers yellow; style branches with single stigmatic area covering inner surface; achenes usually with 8 to 10 nerves. *Odontocline*.
 - C. Flowers of Jamaican species whitish; style branches with paired stigmatic lines; achenes with 5 to 8 nerves. *Pentacalia*.

The three indigenous Jamaican genera of the Senecioneae can be briefly summarized as follows:

Jacmaia Nordenstam

Jacmaia incana (Sw.) Nordenstam, Op. Bot. 44: 66. 1978.

Gynoxys incana (Sw.) Less. Synopsis Gen. Composit. 390. 1832; Adams, 1972.

Odontocline Nordenstam

The following key is mostly adapted from that of Adams (1972):

- A. Leaves divided about halfway to midrib in proximal part, the lobes more or less triangular, up to 40 by 12 cm, equally coarsely pubescent on both surfaces; small tree. *O. laciniata*.
- A. Leaves at least on flowering branches entire or at most repand-dentate, smaller in size and otherwise in pubescence; shrubs or vines.
 - B. Leaves on flowering branches distally toothed, each tooth tip a thick gland; 7 to 12 pairs of conspicuous lateral veins prominent beneath when dry.
 - C. Lamina coarsely serrate, elliptic, base obtuse. *O. dolichantha*.
 - C. Lamina with minute teeth, slightly obovate, base short-acute. *O. fadyenii*.
 - B. Leaves on flowering branches entire, or if denticulate then tooth tips not obviously thickened; lateral veins up to ca. 7 pairs, obscure.
 - D. Involucral bracts 5; florets 5 or 6; erect shrub with obtusely tipped leaves. *O. tercentenariae*.
 - D. Involucral bracts 6 to 8 (to 10); florets 8 to 14; leaf tips mostly acute or acuminate; leaves on nonflowering branches narrower and more distinctly toothed.
 - E. Erect or straggly branched shrub, or small tree with brittle branches; leaves on flowering branches cuneate at base; lateral veins forming 70–80° angle with midrib. *O. glabra*.
 - E. High-climbing woody vine; leaves broadly cuneate to rounded at base; lateral veins forming 30–60° angle with midrib. *O. hollickii*.

These can be listed alphabetically as follows:

Odontocline dolichantha (Krug & Urban) Nordenstam, Op. Bot. **44**: 25. 1978.

Senecio fadyenii Griseb. var. *dolichantha* Krug & Urban in Urban, Symb. Antill. **1**: 470. 1900.

S. dolichanthus (Krug & Urban) S. Moore, Jour. Bot. London **67**: 130. 1929.

This entity was reduced to synonymy under *Senecio fadyenii* by Adams (1972).

Odontocline fadyenii (Griseb.) Nordenstam, Op. Bot. **44**: 25. 1978.

Senecio fadyenii Griseb. Fl. Brit. W. Indian Is. 382. 1861; Adams, 1972.

Odontocline glabra (Sw.) Nordenstam, Op. Bot. **44**: 25. 1978.

Senecio swartzii DC. Prodr. **6**: 411. 1838; Adams, 1972.

Odontocline hollickii (Britton ex Greenman) Nordenstam, Op. Bot. **44**: 25. 1978.

Senecio hollickii Britton ex Greenman, Ann. Missouri Bot. Gard. **3**: 201. 1916; Adams, 1972.

Odontocline laciniata (Sw.) Nordenstam, Op. Bot. **44**: 25. 1978.

Cineraria laciniata Sw. Fl. Ind. Occ. **3**: 1352. 1806.

Senecio swartzianus Bueck, Index DC. Prodr. **2**: vi. 1840; Adams, 1972.

Odontocline tercentenariae (Proctor) Nordenstam, Op. Bot. **44**: 25. 1978.

Senecio tercentenariae Proctor, Bull. Inst. Jamaica Sci. **16**: 75. t. 33. 1967; Adams, 1972.

Pentacalia Cass.

This taxon, originally based on a Colombian species, was distinguished by Robinson and Cuatrecasas (1978, p. 38) from *Senecio* by "the fruticose to scandent habit with woody stems, the distinctly petiolate usually non-stipitate leaves, the minutely fistulose or non-fistulose receptacles, the tails on the anthers, and the rather stout 5-ribbed achenes. . . ." The separation of *Pentacalia* from *Odontocline* (the latter an endemic Jamaican genus), although primarily based on characters not easy to see without special techniques, is made simpler by the consistent difference in flower color. However, it should be noted that the white or whitish color of *Pentacalia* flowers in Jamaica is somewhat anomalous in this genus, which elsewhere usually has yellow flowers.

- A. Heads radiate (rays white); achenes mostly with 8 nerves and with many short mucilage hairs. *P. discolor*.
- A. Heads entirely discoid; achenes with 5 nerves, glabrous.
 - B. Stems, lower surface of leaves, and involucre with white tomentum; corollas ca. 3.5 mm long, bearing few short hairs on outer surface. *P. subdiscolor*.
 - B. Stems, leaves, and involucre essentially glabrous; corollas ca. 4.5 mm long, glabrous. *P. inornata*.

Pentacalia discolor (Sw.) H. Robinson, comb. nov.

Cineraria discolor Sw. Prodr. 114. 1788.

Senecio discolor (Sw.) DC. Prodr. **6**: 412. 1838; Adams, 1972.

Although this species differs from typical *Pentacalia* in having eight (vs. five) nerves in the achene, it nevertheless falls within the broad concept of the genus. The setae on the achenes release mucilage from the tips when they are ruptured. Such setae are not common in *Pentacalia* but are known elsewhere in the Senecioneae. *Pentacalia discolor* is a very common and widespread species in Jamaica and is locally called "whiteback." It has frequently been used as an ingredient of "bush tea" and as such has been implicated as a carcinogen, especially in cases of liver cancer among children. Adams (1972) pointed out that although this species is endemic to Jamaica,

it is closely related to a Cuban species. The latter should therefore be known as *Pentacalia almironcillo* (Gómez Maza) Proctor, comb. nov., based on *Senecio almironcillo* Gómez Maza, Ann. Hist. Nat. Madrid 19: 277. 1890.

***Pentacalia inornata* H. Robinson, sp. nov.**

MAP 42.

Ab speciebus affinis plurimis in corollis albis differt, ab speciebus affinis Jamaicensibus in caulibus foliis et squamis involucri distincta.

Shrub with arching branches 2–3 m long; stems becoming pale brownish and subcarnose, slightly striate, glabrous. Leaves alternate; petioles 8–11 mm long; blades narrowly ovate, 5–8 by 1.5–2.5 cm, acute to short acuminate at apex, short-acute at base, margins subtly remotely mucronate-denticulate, both surfaces glabrous, adaxial surface with prominulous veins, abaxial surface slightly paler, secondary veins pinnately arranged, with 6 or 7 on each side. Inflorescences terminal on leafy branches, pyramidally paniculate with corymbose parts, peduncles 2–5 mm long, with appressed tomentum. Heads 6–7 mm high and ca. 3 mm wide; subinvolucral bracts linear, ca. 1 mm long, forming short calyculus; involucral bracts 8, oblong, ca. 5 mm long and to 1.3 mm wide, apices short-acute, glabrous. Flowers disciform, 10 to 14 per head; corollas white, ca. 4.5 mm long, externally glabrous, the tube cylindrical, wider below, strongly indurated, ca. 2 mm long, with throat narrowly funnelform, ca. 1.5 mm long, the lobes ca. 1 mm by 0.5 mm; anther collar ca. 0.3 mm long, the thecae ca. 0.8 mm long, with tails to 0.15 mm long, the anther appendages oblong, ca. 0.25 by 0.15 mm; apices of style branches very short fringed abaxially. Achenes submature, ca. 3 mm long, 5-costate, glabrous; pappus setae ca. 35 in 1 or 2 series, ca. 3 mm long, very easily deciduous, with apices not or scarcely broadened. Pollen grains ca. 30 μ m in diameter.

St. Ann: James Webster Patent, along road #144 between Mason River and Stepney, 2100 ft, *Proctor* 32855, March 4, 1972 (holotype, us), *Proctor* 32792, Jan. 14, 1972, *Proctor* 32833, Feb. 12, 1972, *Proctor* 32863, March 31, 1972. **Clarendon:** stream gully 0.9 mi by road E of Reckford, ca. 2000 ft, *Proctor* 37553, Jan. 7, 1978, *Proctor* 38111, March 29, 1979.

Pentacalia inornata is the only glabrous member of the genus in Jamaica, but in this respect it is more like most of its congeners in Central America and northern South America. The denticulate margins of the leaves indicate that this and the other Jamaican species are most closely related to the typical element of *Pentacalia*, which is distributed primarily in the northern Andes.

Pentacalia inornata is an arching or scrambling shrub with stems up to 3 m long; the flower heads are "creamish." This species has been found in thickets on rocky limestone hillsides and on the steep bank of a stream.

***Pentacalia subdiscolor* H. Robinson, sp. nov.**

MAP 42.

A *Pentacalia discolor* in capitulis discoideis et achaeniis 5-costatis distincta.

Erect shrub 2 m high, with stems, abaxial surfaces of leaves, pedicels, and involucre covered with appressed, grayish white tomentum; stems becoming glabrous, irregularly rugulose when dry. Leaves alternate; petioles 8–11 mm long; blades narrowly ovate, 6–9 by mostly 1.8–2.5 cm, acute at apex, short-acute at base, margin subtly remotely mucronate-denticulate, adaxial surface glabrous with prominulous veins, abaxial surface grayish white tomentose, secondary veins pinnate, with ca. 7 or 8 on each side. Inflorescences terminal on leafy branches, pyramidally paniculate with densely corymbose parts, peduncles 2–5 mm long. Heads ca. 5 by 2.5 mm; subinvolucral bracts ca. 5, ca. 1 mm long in short calyculus; involucral bracts mostly 8, oblong, ca. 3.5 by 1.3 mm, with short-acute apices, becoming glabrous on part of outer surface. Flowers disciform, ca. 14 per head; corollas white, ca. 3.5 mm long, the tube cylindrical, ca. 1.5 mm long, with throat narrowly funnelform, ca. 1.3 mm long, both tube and throat sparsely minutely puberulous externally, the lobes ca. 0.9 by 0.4 mm; anther collars ca. 0.25 mm long, thecae ca. 0.8 mm long, with tails to 0.15 mm long; apices of style branches abaxially and laterally short fringed. Achenes submature, ca. 1.8 mm long, 5-costate, glabrous; pappus setae ca. 35 in 1 or 2 series, ca. 3 mm long, very easily deciduous, with apices not or scarcely broadened. Pollen grains ca. 30 μ m in diameter.

St. Ann: James Webster Patent, along road #144 between Mason River and Stepney, ca. 2100 ft, *Proctor* 32382, Feb. 12, 1972 (holotype, us), *Proctor* 32864, March 31, 1972; Douglas Castle distr., 2200–2300 ft, *Proctor* 35683, April 9, 1976. **Trelawny:** near Crown Lands road extension 4.5–5 mi NW of Troy, ca. 1750 ft, *Proctor* 34708, Jan. 26, 1975.

Pentacalia subdiscolor is similar to *P. discolor* in the whitish pubescence of the leaf undersurface but differs sufficiently in details, especially in achene structure, to make close relationship seem doubtful. The relationship is much closer to the partly sympatric *P. inornata*, and the two might be considered pubescence variants except for the secondary differences in leaf acumination, head size, and corolla size and texture. The presence of some hairs on the corolla is probably a reflection of the general pubescence seen on other parts of the plant.

Pentacalia subdiscolor is recorded as an erect or arching shrub 2 m tall, with whitish, ill-scented heads. It grows in thickets on rocky limestone hillsides.

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NOTES ON PEPEROMIA (PIPERACEAE) IN THE
SOUTHEASTERN UNITED STATES

DAVID E. BOUFFORD

THE PIPERACEAE consist of approximately 4000 species distributed in the tropics and subtropics of both the Old and New Worlds. A few species reach temperate latitudes in eastern Asia, where *Piper kadsura* extends to about 35°N latitude, and off the eastern coast of North America, where the family is represented on Bermuda at about 32°20'N latitude. Both regions have climates that are modified by warm oceanic currents. Three species of *Peperomia* are apparently native in Florida, and about five additional species have been collected as growing "wild" in the southeastern United States or have at least been attributed to that region.

The Piperaceae were first recorded in the continental United States in 1822, when Nuttall described *Piper leptostachyon* (= *Peperomia humilis* A. Dietr.) from eastern Florida. Chapman did not include the family in the first edition of his *Flora of the Southern United States* (1860); his first mention of them was in 1883, when he listed two species of *Peperomia* (*P. magnoliaefolia* (Jacq.) A. Dietr. and *P. leptostachya* (Nutt.) Chapman) in the supplement at the back of the second edition of his *Flora*. The Garber collection that he called *P. magnoliaefolia* is actually *P. obtusifolia*. Small (1903) treated the same two species in his *Flora*, as well as five species in the genera *Micro-piper* and *Rhynchophorum* (both now considered synonyms of *Peperomia*) in his *Manual* (1933). Long and Lakela (1971) recognized six species of *Peperomia* as growing naturally in South Florida. Further discussion on the history of the discovery of *Peperomia* in Florida can be found in a paper by Small (1931).

In the treatment of the Piperaceae for the *Vascular Flora of the Southeastern United States*, I am recognizing eight species of *Peperomia* and two species of *Piper* as growing naturally (or at least as having been collected outside of cultivation) in this region. In the Southeast all but one are restricted to Florida. The following nomenclatural notes that could not be included in the format of that publication are an attempt to provide synonymy for the species of *Peperomia* occurring in the southeastern United States. Additional notes as an aid to the identification of the species and reasons for a taxon's inclusion in the flora of this area are also given. Dot maps for the taxa in the Southeast (based on specimens at A, FLAS, FSU, GH, LSU, NCU, NLU, NY, SMU, USF, and VAL), maps to show the distribution of those taxa in the West Indies (based on specimens at A and GH), and keys to the genera of Piperaceae and the species of *Peperomia* in the southeastern United States are provided.

For convenience the species are listed in alphabetical order. A finding list of synonyms and currently accepted names is included as an appendix.

KEY TO THE GENERA OF PIPERACEAE IN THE SOUTHEASTERN UNITED STATES

1. Shrubs or small trees; floral bracts fringed with whitish hairs. *Piper*.
1. Herbs; floral bracts glabrous, sometimes covered with glandular dots. *Peperomia*.

KEY TO THE SPECIES OF PEPEROMIA

1. Stems pubescent; leaves opposite or whorled. *P. humilis*.
1. Stems glabrous; leaves alternate.
 2. Plants covered with numerous black, glandular dots. *P. glabella*.
 2. Plants without black, glandular dots, occasionally leaves with yellowish resinous or pellucid dots.
 3. Leaves broadly cuneate, attenuate, or acuminate at base, tapering smoothly to petiole.
 4. Beak of fruit mammiform or conical, less than 0.2 mm long; leaves elliptic, lanceolate, or oblanceolate; petioles slightly dilated and clasping at base, decurrent in lines or wings along stem. *P. alata*.
 4. Beak of fruit elongate, 0.5–1 mm long; leaves obovate, spatulate, or ovate; petioles not dilated at base, if appearing to be clasping then not decurrent in lines along stem.
 5. Peduncles with microscopic, spiculelike hairs; beak of fruit filiform above conical base, abruptly hooked near apex. *P. obtusifolia*.
 5. Peduncles glabrous; beak of fruit tapering smoothly from broadened base to sharply acute apex, straight, bent, or gradually hooked from about the middle. *P. magnoliifolia*.
 3. Leaves rounded, truncate, cordate, or auriculate at base.
 6. Leaves auriculate at base, sessile or subsessile and more or less clasping the stem. *P. amplexicaulis*.
 6. Leaves rounded, truncate, or cordate at base, petiolate, never clasping the stem.
 7. Leaves less than 5 mm long, orbicular to depressed-orbicular, pubescent; plants creeping. *P. emarginella*.
 7. Leaves more than 6 mm long, broadly ovate to deltate, glabrous; plants erect. *P. pellucida*.

Peperomia alata Ruiz & Pavon, Fl. Peruv. Chil. 1: 31. 1798.

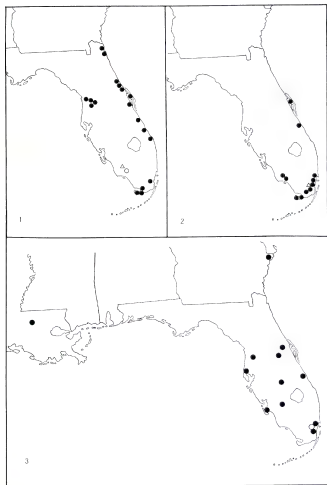
MAPS 1, 4.

The single specimen seen, labeled "Florida, Collier County, Big Cypress Swamp, W of Deep L., 5 February 1939, W. C. & M. W. Muenscher 14219" (NY), is tentatively attributed to this species. *Peperomia alata* is common and widespread in Central and South America and in the Lesser Antilles. The characteristic wings on the stem of this specimen are not as conspicuous as on many plants from those areas, but otherwise it matches *P. alata* well.

Peperomia amplexicaulis (Sw.) A. Dietr. in L. Sp. Pl. ed. 6. 1: 144. 1831.

MAPS 3, 5.

Piper amplexicaule Sw. Prodr. 16. 1788.



MAPS 1-3. Distribution of *Peperomia* in the southeastern United States: 1, *P. alata* (circle), *P. glabella* (triangle), *P. humilis* (dots); 2, *P. magnolifolia* (triangle), *P. obtusifolia* (dots); 3, *P. amplexicaulis* (circle), *P. pellucida* (dots).

According to Adams (1972), *Peperomia amplexicaulis* is endemic to Jamaica. However, it has been collected once in Florida (Dade County, near Cutler, W. G. *Atwater* 626, FLAS). In size and habit it resembles *P. magnoliifolia* and *P. obtusifolia*, but it can be recognized by the narrowly to broadly oblanceolate, sessile to subsessile, auriculate, and more or less clasping leaves.

Peperomia emarginella (Sw. ex Wikström) C. DC. Prodr. **16**(1): 437. 1869. MAP 6.

Piper emarginella Sw. ex Wikström, Kongl. Vetensk. Acad. Handl. **1827**: 56. 1828.

Peperomia emarginella is easily recognized by its small size, creeping habit, short spikes, and orbicular to suborbicular leaves, which are loosely covered with rather long, multicellular hairs. The single specimen, labeled only "Alto, 7-16-1915, F. & S. 8725" (NY), was included in a loan from NY of Piperaceae from the southeastern United States and is the basis for the inclusion of *P. emarginella* here; presumably Alto is a location in the Southeast. *Peperomia emarginella* occurs in northern South America, Central America, and the West Indies.

Peperomia glabella (Sw.) A. Dietr. in L. Sp. Pl. ed. 6. **1**: 156. 1831. MAPS 1, 7.

Piper glabellum Sw. Prodr. **16**. 1788.

Peperomia glabella is easily recognized by the numerous black dots that cover all parts of the plant. The upwardly curving hairs in lines on the petioles, and often also in thin lines on the stem below the nodes, separate it from *P. nigropunctata*, a more southern species not known from the southeastern United States. *Peperomia glabella* may be a recent introduction to the United States; the only collection I have seen was collected in Collier County, Florida, in 1960 (*F. C. Craighead s.n.; USF 61938*). The plant is common throughout the West Indies.

Peperomia humilis A. Dietr. in L. Sp. Pl. ed. 6. **1**: 168. 1831. MAPS 1, 8.

Piper leptostachyon Nutt. Am. Jour. Sci. **5**: 287. 1822. Type: East Florida, November, 1821, A. Ware s.n. (holotype, not seen; isotype, GH).

Piper humile Vahl, Enum. Pl. **1**: 349. 28 June 1804, not Miller ex Poirlet in Lam. Encycl. Méth. **5**: 473. 11 January 1804.

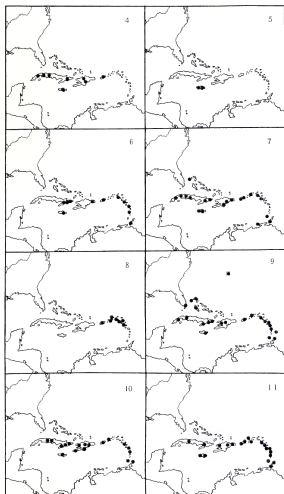
Peperomia leptostachya (Nutt.) Chapman, Fl. So. U. S. ed. 2. 645. 1883, not Hooker & Arnott, Bot. Beechey Voy. 96. 1832.

Peperomia cumulicola J. K. Small, Jour. New York Bot. Gard. **22**: 197. 1921.

Micropiper humilis (Vahl) J. K. Small, Man. SE. Fl. 400. 1933.

Micropiper leptostachyon (Nutt.) J. K. Small, Man. SE. Fl. 400. 1933.

Peperomia questeliana Stehlé & Trel. in Stehlé, Candollea **8**: 77. 1940.



MAPS 4-11. Distribution in the West Indies of the species of *Peperomia* found in Florida: 4, *P. alata*; 5, *P. amplexicaulis*; 6, *P. emarginella*; 7, *P. glabella*; 8, *P. humilis*; 9, *P. magnoliifolia*; 10, *P. obtusifolia*; 11, *P. pellucida*. Based on specimens at A and GH.

Even though *Piper humile* Vahl is illegitimate because it is a later homonym of *Piper humile* Miller ex Poirét, the epithet *humilis* may still be used in *Peperomia*. Article 72 of the International Code of Botanical Nomenclature states that "When a new epithet is required, an author may adopt an epithet previously given to the taxon in an illegitimate name if there is no obstacle to its employment in the new position or sense; the epithet in the new combination is treated as new." The situation here is exactly parallel to the example given in the Code under Article 72. The name *Peperomia humilis* is treated as new, and the binomial must be cited as *Peperomia humilis* A. Dietr., not *Peperomia humilis* (Vahl) A. Dietr.

This is apparently the same plant that is known as *Peperomia questeliana* Stehlé & Trel. in the Lesser Antilles (see Howard, 1973). Comparison of material from Florida with specimens from the West Indies shows no recognizable differences. Even without type material, this species can be unmistakably identified from Nuttall's original description since *P. humilis* is the only species of Piperaceae in Florida with opposite leaves and pubescent stems.

Small (1933) separated *Micropiper humilis* and *M. leptostachyon* on the basis of differences in leaf shape, bract margins, and habitat. While the extremes in leaf shape appear to be discontinuous, there are many plants that are intermediate. I could find no differences in bract margins, and although different populations of *P. humilis* may appear to grow in two distinct types of habitats in Florida, label data on specimens from other parts of the range indicate that plants of this species occupy a wide variety of habitats.

Peperomia magnoliifolia (Jacq.) A. Dietr. in L. Sp. Pl. ed. 6. 1: 153. 1831. MAPS 2. 9.

Piper magnoliaefolium Jacq. Collect. 3: 210. 1798.

Peperomia spathulifolia J. K. Small in Britton & Millsp. Bahama Fl. 101. 1920.

TYPE: "Abaco, in coppice at Eight Mile Bay, dry woods, Florida; Haiti."

Rhynchosporium spathulifolium (J. K. Small) J. K. Small, Man. SE. Fl. 1504. 1933.

Peperomia magnoliifolia is similar in appearance to *P. obtusifolia*, and it is often difficult to distinguish between the two species. *Peperomia magnoliifolia* lacks the microscopic hairs on the peduncles, and contrary to reports that the beak of the fruit is straight, I have found this character to be variable. The beak may be straight, curved, or gradually hooked from about the middle, but not abruptly hooked from near the apex as in *P. obtusifolia*. Also, the beak is subulate from a broadened base in *P. magnoliifolia* but filiform for most of its length above a broadened base in *P. obtusifolia*.

Although Small did not designate a type when he described *Peperomia spathulifolia*, photographs at A of two specimens labeled "Abaco, Eight Mile Bay, L. J. K. Brace 1876" (NY) and five sheets labeled "Florida, Dade County, Hattie Bauer Hammock, J. K. Small & C. A. Mosier 5940" (FSU; GH, 2 sheets; NY, 2 sheets) are probably the basis of the original description. One of the Small and Mosier collections at NY has "Type" written in the upper right corner of the label.

These specimens are not significantly different from *Peperomia magnoliifolia*. The spikes tend to be slightly narrower and more numerous than on most plants of *P. magnoliifolia*, but other characters appear identical. The slender, nodding, branched spikes and cuneate to spatulate leaves are used by Long and Lakela (1971) to separate the two species. The nodding spikes, however, tend to become more erect and rigid as they mature, and sheets of *P. magnoliifolia* from the West Indies occasionally show plants with branched inflorescences. Leaf shape in *Peperomia* is often highly variable and is unreliable in separating closely related taxa.

Peperomia magnoliifolia is a common and widespread West Indian plant and occurs northward to Bermuda. All of the collections I have seen from the southeastern U. S. are from Dade County, Florida, where the species appears to be restricted to only two stations, Hattie Bauer Hammock and Burden's Hammock (see Ward, undated). The two earliest collections I have seen are: Burden's Hammock, 23 February 1905, A. A. Eaton 1218 (GH; NCU); Hattie Bauer Hammock, 18 March 1915, J. K. Small & C. A. Mosier 5940 (FSU; GH, 2 sheets; NY, 2 sheets).

***Peperomia obtusifolia* (L.) A. Dietr. in L. Sp. Pl. ed. 6. 1: 154. 1831.**

MAPS 2, 10.

Piper obtusifolium L. Sp. Pl. 1: 30. 1753.

Peperomia floridana J. K. Small, Torreyia 26: 109. 1926. TYPE: Florida, Dade County, Ross' Hammock near Silver Palm School, 12 November 1906, J. K. Small & J. J. Carter 2478 (holotype, NY).

Rhynchochorum floridanum (J. K. Small) J. K. Small, Man. SE. Fl. 1504. 1933.

Rhynchochorum obtusifolium (L.) J. K. Small, Man. SE. Fl. 1504. 1933.

The microscopically puberulent peduncles and the fruits with filiform, abruptly hooked beaks separate *Peperomia obtusifolia* from *P. magnoliifolia*. There is also a slight difference in fruit shape: the fruits of *P. obtusifolia* tend to be cylindrical while those of *P. magnoliifolia* are ellipsoid. Small described *P. floridana* without distinguishing it from other species. In his *Manual* (1933) he separated it from *P. obtusifolia* on the basis of leaf size and shape and included *P. magnoliifolia* "of Chapman's Flora" as a synonym. The size and shape of the leaves, characters frequently used by Small in separating species of *Peperomia*, break down when large numbers of specimens are examined. *Peperomia obtusifolia* is common in the West Indies and is probably native to southern Florida.

***Peperomia pellucida* (L.) HBK. Nova Gen. Sp. Pl. 1: 53. 1816.**

MAPS 3, 11.

Piper pellucidum L. Sp. Pl. 1: 30. 1753.

Howard (1973) states that *Peperomia pellucida* is the only truly weedy species of *Peperomia* in the Lesser Antilles. It is apparently a recent introduction in the southeastern U. S. (first collected in 1957) and seems to show weedy tendencies there also. Since the time of the original collection in the

Southeast, the species has been found in several scattered localities in Florida as well as in Georgia and Louisiana, most often around nurseries and greenhouses, but also in shaded woods. It will be interesting to see if this plant will continue to expand its range.

Peperomia simplex Ham. Prodr. Pl. Indiae Occ. 2. 1825.

Long and Lakela (1971) attribute this species to southern Florida, but I have seen no specimens from the Southeast. A single sheet of *Peperomia pellucida* at USF was originally misidentified as *P. simplex*, and it may be that Long and Lakela accepted this name but obtained the description for their *Flora* from other sources.

ACKNOWLEDGMENTS

I would like to thank the curators of A, FLAS, FSU, GH, LSU, MO, NCU, NLU, NO, NY, SMU, USF, VAL, and VDB for providing specimens or information from specimens in their herbaria, and George R. Proctor for pointing out the implications of Article 72 of the International Code of Botanical Nomenclature.

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APPENDIX. Finding list.*

Micropiper humilis = ***Peperomia humilis***

Micropiper leptostachyon = ***Peperomia humilis***

*Recognized species of *Peperomia* are in boldface type, synonyms in italics.

- Peperomia alata* Ruiz & Pavon
Peperomia amplexicaulis (Sw.) A. Dietr.
Peperomia cumulicola = *Peperomia humilis*
Peperomia emarginella (Sw. ex Wikström) C. DC.
Peperomia floridana = *Peperomia obtusifolia*
Peperomia glabella (Sw.) A. Dietr.
Peperomia humilis A. Dietr.
Peperomia leptostachya = *Peperomia humilis*
Peperomia magnoliifolia (Jacq.) A. Dietr.
Peperomia obtusifolia (L.) A. Dietr.
Peperomia pellucida (L.) HBK.
Peperomia questeliana = *Peperomia humilis*
Peperomia spathulifolia = *Peperomia magnoliifolia*
Piper emarginella = *Peperomia emarginella*
Piper glabellum = *Peperomia glabella*
Piper humile = *Peperomia humilis*
Piper leptostachyon = *Peperomia humilis*
Piper magnoliaefolium = *Peperomia magnoliifolia*
Piper obtusifolium = *Peperomia obtusifolia*
Piper pellucidum = *Peperomia pellucida*
Rhynchoforum floridanum = *Peperomia obtusifolia*
Rhynchoforum obtusifolium = *Peperomia obtusifolia*
Rhynchoforum spathulifolium = *Peperomia magnoliifolia*

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THE STEMONACEAE IN THE SOUTHEASTERN UNITED STATES¹

GEORGE K. ROGERS

STEMONACEAE Engler in Engler & Prantl, Nat. Pflanzenfam. II. 5: 8.
1887, nom. cons.

(STEMONA FAMILY)

Erect herbs [or subshrubs to scandent vines], usually glabrous [stems and petioles rarely hirsute], with creeping rhizomes [or tuberous roots], bearing raphides in some organs. Leaves distichous [decussate or whorled], simple, petiolate, [rarely sessile], without a sheathing base, exstipulate, often cordiform, with a midrib and [2-]several longitudinal nerves usually diverging near the base and interconnected by \pm transverse veinlets, margins entire; stomata anomocytic. Inflorescences axillary, uniflorous or lax few-flowered cymose clusters [or several in crowded subumbellate clusters]; bracteoles inconspicuous, erect, linear-lanceolate. Flowers nearly actinomorphic [to strongly zygomorphic], perfect. Tepals 4, distinct [or basally connate], 1 pair enclosing the others in bud, green and sometimes reddish or purplish. Stamens 4, epitepalous; filaments short [usually basally connate]; anthers dehiscing introrsely by longitudinal slits; pollen grains monocolpate. Stigma sessile; ovary superior or nearly so, unilocular, bearing several anatropous, bitegmic, crassinucellar ovules on an apical [or basal] placenta. Capsule beaked, compressed, 2-valvate. Seeds with multicellular arillate appendages on and near the funicle; seed coat striate; endosperm fleshy to hard, initially nuclear (*Stemona*); megagametophyte of the Polygonum type (*Stemona*); embryo small, straight. (Fruit and seeds of *Stichoneuron* not known.) (Rox-

¹Prepared for the Generic Flora of the Southeastern United States, a project of the Arnold Arboretum currently made possible through the support of the National Science Foundation under Grant DEB-81-11520 (Carroll E. Wood, Jr., and Norton G. Miller, principal investigators). This treatment, the 87th in the series, follows the format established in the first paper (Jour. Arnold Arb. 39: 296-346, 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area but with information about extraregional members of a family or genus in brackets. References that I have not verified are marked with an asterisk.

I am grateful to Carroll Wood and Norton Miller for their help, including their careful review of the manuscript. Thanks are due also to P. B. Tomlinson for his comments on the manuscript. Shiu-ying Hu, George Staples, and Margaret van Montfrans helped solve some of the problems that emerged. In the illustration "a" and "b" were redrawn from Tomlinson & Ayensu (see references following *Crotonia*) by Sydney B. DeVore. Karen Stoutsenberger drew the others from dissections by K. R. Robertson, which are made from fluid-preserved material collected by P. B. Tomlinson and J. Thieret.

burghiaceae Wallich, Pl. Asiat. Rar. 3: 50. t. 282. 1832; including *Croomia* Nakai, Ic. Pl. Asiae Orient. 2: 159. t. 60. 1937.) TYPE GENUS: *Stemona* Lour. (*Roxburghia* Banks in Roxb.)

Three genera with about 35 species, distributed throughout the monsoon region of eastern Asia, and with one disjunct species of *Croomia* Torrey & Gray in the southeastern United States. Two other species of *Croomia* occur in eastern Asia (Japan to eastern China). The two species of *Stichoneuron* Hooker grow in Bangladesh, India (Assam), and near the border between Malaysia and Thailand. The range of *Stemona* (ca. 30 species) extends from eastern India to eastern China (and Japan, where it was probably introduced), and southward through the Philippines and Indonesia to northern Australia.

The three genera are so distinct morphologically that botanists have frequently questioned the Stemonaceae as a natural assemblage. However, the genera have been separated taxonomically only once, when Nakai segregated *Croomia* and *Stichoneuron* as the family Croomiaceae. Any suggestion of division must take into account several noteworthy shared characteristics, including broad, petiolate leaves with longitudinal arcuate veins and without sheathing bases; partly amphivasal cauline vascular tissue in one or two rings; raphides; two pairs of sepaloid tepals bearing as many epitepalous stamens; and unilocular gynoecium with no style, often slightly sunken in the receptacle. Division of these genera into separate families is further complicated by a set of likenesses linking each of the genera to one of the other two.

Stemona is unique in having appendaged anthers, basal (*vs.* apical) placentation, large flowers, usually twining (*vs.* erect) habit, and highly organized, straight, transverse veinlets connecting the major foliar nerves. *Croomia* and *Stichoneuron* are further set off from *Stemona* by creeping rhizomes, minute pubescence or papillae on the filaments and inner faces of the tepals, and anthers borne obliquely with respect to the filaments.

Stichoneuron stands apart in its crowded, many-flowered inflorescences (*vs.* one or few flowers, usually on long, lax pedicels), major foliar nerves diverging from the midrib (*vs.* from the leaf base, but divergence from the midrib characterizes *Stemona japonica* Franchet & Sav., $2n = 14$), occasional pubescence of vegetative organs, and smooth (*vs.* papillose) leaf margins. Although seeds and fruits of *Stichoneuron* are unknown and its pollen and floral anatomy are scarcely known, each of these is a point of resemblance between *Croomia* and *Stemona*. In these two genera the seeds are striate and bear a tuft of arillate appendages, the flattened two-valved capsules have a short neck, the pollen is sometimes reticulate, and the vascularization of the ovary is similar.

Only in *Croomia* do the stems appear to lack vessel elements and have the vascular tissue in one ring (*vs.* in two), and only in this genus are there frequently free vein-endings in the leaf blade. *Stemona* and *Stichoneuron* are further distinguished by a tendency toward connation of the filaments and of the tepals; connation of the filaments occurs sporadically in *Croomia*.

Floral morphology has caused confusion, especially in *Stemona*, where two strange projections extend beyond the locules of each anther. One is vascularized and appears to be a prolongation of the connective; the other is a solid parenchymatous adaxial appendage inserted immediately distal to the locules. These unusual stamens have been interpreted as involving petals and nectaries. Comparison of early interpretations is available in Kunth, and Swamy provides a detailed recent view. Lachner-Sandoval observed that in some species the appendages block outcrossing, and that in *S. javanica* (Kunth) Engler pollen tubes grow from the anther to the stigma. Reports of perigyny pertain to all three genera, and authors are divided in opinion about the number of carpels comprising the gynoecium (see discussion under *Croomia*).

Taxonomic placement of the family has likewise generated diverse opinions (summarized in Burkill). Evidently because of the four-parted flower, vascular cylinder(s) in the stem, and some other superficial resemblances to dicotyledonous families, certain early authors placed each of the genera separately within that assemblage. Others saw an affinity with the aroids, but most have preferred placement in or near the Liliales and allies (especially the Asparagi of Jussieu or its components, which included *Dioscorea* L.). In recent treatments the Dioscoreaceae and its relatives have received the most attention as potential allies of the Stemonaceae. When Hutchinson separated the Dioscoreales from the Liliales he included the Stemonaceae in the former, and Burkill thought that the family originated from "proto-Liliales" in the vicinity of the Dioscoreaceae. Several authors have mentioned similarities to the Dioscoreales: for example, prolongation of the connective (*Stemona*); a distinct pith in the stem; a similar arrangement of metaxylem vessels in common and cauline bundles (*Stemona* and *Stichoneuron*); and tendencies toward an inferior position of the ovary, dwarfing, twining (*Stemona*), and rhizomes. Nevertheless, opinion is nearly unanimous that confidence in any placement must await accumulation of more information.

Uses in Asia are reported for all three genera. For example, *Croomia japonica* Miq. has been used as a treatment for rheumatism, and *Stichoneuron caudatum* Ridley as a tonic and (as suggested by a local name) as an abortifacient. Several species of *Stemona* are used in a number of ways throughout their ranges; at least three species are cultivated, especially *S. tuberosa* Lour., which is a source for candied roots and is eaten as a potherb. Extracts from underground organs of this and other species (known as *pai pu* in China and by the pharmaceutical name *Radix Stemone*) have antiseptic properties and are allegedly useful against rheumatism, various respiratory ailments, parasitic worms, skin diseases, lice, parasites on cattle, and termites. The genus has attracted the attention of chemists, resulting in an extensive literature. At least 16 alkaloids, which (according to Hegnauer) are usually distinguished by a lactone arrangement, have been isolated. Useful summaries of the chemical work are presented by both Edwards and Hegnauer.

Stemona tuberosa, a climbing vine with large, green and red, fetid flowers, is sometimes grown as a novelty in greenhouses.

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1. *Croomia* Torrey & Gray, Fl. N. Am. **1**: 663. 1840.

Erect, glabrous herbs to 35[–60] cm tall, with annual leafy shoots terminating persistent rhizomes, these bearing sheathing scale leaves sparsely along the horizontal portion and clustered at the upturned portion (the base of the leafy shoot). Scale leaves reddened when protruding above ground and with conspicuous longitudinal nerves not interconnected by transverse veinlets. Foliage leaves 3–6, distichous, clustered above a bare, ribbed, vertical internode, cordiform with an attenuate apex [or elliptic-ovate, cordate to rounded at base and acute to acuminate at apex], bearing 5–11 abaxially prominent longitudinal nerves, the two flanking the midrib extending to the apex, the others forming a marginal commissure, interconnected by \pm transverse, anastomosing veinlets, often with free vein-endings, the leaf margins bearing bulbous papillae. Inflorescences long-pedunculate, nodding from leaf axils, (1 or) 2 or 3[–several]-flowered, with long, articulated pedicels, each subtended by a small, nearly linear, erect bracteole and with another near the middle, this in turn often subtending another pedicel. Flowers ca. 1 cm in diameter; tepals 4, green, often tinged with purple, free, nearly equal [or one much larger than the others], spreading, oblong-elliptic to ovate, often with recurved margins, papillose on the inner surface, with 3–5 nonanastomosing nerves. Stamens 4; filaments purple (in ours), ca. half the length of the tepals, broad and thickened, papillose; anthers orange, borne nearly perpendicular to the filaments, oval; pollen grains globose to ovoid, reticulate,



FIGURE 1. *Croomia*. a-m, *C. pauciflora*: a, flowering plant with rhizome, $\times \frac{1}{2}$; b, same, from above, $\times \frac{1}{2}$; c, flower bud just before opening, tepals somewhat re-

30–50 μm in the largest dimension. Ovary broadly conical, with 1 or 2 longitudinal groove(s) and a papillose stigmatic knob, bearing 2–6(–8) pendent ovules. Fruit flattened, broadly bottle shaped, the 2 valves opposite the inner tepals. Seeds globose-ovoid, dark colored, striate, bearing a tuft of multicellular appendages along and near the funicle. Embryo minute, clavate-capitate, broadened at the cotyledonary end. TYPE SPECIES: *C. pauciflora* (Nutt.) Torrey & Gray (*Cissampelos pauciflora* Nutt.). (Named for the lawyer and botanist Hardy Bryan Croom, 1797–1837, who collected in the Southeast and died with his family in a shipwreck off the coast of North Carolina.)

Probably three species: *Croomia pauciflora* in the southeastern United States; *C. japonica* Miq. (*C. kiusiana* Makino) of southern Japan, the Ryukyu Islands, and eastern China; and *C. heterosepala* (Baker) Okuyama (*C. japonica* Makino, *C. japonica* Miq. var. *heterosepala* Baker) of southern Japan. The Japanese species are known by the local names *hime-nabewari* and *nabewari* (*hime* = little; *nabe* = pot; *wari* = to break). They differ from the American species in their larger flowers, shorter petioles, more numerous nodes along the rhizome, and lesser tendency toward cordate leaf bases. These species, especially the populations in China, need further investigation.

Croomia pauciflora grows on various substrates (probably best on limestone) on rich, loamy, shaded slopes from the southern Appalachians of Alabama, southward (in similar habitats) into the Coastal Plain, across most of that state, and into Georgia and Florida along the Chattahoochee and Apalachicola rivers in ravines, on bluffs, and on islands. In Florida it grows in the shade of *Torreya taxifolia* Arnott and, according to Harper (1942), is associated with many herbs of Appalachian affinity.

Spreading by rhizomes, *Croomia pauciflora* forms abruptly bordered, probably clonal, colonies with sometimes hundreds of upright shoots. At the southern end of its range, flowering is during March and April; farther north, in May. It is reported to remain green through the summer. The section of rhizome corresponding to a leafy shoot bears five or six distichous scale leaves. The second scale leaf from the basal end subtends a bud from which a branch may arise. The third scale is perpendicular to the plane of distichy and subtends a bud that begins new rhizomatous growth the following year (see Tomlinson & Ayensu).

The species is rare and apparently vulnerable to disturbance, as well as slow to propagate and spread. It is thus listed as threatened at the national

volute, $\times 6$; d, open flower, stamens dehiscent, $\times 6$; e, flower, one tepal and stamen removed, ovary in vertical section, placentation apical, ovules anatropous, $\times 6$; f, undehiscent stamen, adaxial side, $\times 12$; g, young fruit, $\times 2$; h, same, in vertical section, arils developing from seeds, $\times 3$; i, immature seed nearly covered with strands of aril, $\times 6$; j, same, part of aril removed to show funiculus (note that some of aril is produced from funiculus), $\times 5$; k, opened fruit, $\times 2$; l, mature seed, aril removed, $\times 6$; m, same, in vertical section, seed coat and embryo unshaded, endosperm stippled, oriented as seed in "l," $\times 5$.

level (Ayensu & Filippis) and at the state level in Georgia and Alabama. In Florida, where feral pigs feed upon the rhizomes, it is designated as endangered (Ward).

Asa Gray assigned *Croomia* to the Berberidaceae but later perceived its relationship with *Stemona* and added it to the Stemonaceae (Roxburghiaceae).

As an anatomical curiosity, *Croomia* has been the subject of several studies. It differs from most monocots in that the vascular systems of the upright stem and rhizome are organized into discontinuous cylinders with pith and cortex on either side. Some of the vascular tissue is amphivasal, taking the form of discrete bundles in the upright stem and a dissected cylinder in the rhizome. Both *Stemona* and *Stichoneuron* have raphides in some organs and vessel elements in the stem. Whether or not these are present in *Croomia* is pertinent to the question of the circumscription of the family, but there are contradictions in the literature concerning both. I have seen scattered isodiametric and elongate crystals in the stem and petiole of *C. pauciflora* but have found vessel elements only in the root.

Tomlinson & Ayensu interpreted the ovary as being unicarpellate, with two vascular bundles corresponding to the dorsal and ventral bundles of a conduplicate carpel; they suggested that the similar ovary of *Stemona* may be of the same structure, although it has a basal placenta. Others have described the ovary of *Stemona* as bicarpellate. Swamy interpreted the two bundles as the dorsal bundles of a pair of carpels and considered the ventral bundles to be represented by the small traces that extend from the receptacle to the basal ovules. Most authors have described the flowers as tending toward perigyny, but Ayensu thought the ovary "without question" to be superior.

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Starting with Volume 64 (1983), the cost per volume will be \$30.00 for individual and institutional subscriptions.

ERRATA

On page 728 of Volume 61, no. 4, and page 441 of Volume 62, no. 4, *Kaunbachia* should read *Kaernbachia*. The correct family for this genus is the Staphyleaceae.

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CONTRIBUTIONS TOWARD A GENERIC FLORA
OF THE SOUTHEASTERN UNITED STATES

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Editors of the Generic Flora: Carroll E. Wood, Jr., and Norton G. Miller



GEORGE R. COOLEY (photograph taken in 1969).

This issue of the Journal of the Arnold Arboretum consists of nine papers devoted to the genera of various families of flowering plants of the southeastern United States. There are now ninety-six papers and more than two thousand pages in the series. The work has received much support from the National Science Foundation, but it was GEORGE R. COOLEY who first made the Generic Flora of the Southeastern United States possible through gifts to Harvard University. His energy and enthusiasm were important in the early years of the Generic Flora project. Mr. Cooley has also stimulated other botanical research in the United States, especially in the Southeast.

He established and has maintained the "Cooley Award," which since 1955 has been given for the best paper presented at the annual meeting of the American Society of Plant Taxonomists. This award has had a double effect in that it has encouraged young plant systematists and has greatly improved the overall quality of the papers presented.

George Cooley has also been most active in the work of The Nature Conservancy and has played an important role in its program of acquiring and preserving whole habitats. He was a member of its Board of Governors for many years, and in 1974 he was given the unique Chairman's Special Award for his efforts.

It is thus with great appropriateness and with gratitude that this issue of the Journal is dedicated to him.—C. E. W., Jr., & N. G. M.

THE SPARGANIACEAE
IN THE SOUTHEASTERN UNITED STATES¹

JOHN W. THIERET

SPARGANIACEAE Rudolphi, Syst. Orb. Veg. 27. 1830, nom. cons.

(BUR-REED FAMILY)

A monogeneric family of perennial, rhizomatous, monoecious, marsh or aquatic, herbaceous monocotyledons distinguished by distichous, linear, sheathing leaves; simple or branched stems; flowers in dense, globose heads on the upper part of the stem or on the branches, the staminate heads distal to the carpellate; perianth of 1-6 tepals; carpellate flowers with 1 ovary; and fruit drupelike. TYPE GENUS: *Sparganium*.

Engler grouped Sparganiaceae with Typhaceae and Pandanaceae in the Pandanales, placing the order at the beginning of the monocotyledons. That these families are primitive is an idea that is no longer tenable (indeed, in Wettstein's system they *close* the monocotyledons). Their affinities, however, remain partly unsettled. Sparganiaceae and Typhaceae, now generally considered to be the sole families of Typhales, are so closely related that they may even be confamilial (see below), but their relationship to Pandanaceae is equivocal. One suggestion is that they are "very closely related to Pandanales" and have "a common origin" (Takhtajan); another, that "whatever similarity there is between . . . Pandanaceae and . . . Typhales reflects parallelism or convergence, rather than inheritance from a common ancestry" (Cronquist, 1981; see also Hutchinson, and Thorne). (For further discussion, see Briggs & Johnson; Cronquist; Harada; Mallick & Sharma; Sharma; and Takhtajan.)

¹Prepared for the Generic Flora of the Southeastern United States, a project of the Arnold Arboretum currently made possible through the support of the National Science Foundation, under Grant DEB-81-11520 (Carroll E. Wood, Jr., and Norton G. Miller, principal investigators). This treatment, the 88th in the series, follows the format established in the first paper (Jour. Arnold Arb. 39: 296-346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with supplementary information about extraregional members of a family or genus in brackets [].

I am indebted to Carroll Wood and Norton Miller for their careful review of the manuscript and for other aid, and to the staff of the Lloyd Library, Cincinnati, for help in bibliographic matters. The illustration was drawn by Karen Stoutsenberger, under the supervision of Dr. K. R. Robertson and Dr. Wood, largely from material collected by Dr. Robertson.

Hutchinson regarded the Typhales as "a reduced and very advanced group derived from the Liliaceous stock, not through the Araceae, but perhaps from the same stock that has also given rise to the Xanthorrhoeaceae. . . ."

Rejecting liliaceous ancestry for the order, Cronquist considered it to be "a separate line from a generalized commelinalean ancestry, parallel in some respects to the other groups with reduced flowers." His assignment of Typhales to the Commelinidae followed the "arguments of stomatal organization [stomata with two subsidiary cells (Stebbins & Khush), thus differing from Liliaceae, which have no subsidiary cells] and vessel distribution [vessels in all vegetative organs; vessels of Liliaceae are confined chiefly to the roots]. . . ." Further, Typhales have starchy endosperm, which is "standard in the Commelinidae but rare in the Liliales."

Thorne characterized the Typhales as "little more than anemophilous, palustrine aroids." He placed them in his Arales, consisting of Araceae, Lemnaceae, and Typhaceae (including *Sparganium*). In this connection, it is of interest to note that the rust *Uromyces Sparganii* C. & P. has both *Sparganium eurycarpum* and an aroid, *Acorus Calamus* (see Savile), as the hosts of its perfect stage; some think that this indicates relationship between these two angiosperms.

Pre-Englerian authors placed *Sparganium* and *Typha* together in the Typhaceae. The tradition of separating these genera as different families was started by Engler and followed by almost all subsequent workers until recently, when D. Müller-Doblies reexamined the relationship between the genera. He concluded that "the five different characters by which Engler justified the family Sparganiaceae are wrong or, in two cases, without any significance. . . . The few remaining but very obvious differences may be explained to a large extent [*sic*] as an adaptation of *Typha* to anemochory. They are far beyond [i.e., below] the minimum of differences required for separated families. The family Sparganiaceae is dropped and the Typhaceae s.l. have been described." The two taxa are similar in many ways: ecologically, cytologically, chemically, embryologically, and morphologically; their union in one family (by post-1970 authors, for example, Casper & Krausch; D. Müller-Doblies; U. Müller-Doblies; Takhtajan; and Thorne) may now — but for tradition — be difficult to gainsay.

1. **Sparganium** Linnaeus, Sp. Pl. 2: 971. 1753; Gen. Pl. ed. 5. 418. 1754.

Perennial, rhizomatous, monoecious, marsh or aquatic, herbaceous plants with fibrous roots. Stems emerged [or floating], simple or branched. Leaves basal and cauline, submersed, floating, or emerged, sessile, distichous, linear, sheathing, more or less flattened to V-shaped or triangular in cross section, with many longitudinal veins, these connected ladder-runglike by cross diaphragms; stomata paracytic. Inflorescences of globose, many-flowered heads on the upper part of the stem and on the branches, inflorescence axis more or less zigzag; staminate and carpellate heads separate, the branches sometimes bearing only staminate heads; staminate heads distal, soon falling, the naked axis usually persisting; carpellate heads proximal, those of the

main stem axillary or supra-axillary to leafy bracts. Each flower subtended by a bract that is sometimes difficult to distinguish from the tepals. Staminate flowers with 1-6 tepals; androecium of 1-8 stamens, sometimes with partly united filaments; anthers 4-sporangiate, introrse to extrorse, the tapetum amoeboid at first, later periplasmodial, the pollen monoporate, more or less spheroidal or ellipsoid, binucleate when shed. Carpellate flowers with (2 or) 3 or 4 (or 5) persistent tepals; gynoecium of 1 (or 2) [3] carpels, usually pseudomonomerous; stigma 1 (or 2) [3]; style 1, usually persisting as a beak on the fruit; ovary 1- (or 2-) [3-]locular, the locule with a single bitegmic, crassinucellar, anatropous, pendulous ovule, the outer integument longer than the inner; megagametophyte development of the Polygonum type; endosperm Helobial in development. Fruits drupelike, crowded in a burlike head, the exocarp spongy, the endocarp hard and with a "germination pore" at its distal end, the inner opening of the pore occluded by a "micropylar cap" or "plug" derived through enlargement of the micropylar part of the integuments; seeds with starchy endosperm and large, straight embryo. TYPE SPECIES: *S. erectum* L.; see P. A. Rydberg, N. Am. Fl. 17: 5. 1909. (Name from Greek, *sparganion*, a swaddling band, in apparent allusion to the long, narrow leaves.)—BUR-REED.

A genus of about 15 species, primarily North Temperate but also in the Arctic, extending in the New World from Alaska, the Mackenzie Delta, Hudson Bay, and Greenland, south to the southern United States and Baja California; and in the Old World from Iceland and northern Eurasia, south to northern Africa, Turkey, Iran, Afghanistan, Assam, China, and Japan; also Indonesia (Sumatra and New Guinea), eastern Australia, and New Zealand.

About nine species of *Sparganium* are known in North America. The three in the southeastern United States belong to subgenus *XANTHOSPARGANIUM* Holmb. (perianth segments thin, uniformly light brown; seeds without longitudinal ridges). *Sparganium americanum* Nutt. occurs throughout our area (see distribution map in Beal, 1960, supplemented by Mississippi records in Jones), growing in shallow water or on wet shores of ponds, streams, and swamps. Beal (1960) described *S. americanum* as "a complex polymorphic species exhibiting extensive variation in height, leaf width, thickness and texture, degree of branching of the inflorescence, position of pistillate heads, size of fruit and length of style and stigma." He distinguished two "well defined" races: (1) the "coastal race," of Coastal Plain distribution, characterized by stigmas 1.5 mm or more long, leaves "wide for the species," and inflorescence branches two to five; and (2) the "Appalachian race," of Appalachian and Ozarkian distribution, characterized by stigmas 0.9 mm or less in length, leaves "narrow for the species," and inflorescence simple to sparingly branched. The races overlap morphologically, with intermediate plants (the "ubiquitous race") scattered throughout the range of the species.

In much the same habitats as *Sparganium americanum* but of limited distribution in the Southeast are *S. androcladum* (Engelm.) Morong, reported in our area only from western North Carolina (Beal, 1960) and northwestern

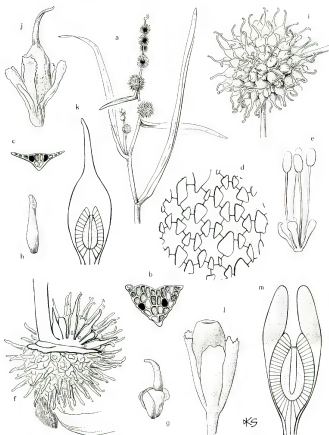


FIGURE 1. *Sparganium*. a-m, *S. americanum*: a, tip of flowering stem with axillary branch, the staminate heads distal to the larger, carpellate ones, $\times \frac{1}{2}$; b, diagrammatic cross section of leaf near base showing diaphragms (stippled) surrounded by supporting tissue, $\times 3$; c, same, near tip of leaf, $\times 3$; d, detail of diaphragm to show individual cells (lightly shaded) and air spaces (unshaded), $\times 150$; e, staminate flower with tepals and stamens, $\times 6$; f, carpellate inflorescence ($\frac{1}{4}$ removed) subtended by bract, immediately after anthesis, $\times 3$; g, carpellate flower with gynoecium and tepals, $\times 6$; h, gynoecium, $\times 6$; i, infructescence, $\times 2$; j, fruit with persistent perianth, $\times 5$; k, diagrammatic vertical section of fruit, endocarp hatched, endosperm

Louisiana (MacRoberts), and *S. chlorocarpum* Rydb.,² reported by Beal from eastern Tennessee.

According to Beal, reports of *Sparganium eurycarpum* Engelm., $2n = 30$, subgenus SPARGANTUM (subgen. *Melanosparganium* Holmb.) (perianth segments thick, with dark brown to black apex; seeds with 6–10 longitudinal ridges), from the Southeast as far south as Florida, are based on misidentification of robust plants of *S. americanum*.³

Some species of *Sparganium* are distinctive; others seem not to be. Many characters used to distinguish taxa in the genus are (as in many other aquatic plants) inconstant or readily altered by environment. According to Mason, characters such as presence or absence of supra-axillary heads, cross-sectional shape of leaves, position of tepals, and shape of fruits appear to be quite meaningless. Nomenclature of the genus is frustrating. *Sparganium* is much in need of study with the use of modern techniques.

Several hybrids involving about 10 taxa in various combinations have been reported, but apparently none has been verified experimentally. The hybrid *Sparganium emersum* \times *S. angustifolium* appears to be fully fertile, but *S. emersum* subsp. *erectum* \times *S. erectum* subsp. *neglectum* (= *S. erectum* subsp. *oocarpum*; *S.* \times *tardivum* Topa) shows "very poor fertility" (Cook, 1961b). Almost nothing is recorded about breeding behavior of other putative hybrids.

Chromosome counts, some undocumented, are available for many of the species, all of which are diploids with $2n = 30$. In only one instance (Harada) has a different number been reported: $2n = 3x = 45$ in some root-tip cells of *Sparganium stenophyllum*. (Other root tips of this species collected from the same place showed $2n = 30$.)

The fossil record of *Sparganium*, based mostly on fruits, but also on pollen (Muller) and leaves, extends back to the Paleocene (Daghlian). The genus provides an impressive example of evolutionary reduction in the number of locules: *S. multiloculare* of the British Bembridge Beds (Oligocene) had five-, four-, three-, and two-locular forms; forms of *S. ramosum* (i.e., *S. erectum*) from interglacial deposits are four-, three-, or two-locular. The

²*Sparganium chlorocarpum* Rydb. is included in the synonymy of *S. emersum* Rehman by Cook (1961b).

³The Eurasian *Sparganium erectum* subsp. *erectum* was said by Casper and Krausch to range in the eastern United States south to Florida. This report apparently rests on Cook's suggestion (1961b) that *S. eurycarpum* (attributed to Florida by Cook, Muenscher, Rydberg, and Small, *inter alios*) is seemingly the same as *S. erectum* subsp. *polyedrum* (i.e., subsp. *erectum*). Curiously, though, Casper and Krausch did not include *S. eurycarpum* in the synonymy of *S. erectum*.

stippled, embryo unshaded, $\times 6$; l, remains of floating fruit collected very late in season, style and central part of fruit above endocarp decayed away, $\times 6$; m, same in vertical section, spongy flotation tissue shaded, endocarp hatched, endosperm evenly stippled, embryo unshaded, $\times 10$.

ovary today is usually one-locular, although in a few species (e.g., *S. erectum* and *S. eurycarpum*) there are typically two locules, occasionally or rarely one or three. Apparently three is the maximum in *Sparganium* today.

Comparative studies of extant species reveal examples of further reduction. Ovaries with two or three locules may show abortion of one or two ovules and may have only one normal locule, the other(s) being rudimentary. One-locular gynoecea may bear a well-developed to rudimentary second stigma, indicating that they are dimerous structures. The dimerous nature is also shown by the vascularization and by the excentric position of the locule (Eckardt). Most of the time, however, one-locular gynoecea show no recognizable remains of an additional carpel. Thus, in *Sparganium* the gynoecea are pseudomonomerous—i.e., they appear to be monomerous in most species but actually incorporate more than one carpel in their make-up or are strictly one-carpellate by reduction from coenocarpous ancestry. In *Sparganium*, "pseudomonomy has reached the last stage of reduction" (D. Müller-Doblies).

Flowers of *Sparganium* are protogynous and anemophilous. Morphology of the densely many-flowered staminate head is difficult to interpret at anthesis, resulting in despairing and inaccurate descriptions such as that of Fernald (1950), who wrote of the staminate flowers as being "3-androus" and "naked" and as having "minute scales irregularly interposed." That these flowers are composed of one to six tepals and one to eight stamens is confirmed in developmental studies, most recently by U. Müller-Doblies.

The ripe fruits drop into the water, where they can float for at least a year, possibly up to 2.5 years (Guppy, 1897). Eventually the spongy exocarp may rot off, leaving only the endocarp. Dispersal is hydrochorous and both epi- and endozoochorous (mostly by water birds).

At the distal end of the endocarp is a pore through which the embryo emerges in germination. The inner opening of the pore is blocked by a "micropylar plug" ("Samendeckel" of Hegelmaier) formed by enlargement of the integuments (and possibly also the apex of the nucellus; Campbell, 1899). Germination can be delayed as long as several years after maturity, apparently by the restraining influence of the micropylar plug. After decay (?) or removal of the plug, and in a fully saturated atmosphere or under water, germination readily occurs.

Some bur-reeds, but not those of the Southeast, are typically "floating-leaved" species, with flaccid, flat or weakly keeled leaves of obvious dorsiventral internal structure. Others, including those in the Southeast, are typically "emergent" species, with robust, relatively stiff, strongly keeled leaves not obviously dorsiventral. The distinction between the types is not absolute. Kaul (1976) suggested that floating-leaved species are neotenous forms derived from emergent species, a hypothesis supported by the observation that floating seedling-leaves of emergent species are anatomically similar to adult leaves of floating-leaved species. He (1973) regarded *Sparganium* as a genus in transition from the emergent to the floating habit.

In rivers and streams (i.e., in flowing water) emergent species of *Sparganium* such as *S. americanum* may produce completely submersed, sterile

plants, often in dense colonies. The leaves of such plants are ribbonlike and flaccid, resembling those of several other genera (*Alisma*, *Butomus*, *Sagittaria*, *Scirpus*, and *Typha*) that can develop similar underwater leaves (Luther, Voss). Emergent bur-reeds may also produce floating leaves, especially in deeper water.

Bur-reeds are among the plants that can choke waterways, a matter of considerable economic significance in some areas (as in England and Wales; Robson). The fruits of *Sparganium* are important food for water birds; the fruits, stems, and leaves are eaten by mammals (e.g., muskrat, moose). The Klamath Indians of Oregon used the starchy rhizomes of bur-reeds for food (Coville). Certain species of black flies — among the insects most notorious as annoyers of animals and people — choose submersed plants in running water as a larval and pupal substratum; *Sparganium* may rank high among the choices (as in central Maine, where the black fly *Simulium penobscotensis* is a serious summertime nuisance). A few species of *Sparganium* are grown as "bog plants." The unripe fruits of *S. erectum* ("*S. ramosum*") "made into an infusion with sourish red wine and cinnamon" are "good against fluxes of the belly and bleedings of all kinds" (Steinmetz). (The fruits of any other species of bur-reed could probably be used with equal efficacy.)

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THE CASUARINACEAE IN THE SOUTHEASTERN UNITED STATES¹

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CASUARINACEAE R. Brown in Flinders, Voy. Terra Austral. 2: 571. July–Aug. 1814. "Casuarineae." [Mirbel, Ann. Mus. Natl. Hist. Nat. 16: 451. 1810, "Casuarinées"], nom. cons.

(BEEFWOOD FAMILY, SHE-OAK FAMILY)

A unigeneric family of evergreen [shrubs and] trees with minute, whorled, basally connate, scalelike leaves and thin, ridged and grooved [or quadrangular], articulated branchlets. Plants monoecious or dioecious, with reduced anemophilous flowers, the staminate flowers whorled in terminal, simple [or compound], bracteate spikelets; the carpellate flowers whorled in bracteate, globose to ellipsoid heads, usually on short, lateral branchlets. Ovules semi-anatropous, bitegmic, crassinucellate. Infructescence woody and cone-like, bearing winged, indehiscent samaras, each enclosing a single seed without endosperm. TYPE GENUS: *Casuarina* Adanson.

1. *Casuarina* Adanson, Fam. Pl. 2: 481, 534, 1763.

Plants to ca. 25(–45) m tall, to ca. 70 cm [–1 m] in diameter. Trichomes unicellular or uniseriate, often branched. Calcium oxalate crystals often single or clustered in parenchymatous tissues, sometimes in phloem fibers. Leaves in whorls of [4 or] 5–16, the free tip of each protruding as the extension of a cauline ridge, linear to narrowly elliptic-lanceolate or narrowly deltoid [or ovate], erect or recurved, usually pubescent along the margins but

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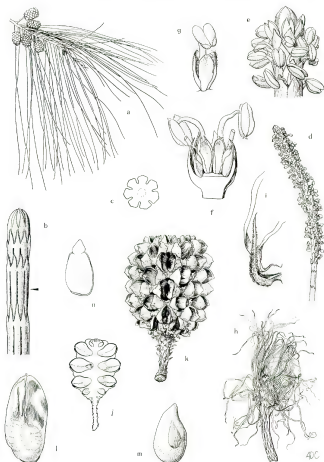


FIGURE 1. *Casuarina*. a-n, *C. equisetifolia*: a, fruiting branch (infructescences immature), $\times \frac{1}{2}$; b, tip of photosynthetic branchlet, $\times 12$; c, diagrammatic cross section of internode at level marked on "b," hairs omitted from grooves in stem, stele outlined by dots, $\times 18$; d, staminate inflorescence, $\times 2$; e, tip of same, showing 4 whorls of flowers, $\times 8$; f, single node showing 4 of a whorl of 7 flowers, each in a leaf axil, anthers of 2 flowers removed, adaxial side seen, $\times 12$; g, single staminate

often becoming glabrous, with 1[-3] median vein(s). Branchlets whorled, with the ridges of an internode aligned with grooves on the adjacent internodes, puberulent or tomentose, often becoming glabrous or nearly so [usually glabrous in the *Gymnostomae*], the indument usually most concentrated in or confined to the grooves, sometimes glaucous; stomata transverse, distributed mostly on the branchlets, rubiaceous or nearly so, with a variable number of polar cells. Wood with growth rings poorly defined or absent; vessel elements mostly solitary, with simple or scalariform, steeply oblique to transverse perforation plates, often with gum deposits, tertiary spiral thickenings, and tyloses; ground tissue usually composed of vasicentric tracheids intergrading with fiber-tracheids, the fibrous elements often with tertiary spiral thickenings; xylem parenchyma apotracheal banded and usually diffuse; rays highly variable, uniseriate to broadly multiseriate, often of the aggregate type. Each staminate flower subtended by a bract covering 2 small, sometimes slightly protruding bracteoles, the bracts deltoid to subulate or narrowly lanceolate [rarely orbicular], arranged like the sterile leaves and basally connate [sometimes these whorls separated by exposed sections of internode], usually with shaggy pubescence, especially along the margins; the paired bracteoles enclosing 2 perianth segments (sometimes called petals or inner bracteoles), the adaxial one larger and usually forming a hood over the anther and the other segment [the abaxial segment sometimes not developing], both sometimes broken off by growth of the exerted single stamen; stamen with the filament bent in the bud, anthers broadly oblong-elliptic, the epidermis degenerating and replaced with a fibrous layer, the 2 locules tending to separate at the often apiculate ends, dehiscing by longitudinal lateral slits. Pollen grains 2-nucleate when released, medium sized, usually oblate to oblate-spheroidal, rounded to semi-angular in polar view, (2 or) 3(-7)-porate or -pororate, the usually protruding pores often operculate, exine with or without columellae, nearly psilate to rugulate or spinulose. Whorls of carpellate flowers alternating with adjacent whorls and condensed into capitula, each flower subtended by a pair of minute, pubescent bracteoles within a usually tomentose, subulate to broadly deltoid or broadly orbicular bract (the broader shapes perhaps reflecting changes with development of the infructescence), sometimes with an attenuate apex; gynoeceium 2-carpellate; ovary flattened, with 1 fertile locule and a small sterile locule; ovules 2[-4] with 1 maturing,

flower, from abaxial side, showing 2 lateral bracteoles, abaxial "petal," and tip of adaxial "petal," $\times 12$; h, carpellate inflorescence, $\times 3$; i, single primary bract with carpellate flower, the minute ovary with a bracteole on either side; styles only partly shown, $\times 12$; j, developing infructescence, in vertical section, showing 6 developing fruits, one in diagrammatic section to show 2 ovules (note primary bract subtending each fruit, heavy secondary bract behind each fruit), $\times 2$; k, infructescence from which fruits have fallen (note pairs of greatly enlarged secondary bracts (bracteoles; cf. i), each above a primary bract), $\times 2$; l, mature fruit, $\times 6$; m, seed, with delicate seed coat and rudiment of aborted ovule, $\times 10$; n, embryo, oriented as in seed (radicle up), $\times 10$.

the micropyle superior; style short, surmounted by 2 long, exerted, reddish stigmas. Inflorescence globose to cylindrical; bracts becoming variably deformed and woody, often apiculate at the apex; bracteoles enlarging greatly, becoming woody, usually conspicuously puberulent toward the apex on both sides, their jutting, rounded to acute [to truncate or acuminate] apices becoming the most conspicuous components of the infructescence [sometimes bearing an abaxial projection], coming superficially to resemble paired valves of a capsule enclosing the seedlike samara. Samara flat, elliptic to obovate, rounded to acute at the apex, sometimes apiculate due to the persistent base of the style, conforming to the outline of the enclosing bracteoles and thickened at the basal end, membranaceous-winged at the opposite end, the wing traversed by a dark-colored nerve. Seed solitary, the pericarp adhering to the seed coat; endosperm originally nuclear with cell formation proceeding from the micropylar end, eventually completely consumed by the embryo; embryo straight, with flat cotyledons and a superior radicle. (Including *Gymnostoma* L. A. S. Johnson; type species *G. nodiflorum* (Thunb.) L. A. S. Johnson.) TYPE SPECIES: *C. equisetifolia* [L. ex] J. R. & G. Forster.² (Name from the resemblance of the branchlets to the plumage of the cassowary bird, *Casuaris*.) Rumphius, the acknowledged originator of the generic name, mentioned the common name "Casuaris-Boom, a foliorum forma." He remarked further that the pattern of striations in the wood resembles feathers even more than does the foliage.

A genus of approximately 55 species distributed mostly in or near Australia including New Caledonia and Fiji, with the southernmost species in Tas-

²The correct name for the species long known as *Casuarina equisetifolia* has been a matter of controversy. Linnaeus published the name *Casuarina equisetifolia* in the *Amoenitates Academicæ* (4: 143, 1759), but arguments for setting the valid publication at both an earlier and a later date have been made. In the Linnaean dissertation (Stickman's *Herbarium Amboinense*, 1754), on which the work of 1759 is based, Fosberg and Sachet (see also Fosberg) noticed that the misspelled name *Casaarina litorea* preceded *C. equisetifolia*. Citing ICBN Art. 42, they stated that reference to the description and figure in Rumphius's pre-Linnaean *Herbarium Amboinense* validated both the generic and the specific names. Fosberg proposed amending Art. 23 of the ICBN to consider the Rumphian names in Stickman's dissertation as invalidly published. In response, Voss and Greuter asserted that under Art. 34.1(a) most botanists would consider these names as already invalid "since they were not accepted by Linnaeus upon publication." The XIII Botanical Congress referred the matter to the editorial committee (Taxon 30: 906, 1981), with the result that Stickman's Rumphian names will appear in the 1982 edition of the ICBN as an example of names not accepted by the author in the original publication. (However, note that *C. equisetifolia* appeared as a replacement for *C. litorea* in 1759, not 1754.)

As an objection to the genus being validated by reference to Rumphius, Friis noted that "Although the Code is not absolutely clear on this point it has consistently been stressed by Rickett and Stafleu . . . that monotypic new genera cannot be validated by references to pre-Linnaean literature only." If Rumphius's description does not validate the generic name, it cannot validate the combination *Casuarina litorea* either according to Art. 43.1.

In contrast to Friis, Bullock found Stickman's or Linnaeus's (1754, 1759) "Generis proprii, singularis arbor, Equiseti Structura" insufficient as a validating description. He suggested that Adanson gave valid publication to *Casuarina* and that the Forsters did so for *C. equisetifolia*.

mania and the northernmost in southeastern Asia. The original eastern and western limits are defined by the only naturally widespread species, *Casuarina equisetifolia*. This appears to be indigenous around the Indian Ocean and eastward to part of Polynesia, where the extent of introduction by humans and subsequent naturalization is unclear (Smith), an uncertainty common to the history of this and various other species in tropical and subtropical regions.

Casuarina equisetifolia, *C. Cunninghamiana* Miq., and *C. glauca* Sieber ex Sprengel are cultivated and have become naturalized in the southeastern United States, mostly in Florida. Reports of *C. lepidophloia* F. Mueller (*C. cristata* Miq.) in Florida apparently result from misidentifications of *C. glauca* (see Bailey, Morton). Other species have been introduced, but either they are now absent or their presence is not well documented (e.g., a list of several such species appears in Eick).

The most common species, *Casuarina equisetifolia* (*C. litorea* [Rumph. ex] L. and many other synonyms) (with at least three taxonomic varieties), Australian pine, beefwood, was available from a nursery in Florida at least as early as 1887, as were several other species that have been less successful. Trees of *C. equisetifolia* differ from the other species naturalized in Florida in having an open, irregular crown; prominent ribs on the branchlets; infructescences usually more than 13 mm in diameter vs. narrower in *C. Cunninghamiana* (infructescences of *C. glauca* do not develop in Florida); and samaras usually 6–8 mm long vs. 3–4.5 mm in *C. Cunninghamiana*. *Casuarina equisetifolia* is usually monoecious, highly tolerant of salty soil, and prolific in fruit production. It flowers in Florida from late winter to October, with individual trees flowering twice per season. About 45–50 days pass between pollination and fertilization (Swamy).

Casuarina glauca, native to Australia (where it is called swamp oak) and restricted to South Florida in the southeastern United States, is dioecious and tolerant of salt; it has a strong tendency to sucker. In order to combine its attractive, dark green, dense, erect crown with a root system that does not sucker, scions of this species are grafted onto rootstocks from *C. equisetifolia*. Branchlets of *C. glauca* usually have 12–16 leaves per whorl vs. 6–8 in *C. equisetifolia*, and 6–11 in *C. Cunninghamiana*. *Casuarina glauca* has the thickest branchlets (usually more than 0.85 mm vs. a narrower diameter) and the longest internodes (usually 8–13 mm vs. usually less than 10 mm in *C. equisetifolia* and *C. Cunninghamiana*). That *C. glauca* hybridizes with *C. Cunninghamiana* is well established by anatomical, morphological, and serological criteria (Bailey *et al.*, El-Lakany *et al.*, El-Osta *et al.*, Saleh & El-Lakany). The other two possible hybrid combinations may occur in Florida as well.

Casuarina Cunninghamiana is native to eastern Australia, where it is called "River-[She-]Oak" from its tendency to line streams in pure stands, although it also grows well on drier sites. This is the least salt tolerant among the species in Florida. Trees of this species may attain the largest sizes to be found in *Casuarina*—in Australia the trunk sometimes exceeds a meter in diameter. *Casuarina Cunninghamiana* has ascending branches and a py-

ramidal crown; it sometimes suckers from the roots. Distributed from South Florida northward and westward to Tallahassee and to southern Louisiana, these (at least usually) dioecious trees flower from late summer through November, and occasionally later (e.g., in February.)

Using mostly characters of the bracteoles in the infructescence, Miquel (1868) divided *Casuarina* into the sections (EU-)CASUARINA and ACANTHOPITYS. Benthham and Mueller retained ACANTHOPITYS but split section CASUARINA into sections TRACHYPITYS and LEIOPITYS. The latter contains the three species naturalized in Florida and, because it contains the type species of the genus, should be called section CASUARINA. Refinement of Benthham and Mueller's classification with an anatomical characterization of the sections appeared in Moseley's monograph on the wood anatomy of the Casuarinaceae. Poisson accepted Benthham's sections, collected them as his *Divisio Casuarinae Cylindricae seu Cryptostomae*, and proposed the new *Divisio Casuarinae Tetragonae seu Gymnostomae* (corresponding to Loew's "Typus nodiflorae") for seven species from New Caledonia, Sumatra, and some other nearby islands. These differ from the Cryptostomae in having quadrangular stems with only four leaves per sheath (*vs.* stems usually cylindrical with pilose grooves and more than four leaves per sheath); sparse, pseudoverticillate branches; usually compound staminate inflorescences; and squared (*vs.* rounded) infructescences with exserted bracteoles and 8-ranked scales, which are broadened at the base.

The genus *Gymnostoma*, recently segregated from *Casuarina* by L. A. S. Johnson, seems to correspond closely to the Gymnostomae in description and distribution. Stating that the new genus "is not formally based on" Poisson's taxon, Johnson published *Gymnostoma* with little elaboration in a note that is preliminary to an upcoming revision of the Casuarinaceae in which he will recognize four genera.

Others have agreed that *Casuarina* can be divided. Anticipating Johnson's publication, Chanda found *Gymnostoma* to differ from *Casuarina* by having "distinctly striate" (*vs.* striate, faintly striate, or nonstriate) punctitegillate pollen. Kershaw (also in anticipation of *Gymnostoma*) did not fully confirm Chanda's distinction, but concluded that pollen of *Gymnostoma* tended to be smaller, and to have a larger polar index, fewer pores with smaller protrusions, and less frequent cracks in the exine. The chromosome number is known for only one species of Gymnostomae, *C. papuana* S. Moore, $2n = 16$; all counts in the Cryptostomae are different (Barlow, 1959a). Stomata of Gymnostomae are sunken, are separated vertically by only one or no subsidiary cells, are not restricted to cauline grooves or adaxial surfaces of leaves, and have thicker lamellae in the guard cells (Flores, 1977). Moreover, Moseley's study of the wood anatomy of Casuarinaceae supports the recognition of *Gymnostoma*. (For more detailed general comparisons of these two groups see Christophel; Flores, 1977; and Smith.)

Other than by providing limited evidence that the Gymnostomae comprise a distinct group, Barlow's (1959a) informal subdivision of *Casuarina* on the basis of chromosome counts hardly coincides with any of the infrageneric

classifications mentioned above. Barlow divided the Cryptostomae into groups A and B. Members of group A (including the species in Florida) are like the Gymnostomae in having few chromosomes ($n = 9$, but see Darlington & Wylie) and a distribution not limited to Australia. The $n = 8$ or 9 of the Gymnostomae or Cryptostomae Group A are thought to be the base numbers from which the diploid numbers, $2n = 20-28$ (and to 56 with polyploidy), in the entirely Australian group B were derived. Barlow (1959a, b) found species of the problematic *Casuarina* "Distyla complex," which was revised by Macklin and belongs to group B, all to have diploid numbers of 22, and he found sexual tetraploid individuals in most of them. Triploid carpellate plants of two species of the Distyla complex yield mixed triploid and tetraploid progeny, with a high frequency of heteroploid double embryos. In such cases haploid pollen fertilizes unreduced eggs, producing tetraploid embryos, and initiates pseudogamous development of unreduced triploid synergids. Apomictic embryos derive (without pseudogamous initiation) from triploid parents in two other species (Barlow, 1959b). Palynological characters serving to distinguish Barlow's groups were tabulated by Kershaw, who found the sequence *Gymnostoma*, group A, group B, and the Distyla complex to "form a series of increasing morphological complexity."

Treub's classic monograph of the embryology of three species of *Casuarina* is a source of numerous surprises, not all of which have withstood subsequent research (Frye, Juel, Swamy). Among his apparently accurate observations are that the branching pollen tube reaches the embryo sac (i.e., megagametophyte) by growth through the placenta and chalaza (chalazogamy) rather than by the more typical passage through the micropyle (porogamy); a massive sporogenous tissue produces several megaspores and several (to 20 or 25) embryo sacs (according to Swamy, probably leading occasionally to polyembryony); tracheids develop in the sporogenous tissue of some species; and the embryo sacs elongate basally into the chalaza. Frye reported that in *C. stricta* Aiton the chalazogamous pollen tube grows within the embryo sacs, but Swamy thought that the tube passed only between them.

Among Treub's probably inaccurate observations are that antipodal cells, and sometimes synergids, are absent (the embryo sac is of the eight-celled Polygonum type); the endosperm begins to divide before fertilization; the sporogenous tissue develops from two distinct groups of cells; the unfertilized egg is enclosed in a cellulose wall; the tip of the pollen tube becomes detached and is carried along by growth of the embryo sac; and the sperm is probably released into the embryo sac far from the egg.

Treub listed several supposedly primitive embryological features of *Casuarina* and segregated it as the subdivision Chalazogames, establishing the Porogames for the other angiosperms. *Casuarina* represented to him a fundamental split within the flowering plants and not, he emphasized, a group intermediate to the gymnosperms. Chalazogamy and multiple megaspores and embryo sacs were accepted as primitive by both Engler and Wettstein, who, from this and other observations—primarily the incomplete, anemophilous flowers and the vegetative resemblances to some gymno-

sperms—regarded *Casuarina* as primitive, not far removed from the gymnosperms, and placed the Casuarinaceae in the Archichlamydeae and Monochlamydeae, respectively. Wettstein explained that imperfect flowers with uniseriate perianths could have arisen from reproductive clusters on gymnosperms like *Ephedra*, with the carpellate flowers and whorls of staminate flowers of *Casuarina* as intermediates. Nevertheless, he thought that *Casuarina* probably represented a line of descent from the gymnosperms distinct from the origin of the other angiosperms.

Such incomplete, usually anemophilous flowers are now interpreted by most botanists to be specialized reductions from more complex, insect-pollinated ancestors. Wood, phloem, and pollen all indicate that *Casuarina* is fairly specialized (Erdtman, Moseley, Tippe). Its embryological oddities are also not strong evidence for labeling *Casuarina* as primitive. Chalazogamy probably evolved from porogamy, and the production of many megaspores occurs in diverse angiosperms (Moseley, Tippe). Both characteristics are found in the hamamelidalean families (Swamy, Tippe), to which the Casuarinaceae are allied by most who have considered their placement.

Similarity to the hamamelidalean assemblage is apparent not only in the small anemophilous flowers and the embryological characteristics, but also in the wood anatomy (Metcalf & Chalk, Moseley, Tippe) and pollen (Erdtman). The Betulaceae have received the most attention as the possible closest relatives of *Casuarina*, with likenesses apparent in the pollen (Erdtman, Kedves *et al.*), aspects of the embryology (Benson *et al.*), and paired vascular traces in the filaments (Eames). Poisson listed many similarities between *Casuarina* and the Myricaceae; Erdtman noticed palynological resemblance to this family and to Juglandaceae. Nonetheless, most authors perceive the Casuarinaceae as sufficiently isolated to comprise an order, the Casuarinales (or Verticillatae), which is placed in the subclass Hamameli[d]dae or superorder Hamamelidiflorae (Cronquist, Takhtajan, Thorne).

The chemistry of *Casuarina* remains too inadequately studied to be important in its taxonomy (Mears). The following phenolic compounds have been detected in several species or as indicated: catechin, cinnamic acids, cupressuflavone, cyanidin, delphinidin (*C. stricta*), ellagic acid, hinokiflavone, kaempferol, and quercetin. "Casuarin" from *C. equisetifolia* appears to be a mixture of d-galocatechin and d-catechin (Roux). (For tables of species and compounds see Bate-Smith, Natarajan *et al.*, and Saleh & El-Lakany.) Biflavonoids (hinokiflavone and cupressuflavone in *Casuarina*) are known from only seven families of angiosperms but are common among gymnosperms (Geiger & Quinn). Similarly, Natarajan *et al.* mentioned that juniperic acid reported from *C. stricta* is "considered to be a typical gymnosperm constituent." At least some of the other phenolic compounds are consistent with hamamelidalean affinity (Bate-Smith, table 2; Hegnauer; Natarajan *et al.*). In *C. Cunninghamiana* three sterols amount to over three mg per gram of dry weight of the roots (Knights & Wheeler), and haemoglobin is contained in the root nodules (Davenport).

Megafossils clearly identifiable as Casuarinaceae have been found in

Eocene and later deposits in Australia (Christophel, Lange, Patton, Pike), with the oldest (according to Christophel) most similar to *Gymnostomae*. A Gondwanalandic distribution is indicated by a Miocene fossil of a fruiting branchlet from Patagonia (Frenguelli). Less certainly identified is the fossil pollen attributed to *Casuarina*. Martin transferred the palynological form-species, *Casuarinidites cainozoicus* Cookson & Pike and *Triorites Harrisii* Couper, to *Casuarina*. The oldest specimens of the former are Paleocene (Harris). Pollen identified as *T. Harrisii* is common and widespread in Tertiary deposits in Australia and New Zealand, extending back to approximately the Danian-Maestrichtian transition (Couper).

Several authors have studied the unusual photosynthetic branchlets; the most thorough and broadly based study appears in the recent series by Flores. Her tentative opinion (1978) on the long-standing question of the homology of the ridges on the surface of the branchlets was to consider them as axial, limiting her concept of the leaves to the free, scalelike tips. The contrary and often accepted view that the ridges are the decurrent bases of leaves originated with Loew, who coined the term "phyllichnia" for them. As seen in transverse section, each ridge has near the outer surface a sclerenchymatous layer usually shaped like a "T," with the stem extending variably toward an underlying vein and halving the photosynthetic palisade layer. These veins extend into the leaf tips, are alternate with the more internal bundles of the cauline stele, are flanked by flanges of transfusion tissue, and have been reported in a few species to be surrounded by an endodermis (Boodle & Worsdell, Corderoy). Flores (1977), however, was unable to verify the presence of Casparian strips in the alleged outer endodermis in any of the many species she studied. The inner vascular ring is surrounded by an endodermis. Succulent branchlets that sometimes develop in *Casuarina equisetifolia* probably result from exposure to salt spray along seashores (Rao).

Ovule orientation and attachment have been variably described as orthotropous to anatropous and apical to basal. In an effort to correct this confusion, Treub conducted a developmental study of the the ovary of *Casuarina suberosa* Otto & Dietr., which when augmented by later studies allows some clarification. The (usually) two ovules originate parietally on opposite sides of an initially unilocular ovary; as a sterile second locule appears, the ovules become collateral on the septum. The base of the septum could be misinterpreted as the funiculus of a basally inserted orthotropous ovule. The mature ovule is erect, with its integument fused to the septum toward the top of the locule above the attachment of the bent funiculus.

Species of *Casuarina* grow in varied habitats, from rainforest to arid regions, commonly showing tolerance for dry conditions and substrates deficient in nitrogen. *Casuarina equisetifolia*, for example, forms forests on nearly soilless volcanic rock on Polynesian and Melanesian islands. Undoubtedly contributing to such tolerance are the nitrogen-fixing nodules on the roots of this and no fewer than ten other species, including the three in Florida.

That nitrogen is fixed by the microorganisms in the nodules and that the symbiosis contributes to the growth of the tree have been thoroughly demonstrated (Aldrich-Blake, Bond, Gauthier *et al.*, McLuckie, Narasimhan, Tyson & Silver). The endophyte invades a young lateral root near its base through a deformed root hair, stops the longitudinal growth of the root, comes to fill enlarged cortical cells, and initiates production of upwardly growing branch roots. The branch roots, in turn, branch from their own bases, ultimately producing a coralloid mass up to 6–7 cm in diameter (Becking, Callaham *et al.*, McLuckie, Miehe, Torrey; these studies based mostly on *Casuarina Cunninghamiana* and, to a lesser degree, on *C. equisetifolia*). As the branched, septate hyphae follow the growing end of the nodule, polyhedral resting stages are left behind in dead cortical cells. The mycelium produces terminal vesicles that probably have a role in the fixation of nitrogen. (For information on the morphology and growth of the endophyte, see Becking, Gauthier *et al.*, Miehe, Torrey, Tyson & Silver).

Similar nodules form in roots in six other nonleguminous families of angiosperms. Nodules of the Myricaceae most resemble those of *Casuarina* in also having upturned rootlets. The microbial symbionts hosted by each of these families all belong to the family Frankiaceae recently described and assigned to the Actinomycetales by Becking, who named and described the species from nodules of *Casuarina* as *Frankia casuarinae*. *Casuarina* also shares with the other nodulated nonlegumes the characteristic of vesicular-arbuscular endomycorrhizal symbiosis. *Casuarinas* in Florida are infected by species of *Gigaspora* and *Glomus* (Zygomycetes) (see Rose). Warcup recorded ectomycorrhizal associations for three species of *Casuarina* in Australia.

As is often noted, *Casuarina equisetifolia* sometimes grows more than ten feet a year and thus can be a rapidly regenerating source of wood on inferior soils. In India this species is cultivated in plantations and is harvested for fuel after five to seven years (Singh). (According to Morton, it is regarded favorably as a fuel for barbecues in Florida, lending a desirable flavor to the meat.) Wood of *C. equisetifolia* is hard and fine grained. Although several defects diminish its utility in cabinet work, it is commonly used for such rougher items as beams, poles, and handles for tools. Durability in salt water has made the wood of this species and *C. glauca* useful for masts, oars, spars, and docks. The pulp is suitable for manufacture of wrapping paper and coarser products (Guha & Karira).

Branchlets or seedlings of *Casuarina Cunninghamiana*, *C. glauca*, and other species have served as cattle fodder but are of low quality and even toxic (Anderson, Morton). Tannin, dyes for textiles, and ingredients in a wide variety of medicinal preparations (listed by Morton) have been derived from bark of *C. equisetifolia*.

The principal use of *casuarinas* in Florida has been horticultural, although the mature infructescences have been used in necklaces and for buttons. *Casuarina* has been planted along roads, in lawns, in hedges, in sandy areas (as a restraint to shifting), and in citrus groves (as a shelter).

All the species in Florida are susceptible to root rot caused by the basidiomycete *Clitocybe tabescens* (Rhoads). *Casuarina equisetifolia* (and to a

lesser extent the other species) has become an invasive pest in South Florida. It spreads rapidly, aggressively displaces native vegetation, and is difficult to eradicate. The masses of roots and fallen branchlets interfere with the nesting of sea turtles and the American crocodile. Sites invaded by *C. equisetifolia* provide poor habitats for other wildlife. (For information on *Casuarina* as a nuisance, see Craighead, Mazzotti *et al.*, Morton, Toops, Workman & Missimer.)

Zivitz found that three cases of hay fever and asthma near Miami coincided with flowering of *Casuarina equisetifolia* and "*C. lepidopholia*" (*sic*; probably *C. glauca*); he also found pollen of *C. Cunninghamiana* to be antigenic, and thus a likely source of problems in central and western Florida. Morton mentioned additional instances in which pollen from *Casuarina* has evidently caused respiratory irritation.

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THE BATACEAE IN THE SOUTHEASTERN
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BATACEAE Martius ex Meissner, Gen. Tab. Diag. 345, 349, Comm. 260.
1842. "Batideae," nom. cons.

(SALTWORT FAMILY)

A unigeneric family distinguished by nearly linear, opposite, succulent leaves, each with a basal appendage and minute stipules; reduced, anemophilous, imperfect flowers, with a nearly closed sac initially enclosing the staminate flower, and with a 4-locular ovary and sessile stigmas in the carpellate flower, a single, basal-parietal, bitegmatic, anatropous ovule in each locule; and seeds lacking endosperm. TYPE GENUS: *Batis* P. Br.

1. *Batis* P. Browne, Civil Nat. Hist. Jamaica, 356. 1756.

Strong-scented, sprawling, succulent, nearly glabrous, small shrubs rarely more than 1 m tall, main stems to 2(-4) cm in diameter at the base, major branches arching or prostrate and (*B. maritima*) rooting at the nodes, branchlets erect or drooping, initially quadrangular in transverse section, becoming terete; bark light gray, flaking. Large irregularly shaped crystals (sodium chloride?) in most organs (calcium oxalate crystals also reported), and often apparently with clusters of salt crystals being excreted through fissures in the epidermis. Wood with the vessel elements mostly solitary or in radial multiples, the perforation plates simple, sometimes bearing thin-walled tyloses; xylem parenchyma vasicentric and banded apotracheal with storied cells; rays

¹Prepared for the Generic Flora of the Southeastern United States, a project of the Arnold Arboretum currently made possible through the support of the National Science Foundation, under Grant DEB-81-11520 (Carroll E. Wood, Jr., and Norton G. Miller, principal investigators). This treatment, the 90th in the series, follows the format established in the first paper (Jour. Arnold Arb. 39: 296-346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets []. References that I have not verified are marked with an asterisk.

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FIGURE 1. *Batis*. a-n, *B. maritima*: a, staminate inflorescence with portion of leaf (note, in region above opened flowers, unopened spathelets alternating in vertical rows with longer bracts), $\times 5$; b, bract from upper part of staminate inflorescence, $\times 5$; c, spathe, abaxial side, before anthesis, $\times 15$; d, same, after anthesis, stamens and tepals of flower protruding, $\times 15$; e, staminate flower removed from spathe, $\times 15$; f, spathe with flower removed to show line of rupture (note thin abaxial surface and thick adaxial surface), $\times 10$; g, branchlet with carpellate inflorescences (note appendage on lower surface of leaf at base), $\times 1$; h, carpellate inflorescence

mostly multiseriate, with crystals (*B. maritima*); ray cells sometimes perforate; fiber-tracheids with minute pits. Leaves simple, sessile, narrowly elliptic to narrowly oblanceolate, in transverse section nearly triangular to nearly terete with the adaxial surface flattened, rounded to acuminate or mucronate at the apex, with a small deltoid appendage below the insertion; stomata paracytic; stipules paired, inserted on the stem, caducous, blunt, minute, succulent, glandular. Plants dioecious [or monoecious]; staminate flowers (*B. maritima*) 4-ranked, in axillary, ellipsoid, turbinate, or subglobose catkins, these sessile or short-pedunculate and sometimes clustered on short branches, each flower subtended by a broadly ovate, obtuse, and often mucronate fleshy bract, margins membranaceous and erose. [Staminate flowers of *B. argillicola* axillary or terminal (when terminal, flanked by a pair of carpellate flowers), not in catkins, sessile or nearly so, usually on short shoots.] Staminate flowers initially enclosed in a sheath (spathella) that dehisces to form a 2- [sometimes 3- or 4-]lipped cup; tepals (staminodes?) 4 (or 5), white, nonvascularized or with an unbranched midvein, unguiculate [or gradually tapered], the limb abaxially cutinized. Stamens longer than the tepals and alternate with them, exerted beyond the subtending bract; filaments glabrous, [winged]; anthers broadly oblong-elliptic, opening by lateral longitudinal slits, dorsifixed, versatile, [connective prolonged]. Pollen grains yellow (dry), subprolate to prolate, 3- or 4-colporoidate (or 3- or 4-loxocolporoidate), the membrane granular, ovoid region rounded-lolate, sexine solid (without columellae), psilate or nearly so, with local thickenings usually near the equator and often near one or both poles. Carpellate flowers [borne singly in the axils of leaves, usually on short shoots or] (in *B. maritima*) 2-14(-24), arranged decussately in short-pedunculate or sessile, axillary, bracteate, fleshy spikelets, these often clustered on short branches; bracts peltate, caducous, usually broadly ovate to orbiculate, sometimes 3-lobed, the margins erose and membranaceous, rounded to acute and often apiculate at the apex, rounded to cordate at the base. Perianth absent. Gynoecium probably 2-carpellate, 4-locular, the locules uniovulate and filled with parenchyma above the ovule; stigmas 2, fimbriate (extruded stigmatoid tissue); ovules bitegmic, crassinucellar, [slightly campylotropous when young], epitropous, erect. Inflorescence a green, fleshy, roughly cylindrical(-obconic) syncarp with rounded protuberances corresponding to each carpellate flower (apical flowers often not developing), each seed surrounded by a hard layer (composed of elongate, mostly transverse, pitted cells), these

(note decussate arrangement of bracts and flowers), $\times 5$; i, diagrammatic vertical section of inflorescence at level marked by arrow on "j," showing ovules, locules filled with parenchyma (stippled), section to one side of attachment of bracts, $\times 5$; j, diagrammatic cross section at level marked by arrow in "i," section passes through ovules in two locules of each of two flowers, $\times 5$; k, mature syncarp (note scars of stigmas and bracts), $\times 2$; l, single endocarp with seed, $\times 6$; m, embryo oriented as in seed and stone, $\times 6$; n, stem with leaf scar and stipules, inflorescence scar above, $\times 15$.

endocarps (pyrenes) narrowly deltoid, strongly compressed, laterally coherent, (locules often sterile). [Or with a septicidally dehiscent, fleshy fruit derived from one flower, with 4 endocarps (pyrenes).] Seeds without (or possibly with a little) endosperm, club shaped, compressed, the testa membranaceous; embryo slightly curved, compressed, filling the seed, the cotyledons fleshy, oblong, plano-convex, the conical radicle pointing toward the hilum. TYPE SPECIES: *B. maritima* L. (*B. californica* Torrey.) (Name probably from Latin, borrowed from Greek, for another maritime plant or, less likely, from Greek *batos*, bramble, because of the superficial similarity of its syncarps to fruits of *Rubus*).—SALTWORT.

Two species of littoral habitats: *Batis maritima*, common along the east coast of the Americas including the Gulf of Mexico from North Carolina (according to Fulcher not encountered north of South Carolina in recent surveys) to Brazil, throughout the West Indies, along the west coast of the Americas from southern California to northern Peru, on the Galapagos Islands, and in Hawaii (where probably introduced; see Hillebrand, Degener); and *B. argillicola* van Royen, of southern New Guinea and northeastern Australia. There is a doubtful report of an unidentified species of *Batis* in the Marianas Islands ca. 2300 km north of New Guinea (see Fosberg *et al.*).

Only *Batis maritima* is dioecious (*vs.* monoecious), has flowers borne in catkins or spikelets (*vs.* singly or in small clusters), and has highly differentiated bracts subtending the flowers, clawed (*vs.* gradually tapered) tepals, vascular bundles opposite the flat faces of the stem, crystals in parenchymatous tissues, and branches that root. In contrast, some staminate flowers are terminal on short shoots in *B. argillicola*, which also differs in its winged filaments, elongated connectives, smaller leaves, and much stronger tendency toward procumbent cells in the rays. (See further details in van Royen, 1956b, 1958.)

Sunny, periodically wet, saline, maritime habitats seem to be required by both species. They grow in open areas and are often components of mangrove vegetation, especially in association with *Avicennia* (*A. germinans* (L.) L., black mangrove, in the United States). Plants grow either within the stands where abundant light penetrates or adjacent to them, usually on the side opposite open water. In Florida *Batis maritima* has been a major colonizer following loss of mangroves by hurricanes. This species establishes itself on clay, sand, or calcareous substrates on beaches, in salt marshes, in saline mud flats, in hammocks, and in swales on dunes, in addition to growing with mangroves. The plants sometimes form dense tangles and often cover large areas as pure stands. Due to its extensive geographic range and apparent wide ecological amplitude, *B. maritima* is found in association with a variable array of other plants, frequently including *Distichlis spicata* (L.) Greene, and species of *Salicornia* L., *Spartina* Schreber, and *Suaeda* Forskål. ("Batis marshes" are characterized by Craighead; see also Chapman, Davis, Harper, and Rzedowski for information concerning habitat and associates.)

Batis maritima tolerates long periods of waterlogging and a wide range of salinity. Penfound and Hathaway reported it to tolerate a range of 1.33–4.97‰

salt in soil water, and in reference to the salt water marshes of southern Florida, Davis described plants as growing in the most salty situations that will support plant life.

The spongy syncarps of *Batis maritima* float one to two weeks before decay releases the one-seeded endocarps (pyrenes), which float as long as three months until germination (Guppy, 1906, referred to seeds rather than endocarps). Rooting at the nodes seems to enable the development of clones of this species. In tropical regions it flowers throughout the year; in Florida flowering is between April and late summer, mostly early in the season. Fruits are found from midsummer to late autumn; seedlings have been observed during the same period.

The homology of the petallike appendages that alternate with the stamens is unknown; they have been designated petals, tepals, or (most often) staminodes. Johnson considered the cutinized abaxial surface of the limb and the lack of vascular tissue as evidence against their being staminodes, but in *Batis argillicola* the appendages are usually vascularized. They are sometimes so in *B. maritima* according to Eckardt (1960). The spathella opens to resemble a calyx and has been thus interpreted, but is more likely an involucre. Noting that it bears two crests, that it has two basal appendages (as do the foliage leaves), that its two halves continue the decussate phyllotaxy of the shoot, and that there are leaves morphologically intermediate between it and the foliage leaves, van Royen (1956b) and van Heel argued that the spathella in *B. argillicola* is foliar and is homologous to a pair of opposite bracts. The spathella in *B. maritima* receives a single vascular bundle at the base, and some authors (Dammer, 1892; Johnson; van Tieghem) have regarded it as a single unit. In this species the spathella is usually divided by a transverse apical slit with the edges abutting or one overlapping the other; the adaxial side bears a transverse crest, which matches an abaxial thickening on the bract above and usually protrudes beyond the subtending bract. Dehiscence is through the slit or, according to Johnson, by a transverse rift between the original slit and the crest. A central projection has often been observed in some staminate flowers of *B. maritima*. Although this is suggestive of a rudimentary gynoeceium, "imperfect pollen" has been observed in the head of such a structure (Torrey).

It is generally agreed that the gynoeceium is composed of two carpels so joined that the lateral bundles, placentae, and septum lie on a median plane (radial to the axis of the spikelet in *Batis maritima*). The ovary is falsely four-locular by a second perpendicular septum. The median carpellary bundles (which are not consistently present) are in the plane of the false septum (see diagrams in Cronquist; Eckardt, 1960; van Heel). The ovary of *B. argillicola* is unilocular at the base. Although the literature is contradictory about the orientation of the raphe of the ovules, my dissections of *B. maritima* showed that it is abaxial, which agrees with the statements of most observers.

Contrary to earlier descriptions, Fulcher encountered scattered ephemeral clusters of unicellular trichomes toward the ends of branches in *Batis maritima*.

The taxonomic placement of *Batis* is a long-standing and unresolved problem. It has no obvious close relatives; thus the many botanists concerned with this aspect of the genus have variously considered allying it with over 25 disparate families or orders, and they have tended to isolate it at high taxonomic levels. It has consistently been taken to comprise a unigeneric family, and it often stands alone as the order Batales (Batidales); Behnke and Turner elevated it even further as the subclass Batidae. The history of the classification of *Batis* and/or lists of families and orders considered as potential relatives are available in several works, including Eckardt (1960), Fulcher, McLaughlin, and Uphof (1930). A summary emphasizing the recent literature follows.

The reduced, imperfect flowers borne in catkins or spikelets (*Batis maritima*) have led some authors to ally *Batis* with the Amentiferae, where it was most recently placed by Benson. With little explanation Hjeltnquist has opposed this position. Among the catkin-bearing plants the Salicaceae have received the most attention as potential relatives of *Batis* (see Baillon, van Tieghem), but little evidence supports an affinity with this family. The base chromosome number of the Salicaceae is 19, in contrast with $n = 11$ for *B. maritima*. (Goldblatt and Fulcher independently reported $n = 11$, but Engel & Schmidt reported $n = 9$.) After comparing *Batis* to that family, Fulcher concluded an extensive anatomical-morphological study favoring a relationship with the Urticales, possibly as a derivative of Moraceae. Chiefly on the basis of stem anatomy, McLaughlin favored the Centrospermae over the Salicaceae.

Most authors have treated *Batis* as a member of the Centrospermae (Caryophyllales). In habit *Batis* is similar to succulent, halophytic members of the Chenopodiaceae, a resemblance supported by the reduced, imperfect flowers, scarious, uniseriate (or absent) perianths (as well as staminodes), and compact, bracteate inflorescences found among this family and some of its relatives. Moreover, van Heel pointed out that ovules of *B. argillicola* resemble those of various members of the Centrospermae because only the inner integument forms the micropyle; others (Fulcher, van Tieghem) found the micropyle to be formed of both integuments in *B. maritima*.

Rejection of *Batis* as a member of the Centrospermae reflects the modern trend toward emphasizing a suite of technical characters in circumscribing the group. Characters in conflict with its placement in the Centrospermae include seeds with nearly straight (*vs.* curved or coiled) embryos and no perisperm (Eckardt, 1960, 1976), S-type (*vs.* P-type) sieve-tube plastids (Behnke & Turner; Behnke, 1976a), and binucleate, psilate (*vs.* trinucleate, spinulose, tubuliferous/punctate) pollen grains without columellae (Behnke, 1976b; Fulcher; Prijanto, 1970b; Skvarla & Nowicke). RNA-DNA hybridization (Chang & Mabry) and the chromosome number (Goldblatt) likewise favor exclusion. *Batis* lacks betalain pigments, one of the best-known characteristics of the Centrospermae, but also lacks anthocyanin (Mabry & Turner). Because all of these technical characters—except those connected with the morphology of the pollen and seeds—are reported only for *B. maritima*, confirmatory research on *B. argillicola* is desirable.

Batis maritima also differs from the Centrospermae in that it produces myrosinase. Since this enzyme acts on glucosinolates, its presence supports linking *Batis* to the glucosinolate-producing families of the Capparales (Schraudolf *et al.*). Benzylglucosinolate was later confirmed as present in *B. maritima* (Ettlinger *vide* Mabry, 1976). Essentially the same circle of affinity was indicated when Pulle allied the Batales with the Rhoeadales (brief discussion in Eckardt, 1960, 1964). Other characters that *Batis* shares with members of the Capparales include seeds without endosperm, minute stipules, and paired carpels. Placement in or close to the Capparales is consistent with chromosome data (Goldblatt). Moreover, if *Batis* has parietal placentae, a replum in the ovary, and staminodes, these characters provide additional ties to the Capparales.

The Australian family Gyrostemonaceae also produces glucosinolates (Ettlinger & Kjaer) and, like *Batis*, is outstanding in having these compounds but lacking myrosin cells (Carlquist, Rodman). They are also alike and unusual in their psilate (to slightly scabrous in the Gyrostemonaceae) pollen grains with a solid sexine, although *Batis* differs in having compound apertures without opercula (Erdtman; Prijanto, 1970b). The Gyrostemonaceae resemble *Batis* in the absence of betalain and anthocyanin pigments and in having S-type sieve-tube plastids (Goldblatt *et al.*). Additional similarities include succulence, shrubbiness, wide multiseriate rays, storied xylem parenchyma cells resembling short fibers, linear leaves with minute stipules, and reduced, imperfect flowers with uniovulate locules. Van Royen (1956b) mentioned the "striking resemblance" of *B. argillicola* to *Gyrostemon* Desf., as well as to other groups. The presence of both genera in Australia is consistent with this apparent relationship (Carlquist).

However, Goldblatt *et al.* thought that different chromosome numbers indicate that the relationship between *Batis* and the Gyrostemonaceae might not be close (in Gyrostemonaceae $x = 14, 15$). Other traits by which *Batis* differs from the Gyrostemonaceae are paracytic (*vs.* anomocytic) stomata, opposite leaves, spatheas, fewer stamens, lack of diffuse xylem parenchyma, four-locular ovaries with basal-parietal (*vs.* axile) placentae, seeds without arils and endosperm, and nearly straight embryos (*cf.* Carlquist, Cronquist, Thorne). Cronquist included the Gyrostemonaceae in the Batales, which he allied to the Capparales. Goldblatt *et al.* favored placement of *Batis* and the Gyrostemonaceae in the Capparales, which is the placement these taxa received from Dahlgren *et al.* It should be noted that pollen of *Batis* and members of the Gyrostemonaceae is anomalous in that order (Erdtman; Goldblatt *et al.*). Furthermore, glucosinolates are not restricted to the Capparales as usually circumscribed; they are reported, for example, in the Caricaceae, Euphorbiaceae, Limnanthaceae, and Salvadoraceae (Rodman).

Carlquist discussed the possible presence of such compounds among the Sapindales. Drawing mostly upon general morphology and wood anatomy, he considered sapindalean affinities for both *Batis* and the Gyrostemonaceae most likely but regarded them as distinct from each other. Some other modern systematists agree that a position in or near this order is best. Takhtajan thought the Bataceae and the Gyrostemonaceae were related and placed both

in the Sapindales. Thorne tentatively put his suborder Batineae "following" the Gyrostemonaceae (in the Sapindineae) among the Rutales.

The salty leaves and stems of *Batis maritima* are sometimes pickled, used as poultices, and eaten fresh in salads, but the plant is suspected of being poisonous (Duncan; Perkins & Payne). As is true of other halophytes, plants of this species have been burned for ash, which was used in making soap, glass, and medicines. In countries where Spanish is spoken, the colloquial name *barilla* is (was?) commonly associated with the ash and plants of *B. maritima* but is not unique to this species. Various derived preparations have evidently been used to prevent and treat skin disorders, tuberculosis, syphilis, scurvy, and ulcers, and some have been used as a diuretic, as an analeptic, and to remove stones from the bladder and kidneys (see Burlage, Descourtiz, Grosourdy). In Hawaii *B. maritima* has been planted on reclaimed land to suppress wind-blown dust.

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THE GENERA OF OLACACEAE IN THE
SOUTHEASTERN UNITED STATES¹

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OLACACEAE Mirbel ex A. P. de Candolle, Prodr. 1: 531. 1824,
"Olacineae," nom. cons.

(OLAX FAMILY)

Trees or shrubs, sometimes sprawling, mostly glabrous, photosynthetic root parasites [or free-living autotrophs]; unarmed or armed with spines [or hooks]. Leaves alternate, simple, entire, sometimes undulate, evergreen, pinnately veined, petiolate, lacking stipules. Inflorescences axillary few-flowered dichasia, racemes, panicles, or fascicles; bracts sometimes calyciform. Flowers perfect [or infrequently imperfect, and the plants then dioecious], sometimes heterostylous, actinomorphic, mostly small. Calyx 4- or 5-lobed or indistinct and adnate to the ovary [sometimes accrescent and colorful]. Petals 4 or 5, free or connate into a cup or tube, mostly valvate in aestivation. Stamens the same number as the petals and opposite them or 2

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This paper has been written with the generous support of the Illinois Natural History Survey. The vast library facilities of the University of Illinois have been used extensively to check the references. The libraries and herbaria of the Field Museum of Natural History and the Missouri Botanical Garden were also utilized. Specimens of *Schoepfia* and *Ximenia* were loaned by the University of Florida. Information on *Schoepfia* was also supplied by James B. Watson, of the Fairchild Tropical Garden; Daniel F. Austin, of Florida Atlantic University; and Richard P. Wunderlin, of the University of South Florida. Special appreciation is extended to Carroll Wood and Norton Miller for their enthusiasm and dedication to maintaining the high standards for papers in this series. The editorial advice of Stephen A. Spongberg is also acknowledged. The plate of *Ximenia* and *Schoepfia* was drawn by Karen Stoutsenberger under my direction from preserved material collected by C. E. Wood, Jr., the late W. T. Gillis, P. B. Tomlinson, and K. R. Robertson; the fruit of *S. Schreberi* is from J. A. Harris C17123 (GH). Dr. H. Sleumer (Rijksherbarium, Leiden), who is preparing treatments of the family for the *Flora Malesiana* and *Flora Neotropica*, has generously given information from his manuscripts.

[3] times as many and in 2 whorls; staminodia absent [or present]; filaments free or adnate to the corolla [or connate into a tube]; anthers 2-locular, opening by longitudinal [or apical] slits; disc usually present, annular, more or less adherent around the base (*Ximenia*) or apex (*Schoepfia*) of the ovary. Gynoecium of 2-5 united carpels; ovary superior and sessile or inferior, 2- to 5-locular above and below [or 1-locular above]; style simple, terminal, usually elongate, sometimes heterostylous; stigma terminal, entire or 2- to 5-lobed; ovules 1 per locule, pendent from an axile [or free-central] placenta, anatropous or rarely apotropous, tenuinucellar, the micropyle superior, the integuments absent or 1 or 2. Fruit usually a 1-seeded drupe, the endosperm abundant, *ab initio* cellular or Helobial in formation, the embryo straight, minute, apical. TYPE GENUS: *Olax* L.

A morphologically diverse family of about 27 genera and 260 species of the tropics and subtropics. Eight genera are restricted to the New World, six to Asia/Malesia, and five to Africa; three genera occur in both Africa and the Americas, and three are present both in Africa/Madagascar and Asia/Malesia; *Ximenia* and *Schoepfia* are pantropical. Approximately eight genera are monotypic, six have only two or three species, and six have more than ten species. The largest genus in the family is *Heisteria* Jacq., with ca. 65 species in the Americas and three in tropical West Africa. *Olax* is composed of about 50 species of Africa, India, Asia, Malesia, New Guinea, Australia, and Micronesia. The third largest genus is *Schoepfia*, with about 38 species; none of the other genera exceeds 20 species.

In the most recent complete treatment of the family (Sleumer, 1935), three subfamilies are recognized: Dysolacoideae Engler (with four tribes), Olacideae (with two tribes), and Schoepfioidae Engler (with only one genus). This scheme was modified somewhat by Schultze-Motel, who included subfamily Dysolacoideae (and its tribes) within subfamily Schoepfioidae; in addition, the genus *Octoknema* Pierre, treated as a distinct family in *Die natürlichen Pflanzenfamilien*, is included in the Olacaceae as tribe Octoknemeae of subfamily Schoepfioidae.

The placement of Olacaceae at the ordinal and higher levels is confusing, both taxonomically and nomenclaturally, because phylogenists have frequently differed widely in their circumscription of related families, suborders, orders, superorders, and classes. The situation is compounded because there are a number of small genera and families that are frequently allied with Olacaceae. Eighteenth- and nineteenth-century botanists grouped the Olacaceae, in different systems of classification, with numerous families, including Berberidaceae, Humiriaceae, Meliaceae, Pittosporaceae, Rutaceae, Sapotaceae, Styracaceae, and Theaceae. The original suggestion of Robert Brown (1810) that these plants might be allied with Santalaceae was ignored until adopted by both Baillon and Engler. This alignment has been followed in most, although not all, subsequent systems of classification, and for some time there has been general agreement that Olacaceae are closely related to Opiliaceae, Santalaceae, Loranthaceae, Viscaceae, and Misodendraceae. These are considered to be the base families of the order Santales by Cron-

quist, Dahlgren, Kuijt, Schultze-Motel, Takhtajan, and Thorne. Kuijt (1968) stated that "Olacaceae thus emerge as the plexus from which all other Santalalean families take their origin." Hutchinson, Metcalfe and Chalk, and Reed place the Olacaceae, Opiliaceae, and some other small families in the order Olacales, which is still allied with Santalales. Phylogenists concur that the Santalales/Olacales complex is allied with Celastrales and Rhamnales.

Species belonging to at least five genera, including the two in our area, are known to be green-leaved root-parasites. One species, *Heisteria longipes*, is autotrophic (Kuijt, 1969). More studies of additional genera and species are needed.

Chromosome numbers have been reported from only a few species: *Ximenia americana*, $2n = 26$; *Lepionurus sylvestris* Blume, $2n = 20$; *Olex nana* Wallich, $2n = 24$; *Schoepfia fragrans* Wallich, $2n = 24$; *Heisteria parvifolia*, $2n = 38$; and *Strombosia glaucescens* var. *lucida*, $2n = 40$.

The pollen of the Olacaceae is quite diverse. The grains may be 3-colpate, 3-colporate, 3-colporoidate, 3- or 4- (or 5-)porate (angulaperturate), 6-forate (3-diploforate), or brevicolporate. The texture of the exine varies from smooth, minutely verrucose, finely reticulate, or tectate-perforate to prominently reticulate or with massive crustose ornamentation around the mesocolpal areas. Lobreau-Callen presents a detailed comparison between pollen of the Olacaceae and Icacinaceae and also has a table comparing pollen type, secondary xylem perforations, and nodal anatomy.

The number of integuments of the ovule varies from two to none in the Olacaceae, and this has been used as a primary character in defining the subfamilies and tribes. In other families that include parasitic species there is a general correlation between the parasitic habit and a reduction in the number of integuments; this also appears to be the case in the Olacaceae, although information is far from complete. An unusual morphological peculiarity of some members of the Olacaceae is the presence of more than two cotyledons in the embryo. Tribes Colueae and Heisterieae usually have three or four cotyledons, the Olaceae and *Schoepfia* may have two or three, and *Octoknema* (see above) can have up to eight. The related Opiliaceae usually have three or four cotyledons, and the Loranthaceae frequently have two to six. The vascular anatomy of the Olacaceae is also diverse. The leaf bundles are unilacunar, trilacunar, or rarely pentalacunar, and the secondary xylem varies from primitive to advanced with regard to type of perforations, pore distribution, imperforation of elements, wood parenchyma, and ray types (Reed).

Although it might appear from the number of references listed below that Olacaceae have been studied rather extensively (and, for a tropical family, they have been), the family is poorly known in comparison with others in the Santalales. The morphological, anatomical, palynological, and cytological diversity that has been observed thus far, as well as the hemiparasitic nature of some (most?) species, the interesting phytogeographical patterns, and the possibility of well-developed breeding systems and dispersal mechanisms, is tantalizing and indicates that much can be learned from further research, especially that which includes detailed field observations.

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KEY TO THE GENERA OF OLACACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: Mostly evergreen trees and shrubs, glabrous, armed with spines or not, free-living autotrophs or photosynthetic root parasites; leaves alternate, simple, entire, estipulate; inflorescences few-flowered axillary dichasia, racemes, panicles, or fascicles; flowers usually perfect, sometimes heterostylous, actinomorphic, small; perianth of 4 or 5 small sepals and free or connate petals; androecium of 4 or 5 antepetalous stamens or 8-10 in 2 whorls; gynoecium of 2-5 united carpels; ovary superior or rarely inferior, 2- to 5-locular, each locule with 1 anatropous ovule pendulous from an axile placenta, integuments absent or 1 or 2; fruit a 1-seeded drupe with abundant endosperm and a straight, minute, apical embryo.

Branches armed with spines; corollas 6-8 mm long; stamens twice as many as the corolla lobes; ovary superior; fruit yellow, 2-3 cm in diameter. . . . 1. *Ximenia*.
Branches unarmed; corollas 2-3 mm long; stamens the same number as the corolla lobes; ovary inferior; fruit red to black, 5 mm in diameter. . . . 2. *Schoepfia*.

1. *Ximenia* Linnaeus, Sp. Pl. **2**: 1193. 1753; Gen. Pl. ed. 5. 500. 1754.

Trees or shrubs, mostly root parasites; branches of three types: long-shoots with elongate internodes, determinate spine-tipped short-shoots arising from leaf axils of long-shoots, and short spur-shoots produced at the base of each spine branch. Leaves ovate or elliptic [lanceolate, obovate, or orbicular], subcoriaceous, glabrous or glabrescent, the apices emarginate and mucronate, the bases cuneate to obtuse; petioles short, slender, grooved. Inflorescences few-flowered cymes or clusters produced mostly from the axils of a leaf or bract on short-shoots. Flowers fragrant, perfect [or imperfect], pedicellate. Calyx lobes 4 (or 5), small, subtending the corolla, initially valvate in aestivation, not accrescent. Petals 4 (or 5), yellowish to white, free to the base, reflexed, abaxially glabrous, adaxially bearded with 2 dense rows of long trichomes, the petal apices each with a knob that in bud interlocks with those of other petals, valvate in aestivation. Stamens [4 or] 8(-10), partially obscured by the corolla trichomes, 4 (or 5) antepetalous and 4 (or 5) anteseptalous; filaments free, elongate, dorsifixed near the base of the anthers; anthers linear, 2-locular, opening laterally, evidently dehiscent while still in bud; pollen grains tricolporate, binucleate when shed. Disc prominent, surrounding base of ovary. Ovary superior, elongate-conical, base swollen,

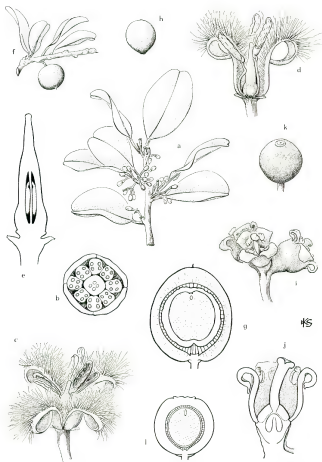


FIGURE 1. *Ximenia* and *Schoepfia*. a-h, *X. americana*: a, tip of branch with flower buds, some leaves removed, $\times \frac{3}{4}$; b, cross section of flower bud with four petals (note adaxial trichomes), eight anthers (the locules stippled), and gynoecium with four ovules, $\times 12$; c, open flower, six anthers shown, two having fallen off, $\times 5$; d, flower, two petals and four stamens removed, $\times 5$; e, gynoecium in vertical section (note two pendent, anatropous ovules, and disc at base of ovary), $\times 12$; f, branchlet

slightly constricted above, 4-locular; style shorter than to equaling ovary; stigma entire, small; ovules linear, anatropous, solitary in each locule, pendent from an axile placenta at top of locule, with 1 integument and a dorsal raphe. Fruit a yellow [red, orange, or purple], 1-seeded, ovoid to ellipsoid, or subglobose drupe; endocarp crustaceous or subligneous, ovoid, minutely pitted, light reddish-brown; seed filling endocarp, seed coat white, thin and spongy; endosperm abundant, rich in oil; embryo minute, apical. LECTOTYPE SPECIES: *X. americana* L.; see N. L. Britton & C. F. Millspaugh, *Bahama Fl.* 112. 1920, and A. S. Hitchcock & M. L. Greene, *Int. Bot. Congr. Cambridge Nomencl. Prop. Brit. Bot.* 195. 1929. (Name commemorating Francisco Ximenes (died 1612), a Dominican priest who translated "Cuatro libros de la naturaleza y virtudes de las plantas y animales que estan recevidas en el uso de medicina en la Nueva-España," by Francisco Hernández, published in Mexico in 1615, the first book on plants published in the New World; see Quinby.)

According to DeFilipps, the most recent monographer, eight species and 12 taxa mostly of tropical and subtropical regions of the Americas, with *Ximenia americana* L. occurring pantropically and *X. Caffra* Sonder in Africa and Madagascar. Most taxa of the genus are xeromorphic and occur in dry, rather severe habitats, such as savannas and scrublands. The genus is represented in our area by *X. americana*, tallow-wood, hog plum, a spinescent, straggly shrub or small tree that occurs fairly frequently in hammock margins, scrublands, coastal sand dunes, sand ridges, shell mounds, and pinelands throughout much of peninsular Florida and the Florida Keys; it is largely absent from the Everglades except on the Everglade Keys. DeFilipps recognized three varieties of *X. americana*: var. *americana* (pantropical—Florida, the West Indies, Mexico and Central America, South America, Africa, Asia, Malesia, Australia, and Pacific Islands); var. *argentinensis* DeFilipps (Argentina); and var. *microphylla* Welw. ex Oliver (Africa).

Ximenia americana is a facultative root-parasite, and plants can grow indefinitely from seed in greenhouse cultivation in pots that do not contain a host plant. In cultivation, parasitism seems to cause neither a visible increase nor a decrease in vigor of either the parasite or host, and under certain conditions haustoria are produced that either attack the parasite's own root system or attach themselves to nonliving objects such as stones, plastic, and charcoal. The haustoria of *X. americana* may be up to 3 cm in diameter, the

with leaves and nearly mature fruit (note small spine at tip of branchlet), $\times \frac{1}{2}$; g, fruit in vertical section, mesocarp stippled in rows, endocarp wall hatched, fleshy inner layer unshaded, endosperm stippled, minute apical embryo unshaded, $\times 2$; h, endocarp removed from fruit, $\times 1$. i–l, *S. Schreberi*: i, cluster of three flowers, $\times 5$; j, flower in vertical section, apex of ovary covered by large disc, $\times 10$; k, fruit, a drupe from an inferior ovary, $\times 2$; l, fruit in vertical section, mesocarp unshaded, endocarp wall hatched, inner layer unshaded, endosperm stippled, embryo near apex unshaded, $\times 3$.

largest of any North American root parasite! Hundreds of haustoria can be produced on the roots of a host species in a single season, and some reports indicate that *X. americana* can cause serious damage in Southeastern forests. (See DeFilipps, Heckel, and Musselman & Mann for information on the parasitic nature of *Ximenia*.)

The flowers of *Ximenia americana* are very fragrant, sometimes likened to jasmine (*Jasminum*, Oleaceae), and are presumably insect pollinated. The only report of compatibility for the species (Zapata & Kalin Arroyo) showed that 334 flowers artificially self-pollinated on seven trees produced no fruit, while artificial cross-pollination of ten flowers on two trees resulted in the production of one fruit.

According to DeFilipps (1976), the fruits of *Ximenia americana* have two types of dispersal mechanisms, which account for its wide geographic distribution. First, the fleshy drupes are eaten by various animals, such as birds and monkeys; second, the pit (endocarp) has an air-filled tissue beneath the outer wall, and the fruits can be water-borne for several months. The seedlings of *X. americana* are unusual in that the first-formed leaves (cataphylls) grow downward into the seed to the space between the petioles of the cotyledons, although no fusion of tissue takes place (see Musselman & Mann). Tomlinson (family references) gives a detailed description of the phenology and growth pattern of the species.

Ximenia belongs to subfamily Dysolacoideae Engler (ovules anatropous with a dorsal raphe and one or two integuments; calyx not accrescent in fruit; ovary superior), which according to Sleumer (1935, family references) includes 16 genera in four tribes. *Ximenia* is the only genus in tribe Ximenieae Engler (hemiparasitic, spinescent trees or shrubs; leaves and bark lacking resin canals or latex tubes; stamens usually twice as many as the petals, half antepetalous, half antepetalous; ovules with one integument).

The endocarps of *Ximenia americana* are rich in oil, and it has been suggested that the species could be grown as a crop in hot, dry areas with poor soil, but this has not yet proven to be feasible.

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2. *Schoepfia* Schreber, Gen. Pl. **1**: 129. 1789.

Unarmed, glabrous, evergreen root-parasitic trees [or shrubs]; distal shoots sympodially branched. Leaves alternate, subcoriaceous, entire or obscurely toothed, elliptic to ovate [obovate, oblanceolate, or spatulate], the apices acute to acuminate [rounded or obtuse]; petioles short, faintly winged. Inflorescences short axillary clusters [or racemes] of 2- or 3-flowered dichasia [or the flowers solitary]; bracts and bracteoles fused to form a 2-lobed, calyx-like structure. Flowers perfect, heterostylous [or not?], sweet scented. Calyx cup shaped, the rim entire or slightly lobed, slightly dilated. Petals 4 or 5, connate into a cylindrical-urceolate [to rotate] tube, orange, pink, red [yellow or greenish], slightly bearded just above the anthers, the tips recurved [or erect] at anthesis and sometimes pubescent. Stamens 4 or 5, adnate to the corolla tube, opposite the petals, included in long-styled flowers, very shortly exerted in short-styled flowers; anthers nearly sessile. Ovary inferior, topped by a thick disc, mostly 2-locular in 4-merous flowers and 3-locular in 5-merous flowers; each locule with an apotropous ovule pendent from an axile placenta; style 1, included in short-styled flowers, shortly exerted in long-styled flowers; stigma terminal, thicker than the style, 2- or 3-lobed. Fruit a fleshy ovoid [ellipsoid or subglobose], red [or yellow] drupe, turning black

at maturity [or not], surmounted by the persistent calyx ring; flesh reddish [or whitish]; endocarp crustaceous; seed solitary, nearly filling the endocarp; endosperm abundant; embryo minute, apical. TYPE SPECIES: *S. Schreberi* J. F. Gmelin. (Name commemorating Johann David Schoepf, 1752–1800, a German physician and botanist who traveled in North America and the West Indies.)

According to Sleumer (pers. comm. and 1980, family references), a genus of 23 species in three sections. Section SCHOEPFIA (sect. *Codonium* (Vahl) Endl.), the largest (19 species), is restricted to the tropics of Central and South America and the West Indies, with one species reaching peninsular Florida. Section SCHOEPFIOPSIS (Miers) Engler includes three species of southeastern Asia (Tibet/China border, China, Macau, Hong Kong, and Japan), and sect. ALLOSCHOEPFIA Sleumer (sect. *Euschoepfia* Engler) is composed of a single species, *S. fragrans* Wallich, which occurs in southeastern Asia and western Malesia (Nepal, Bhutan, eastern Bengal, Assam, Burma, Yunnan province of China, Thailand, Indochina, and northern Sumatra).

Schoepfia Schreberi J. F. Gmelin (*S. chrysophylloides* (A. Rich.) Planchon), graytwig, whitewood, is a shrub or tree to 10 m tall with trunks to 30–45 cm in diameter. It occurs locally, sometimes in abundance, in hammocks, pinelands, and coppices, and on limestone, coral rock, or sand, in Florida from the Everglade Keys northward along the eastern coast to Volusia County and along the western coast to Pinellas County (reports of this species from the Florida Keys may be the result of mistaking Long Key in the Everglades for the island Long Key). This is a wide-ranging species in the West Indies, Mexico, Central America, and northern and western South America.

Schoepfia Schreberi is a photosynthetic root parasite that is not host specific—it has been reported to parasitize the roots of ten different species, both dicots and monocots, in Florida and the Bahamas (Werth *et al.*, 1978, 1979; Piehl, 1973; and Musselman & Mann, 1978). The haustoria are similar to those found in other Santalales but have a distinctive conical or dome shape.

Within the Olacaceae, *Schoepfia* is very distinctive and is the only member of subfam. Schoepfiodeae Engler. Reed (1955, family references), on the basis of wood anatomy and floral morphology, considered the genus to be the most specialized in the family. The calyx is mostly absent, being represented by a lobed ridge at the base of the ovary. The bract and two bracteoles that subtend each flower are united into a cup-shaped, calyciform involucre that encloses the lower part of the flower. The ovary is inferior and two- or three-locular, with each locule containing a single apotropous ovule that lacks integuments. The flowers of *S. Schreberi* are heterostylous, and other members of the genus should be examined carefully for this feature.

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ILLINOIS NATURAL HISTORY SURVEY
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THE VISCACEAE IN THE SOUTHEASTERN UNITED STATES¹

JOB KUIJT

VISCACEAE Batsch, Tab. Affinitatum Regni Veg. 240. 1802, "Viscinac."

(MISTLETOE FAMILY)

Shrubs or herbaceous perennials parasitic on a great variety of host plants, usually foliaceous with decussate [rarely alternate] phyllotaxy, the nodes showing constrictions, the plants thus appearing jointed. Leaves simple and often succulent [rarely squamate], persistent, estipulate, the margins entire. Mode of attachment simple, but haustorial organ usually much fragmented within host. Flower small and inconspicuously colored, actinomorphic, in spikes [or other inflorescences], imperfect, the plants dioecious [or some monoecious]. Perianth uniseriate, consisting of 3 or 4 members, fused with the inferior ovary; or with 1 stamen each and arranged around a central cushion. Anther variously constructed but usually sessile on a perianth member; pollen spheroidal, tricolporate, isopolar, and somewhat echinate. Stigma and style scarcely differentiated; ovarian cavity exceedingly inconspicuous, the ovules undifferentiated, the megaspore mother-cells arising from a centrally located papilla, the usually single seed, therefore, without a proper seed coat. Fruit a 1- (or 2-)seeded berry with viscid tissue surrounding a large chlorophylliferous endosperm and 1 (or 2) straight and poorly developed embryos. (Loranthaceae subfam. Viscoideae Engler, Nat. Pflanzenfam. III. 1: 177. 1889. Excluding Loranthaceae A. L. de Jussieu, Ann. Mus. Natl. Hist. Nat. 12: 292. 1808, "Loranthae," nom. cons., and Eremolepidaceae Van Tieghem ex Kuijt.²) TYPE GENUS: *Viscum* L.

¹Prepared for the Generic Flora of the Southeastern United States, a project of the Arnold Arboretum currently made possible through the support of the National Science Foundation, under Grant DEB-81-11520 (Carroll E. Wood, Jr., and Norton G. Miller, principal investigators). This treatment, the 92nd in the series, follows the format established in the first paper (Jour. Arnold Arb. 39: 296-346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets [].

The illustration of *Phoradendron* was begun in early January, 1964, by the late Dorothy H. Marsh (who drew parts a, b, and g) under the supervision of Carroll Wood, but because of Mrs. Marsh's failing health it could not be completed then. Much later, Karen Stoutsenberger drew the remaining items from dissections made by Kenneth R. Robertson. The materials for the illustration were either living plants from Floyd County, Virginia, or alcohol-preserved specimens of these (a, b, g-l) and specimens from the Gray Herbarium (c-f, Small, Mosier, & Small, 1928, St. Lucie County; Craighead, Popenoe, & Campbell, 1963, Monroe County, Florida).

²*Eremolepidaceae* Van Tieghem ex Kuijt (*Eremolepidacées* Van Tieghem, Compt. Rend. Acad. Sci. Paris 150: 1717. 1910, nomen invalidum; *Eremolepidaceae* Van

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A family of seven genera and 400 species, primarily tropical, but reaching well into Temperate zones on various continents. All genera but *Arceuthobium* Bieb. are restricted to either the New World or the Old. *Phoradendron* Nutt. is represented in our area by only two species, one widespread and the other in southernmost Florida. The only other North American genus of the family, *Arceuthobium*, dwarf mistletoe, is unknown from the southeastern United States, except as pollen in Pleistocene deposits in the Carolinas and Georgia (see Whitehead & Barghoorn and Watts). At present, the nearest station of the eastern dwarf mistletoe, *A. pusillum* Peck, which parasitizes *Picea mariana* (Miller) BSP., black spruce, and *P. glauca* (Moench) Voss, white spruce, appears to be some 500 miles to the north, in northern Pennsylvania. Other species of *Arceuthobium* are sometimes serious pests on conifers in western North America (see Hawksworth & Wiens).

The Viscaceae have been treated by various authors either as a family or as subfam. Viscoideae of the Lorantheae, the other subfamily being the Lorantheae. The small neotropical family Eremolepidaceae has frequently been regarded as part of the Viscaceae, but it warrants separate familial status on the basis of pollen (Feuer & Kuijt, 1978), the predominance of alternate phyllotaxy, and catkinlike inflorescences, as well as the occurrence of epicortical roots in two of its genera. Viscaceae and Lorantheae are usually easily distinguished: the "showy mistletoes" belong to the Lorantheae, while those with inconspicuous flowers are usually members of the Viscaceae. In addition to the minute flowers with a single whorl of perianth members, the Viscaceae are characterized by a fruit with the viscous layer *within* the vascular bundles, a single embryo sac of the Allium type, an embryo with a very short suspensor or none, stamens opposite the perianth segments, the anther opening by pores or transverse slits, spherical pollen, a zygote in which the first cleavage is horizontal, and simple endosperm. In contrast, the Lorantheae usually have perfect flowers with two perianth whorls (the outer one greatly reduced to a calyculus), a fruit with the viscous layer *outside* the vascular bundles, several embryo sacs of the Polygonum type, an embryo with a very long, multiserial suspensor, stamens opposite the petals, anthers opening longitudinally, pollen mostly trilobate, zygote with the cleavage vertical, and compound endosperm.

Barlow (1964), in pointing out these differences, noted that "most of the characters that the two families have in common are also features of the Santalaceae, where hemiparasitism is common (mostly root parasitism) and there are various degrees of reduction and suppression of ovules and elongation of embryo sacs (Johri & Bhatnagar, 1961). It is most likely that the two groups have had independent origins from ancestral stocks in the San-

Tieghem emendavit Kuijt, Brittonia 20: 140. 1968, nomen invalidum).

Plantae parasiticae epiphyticae dioeciae radicibus epicorticalibus evanidis et foliis alternis. Inflorescentiae amenta vel spicae subtentae squamis imbricatis. Flores parvi sessiles monochlamydei; perianthium masculinum tri- vel quadripartitum; perianthium foemineum bi- vel tripartitum. Stamina 3 vel 4 distincti lobis perianthii opposita; antherae biloculares. Ovarium inferum (vel semisuperum). Fructus destitutus staminodia setiformes, textura viscida; endospermium viride; cotyledones embryonis duo. TYPUS: *Eremolepis* Grisebach.

talaceae, so that by placing them in a single family they constitute a diphyletic and therefore unnatural group. The new characters which the groups share are the aerial habit, which in fact has been discovered in several other families of Santalales and which therefore has probably originated several times, and the baccate fruits, which are a consequence of the aerial habit and of independent development. . . . The Loranthaceae and Viscaceae are thus relatively uniform groups characterized by a high degree of reduction in the ovary and by a hemiparasitic habit, these being features also of the Santalaceae, from which they have independently arisen." Kuijt (1968) has subsequently suggested that the Viscaceae and the Loranthaceae are derived from the Santalaceae and the Olacaceae, respectively. The Viscaceae extend into the Temperate Zones of Eurasia and North America, while the Loranthaceae are almost exclusively tropical and subtropical.

It is commonly accepted that mistletoe parasitism involves the transfer of water and inorganic materials from the host to the parasite, which synthesizes its own organic requirements. However, even squamate mistletoes such as *Arceuthobium*, which appear to lack chlorophyll, have at least some. This simple picture of mistletoe parasitism has been complicated considerably by the discovery of the transfer of significant amounts of photosynthates from the parasite to the host—in a sense, an inversion of parasitism.

Host preference also appears to be exceedingly complex. Tropical mistletoes generally show little specificity as to host, although interesting exceptions do exist. If one scans the list of host records of a mistletoe of the Temperate Zone, such as *Phoradendron serotinum* (*P. flavescens*), one gains the impression of a similarly indiscriminating parasite. Lists of hosts, however, tend to obscure significant local differences in preference (see Baldwin & Speese under *Phoradendron*). The possibility of parasitic races seems to be a very real one, although genetic variability in the resistance of the host has too often been ignored as an alternative or additional possibility.

A remarkable embryological peculiarity seems to be restricted largely to the Loranthaceae. The megagametophyte in these plants is an intrusive structure that grows out into the carpel wall and up into the style. The height to which the megagametophyte ascends appears to provide a generic character of some taxonomic stability. It has been demonstrated in some that the megagametophyte may actually reach the stigmatic surface and thus be exposed to the air. Here the egg cell awaits fertilization, after which the proembryo is pushed back down the style to the original point of origin of the gametophyte. The megagametophyte thus seems to have usurped the function of the pollen tube. Unfortunately, the neotropical Loranthaceae are very poorly known in this respect. Members of the Viscaceae seem to have a more orthodox embryology, but apogamy has been reported in *Dendrophthora* Eichler.

The Viscaceae are characterized by two main chromosome groups, the first (including *Arceuthobium*, *Phoradendron*, and *Dendrophthora*) with $x = 14$, the second (*Viscum*) with $x = 10, 11, 12$, and 13 (Wiens & Barlow). There are significant cytological differences between the Viscaceae, the Eremolepidaceae, and the Loranthaceae (see also Barlow & Wiens).

Modern pharmacology has given a certain amount of credence to some of the mistletoe's early uses in folk medicine (see Gill & Hawksworth). Virtually all such work, however, is based on the European *Viscum album* L. Both *Phoradendron* and *Arceuthobium* are unimportant in the materia medica of North America. The berries of *Phoradendron* "contain toxic amines which cause acute stomach and intestinal irritation with diarrhea and slow pulse" (Hardin & Arena) or even death (see *Phoradendron*).

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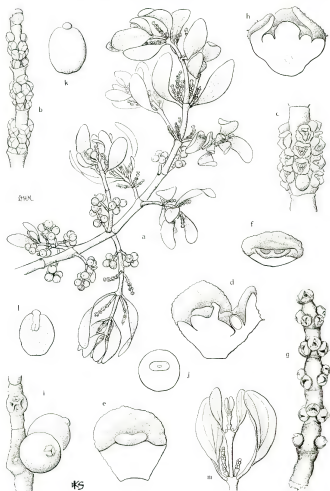


FIGURE 1. *Phoradendron*. a-l, *P. serotinum*: a, portion of carpellate plant with fruits on growth of the previous year and flowers on growth of the current year, $\times 1$; b, tip of inflorescence before flowers have opened, $\times 8$; c, detail of one fertile internode of staminate inflorescence with flowers at anthesis, $\times 12$; d, staminate

1. **Phoradendron** Nuttall, Jour. Acad. Nat. Sci. Philadelphia II. 1: 185. 1847.

Foliaceous [or squamate] shrubby parasites on the branches of woody angiosperms [or gymnosperms], with or without basal cataphylls on lateral branches. Absorptive organ a diffuse and anastomosing system of rootlike strands spreading out laterally into host cortex and phloem, giving rise to radial sinkers through phloem and into wood; secondary haustorial organs absent. Leaves [often] somewhat fleshy. Inflorescence 1–3 axillary [or terminal] spikes in which flowers are produced by intercalary action in 2 or 3 [to several] more or less regular longitudinal series, each resulting flower area topped by a single apical flower in a median position with regard to the bract. Flowers very small, 3- or 4-merous, imperfect [both staminate and carpellate flowers occurring on the same spike] or the plants dioecious. Staminate flower with a sessile, bilocular anther attached to the middle of each perianth segment, the flower terminated by a central cushion and papilla. Carpellate flower consisting of 3 perianth segments united with the unilocular ovary; ovules reduced to a central papilla within which 2 megagametophytes (embryo sacs) develop; stigma sessile, scarcely differentiated. Fruit a berry with 1, rarely 2, seeds consisting of endosperm with embryo and surrounded by viscous tissue. TYPE SPECIES: *P. californicum* Nuttall. (Name from Greek *phor*, thief, and *dendron*, tree, in obvious reference to the parasitism of the plant.)—MISTLETOE.

A large genus distributed from the United States to Argentina, the number of species vastly exaggerated in the only existing generic treatment (Trelease, 1916), which recognized 240. A large number of species have since been added, but it is probable that a reasonable revision of the genus would reduce the total to a hundred or fewer. The primary division of the genus into "Boreales" (lacking cataphylls) and "Aequitoriales" (bearing cataphylls), rank unspecified, seems, in the dim light shed by Trelease's monograph, to be generally workable. *Phoradendron* is closely related to—and often difficult to distinguish from—*Dendrophthora*, a strictly tropical genus (Kuijt, 1961).

A few species are present in the western United States, but only two occur in the Southeast. Of these, *Phoradendron rubrum* (L.) Griseb., a cataphyllous species reported by Cooley (1963) as a parasite on mahogany (*Swietenia Mahagoni*), although widespread in the West Indies, is restricted to south-

flower in vertical section, one sessile anther shown in section to right, disc and sterile gynoecium in center, $\times 50$; e, one perianth lobe removed from flower to show sessile anther, $\times 50$; f, same, from above, to show dehiscence of anther by two apical pores, $\times 50$; g, carpellate inflorescence, flowers open, $\times 8$; h, carpellate flower in vertical section to show large disc and stigma, region of undifferentiated ovules indicated by circle of dots, $\times 50$; i, detail of infructescence with two fruits, $\times 6$; j, cross section of fruit, pericarp (?) unshaded, endosperm stippled, embryo in center of endosperm, $\times 12$; k, seed, oriented as in fruit, $\times 12$; l, seed in section, oriented as in "k," endosperm stippled, embryo unshaded, $\times 12$. m, *P. rubrum*: tip of staminate plant with unopened flowers, $\times 2$.

ernmost peninsular Florida, while *P. serotinum* (Raf.) M. C. Johnston (*P. flavescens* Pursh) has been variously interpreted as including certain western populations or as containing various species in both the eastern and south-eastern United States. The view of Wiens is doubtlessly more reasonable in considering *P. serotinum* as a single species parasitic on a wide variety of dicotyledonous hosts in the area of the Generic Flora. Under this interpretation, *P. serotinum* is distributed from eastern Texas and eastern Oklahoma, eastward along the Gulf Coast to the Atlantic, southward to southernmost Florida, and northward and eastward to southeastern Missouri, southernmost Illinois, Indiana, Ohio, southeastern Pennsylvania, and southern New Jersey. Wiens treated the western populations formerly associated with this species as subspecies of either *P. villosum* (Nutt.) Nutt. or *P. tomentosum* (DC.) Engler.

The work of Baldwin and Speese and of Wiens makes it clear that, at least in the United States, the genus is characterized by a diploid chromosome number of 28. Baldwin and Speese were unable to discover chromosomal differences of any sort between 25 collections of *Phoradendron serotinum* from 15 different host species in Virginia and Arkansas. The considerable amount of damage (malformations, reduced growth rates, and increased predisposition to the attacks of certain insects and decay fungi) done to host trees needs no elaboration.

Baldwin and Speese found that meiosis occurs in staminate buds of *Phoradendron serotinum* in eastern Virginia in July and August. Flowering is in late autumn (October to late November in northern Virginia [Allard] and at least into January in Florida). Pollination of the minute flowers is by insects—presumably Hymenoptera, possibly wasps. Fruits mature the following fall or later, thus requiring up to a year and a half from flower primordium to maturation. The berries are eaten by various birds, which distribute the seeds. In contrast, the seeds of *Arceuthobium* are distributed explosively as the fruits break away from the pedicels. Initial velocities of the viscous-coated seeds may be 90 feet per second, and they may sometimes be thrown as far as 50 feet (see Hawksworth & Wiens, family references).

The superficial likeness of *Phoradendron serotinum* to the European *Viscum album* has made a transfer of the latter's folklore to North America easy. Most *Phoradendron* found on the northern markets at Christmas originates in Texas, New Mexico, Arizona, and Oklahoma, with some from Kentucky, Tennessee, and the Carolinas. The cities in the Southeast seem to draw upon more local sources. Dr. C. E. Wood reports, for example, that the *P. serotinum* sold in Roanoke, Virginia, is trucked in from Floyd, Franklin, and Suffolk counties, with some even from the Carolinas.

The poisonous berries of *Phoradendron serotinum* are mentioned under the family (see Hardin & Arena). Perkins and Payne note that "the berries and tea from the berries [of *P. serotinum*] have caused poisoning deaths of humans & livestock. Symptoms, which appear in 1-2 hours, are nausea, vomiting, profuse diarrhea, sweating, dilated pupils, rapid & labored respiration, shock & death due to cardiovascular collapse in about 10 hrs. Deaths have resulted from using the berries to procure an abortion." The foliage of *P. villosum* has poisoned cattle (Kingsbury).

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THE CARICACEAE IN THE SOUTHEASTERN UNITED STATES¹

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CARICACEAE Dumortier, Anal. Fam. 37, 42. 1829, nom. cons.

(PAPAYA FAMILY)

Shrubs [or trees (to 35 m), rarely herbs] with milky sap. Leaves alternate, estipulate, simple, palmately [or variously] lobed [or palmately compound], terminal on an unbranched [or profusely branched], unarmed [or armed] stem [trunk], [or leaves not congested at stem apex]; abaxial leaf surfaces with external glands [or with glands in the adaxial epidermis]. Plants of most species dioecious, a few monoecious, or polygamous. Inflorescences axillary, irregularly cymose [or flowers solitary], rachises long or short [or peduncles long]. Flowers regular, imperfect or perfect. Calyx 5-lobed [or -toothed, sometimes obscurely so], lobes alternate with [or opposite] those of the corolla. Staminate flowers with 5 petals united into a tube, separate above; stamens 10 in 2 series of 5 each, one series antesealous, the other antepetalous, or stamens 5, either inserted on the corolla tube or arising from near the base of the corolla, the filaments often pilose, free [or basally united] or absent, anthers 2- [or 1-]locular, connective prolonged or not; pollen tricolporate, \pm prolate, 2-celled when shed; gynoecium rudimentary. Carpellate

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The present treatment was developed from a preliminary manuscript prepared in 1960 by K. A. Wilson, to whom I am indebted for a most helpful initial survey of the literature. I have greatly expanded all parts of the original manuscript, drawing information from the abundant literature of the last two decades, from study of herbarium specimens housed in the combined herbaria of the Arnold Arboretum and Gray Herbarium, and from a plant fortuitously under cultivation in the Harvard University Herbaria Building. I thank my colleagues on the Generic Flora project, Carroll Wood and George K. Rogers, who have been ready sources of information and help, and also Barbara Nimblett for her assistance with the typescript. The illustrations are the work of Arnold D. Clapman (Figure 1, a), Margaret van Montfrans (Figure 1, b), and the late Dorothy H. Marsh (Figure 1, c-l). Carroll Wood prepared the dissections. With the exception of Figure 1, b, which was drawn from a living plant of unknown provenance, the illustrations are based upon plants collected in Florida (near Collier-Seminole State Park, Collier Co. [Figure 1, a], and Lower Matecumbe Key, Monroe Co. [Figure 1, b-k]) by Carroll Wood and associates. Alejandro and Carmen Novelo helpfully assisted with some of the literature in Spanish.

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flowers with 5 petals united at the base but appearing mostly free; staminodia absent; gynoecium of 5 united carpels; stigmas 5, flabellate [or petaloid] or variously lobed [or filamentous and branched], the style short or absent; ovary superior or partly inferior, 1-locular or falsely 5-locular by intrusion of the 5 parietal placentae; ovules numerous, anatropous, bitegmic, crassinucellate. Perfect flowers with 5 petals either united into a short tube or mostly free; stamens 10 in 2 series or 5 in 1 series; gynoecium of 5 united carpels, otherwise mostly as carpellate flowers. Fruit a berry, smooth or ridged [or corniculate at the base]. Seeds with a sarcotesta, otherwise tuberculate or ridged [or smooth], the endosperm fleshy, the embryo straight, axile, but located near the micropylar end of the seed. (Papayaceae Blume.)
TYPE GENUS: *Carica* L.

A family of four (possibly three) genera and about 35 species; represented in our area by one species of *Carica* L. The other genera are *Cylicomorpha* Urban (two species, tropical Africa), *Jarilla* I. M. Johnston (*Mocinna* Cerv. ex Llave) (one species, Mexico and Guatemala), and *Jacaratia* Endl. (*Pileus* Ramírez) (six species, mainly of tropical areas of Mexico and Central and South America).

The family is characterized by pentamerous, usually imperfect flowers; parietal placentation; generally large, pendent fruits (berries); and milky sap in anastomosing, articulated laticifers. While plants of *Carica Papaya*, the best-known member of the family, generally consist of single, unbranched stems with terminal crowns of long-petiolate leaves, species of *Jacaratia* are tall, profusely branched trees.

Because much of what is known about the Caricaceae is based on study of *Carica Papaya*, it is not at present meaningful to generalize about the family with respect to such biologically important topics as chemistry, cytology, palynology, anatomy, floral biology, and ecology.

The family has been monographed by Badillo (1971), who consolidated species concepts in *Carica*, *Jacaratia*, and *Jarilla*, in addition to introducing much new information of taxonomic value. Badillo's monograph is fully illustrated with line drawings for all the species he accepted and has distributional maps for most of them.

The family was put near the Passifloraceae in the systems of Bentham and Hooker, and of Engler and Prantl. Modern classification schemes (Cronquist, Dahlgren, Takhtajan, Thorne) also recognize this relationship, as shown by the placement of the two families in a variously circumscribed Violales. However, an affinity with the Capparales and Euphorbiales is also indicated by the occurrence of the glucosinolate-myrosinase system, as well as by certain anatomical similarities (Rodman). Airy Shaw (in Willis) stated that the Caricaceae are related to the Passifloraceae and (through *Jatropha*) to the Euphorbiaceae. Corner indicated that there is an important difference in seed-coat structure among various Caricaceae and Passifloraceae; his investigations stress the similarity of seed-coat structure between the Caricaceae and the Flacourtiaceae, a family also in the Violales in most modern systems of classification.

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1. *Carica* Linnaeus, Sp. Pl. 2: 1036. 1753; Gen. Pl. ed. 5. 458. 1754.

Small trees with unbranched (rarely branched), soft-wooded stems with milky sap and alternate, estipulate, simple, [unlobed or] palmately [or pinately] lobed [or palmately compound] leaves borne on the upper part of the stem in a terminal crown. Plants dioecious, polygamous, [or monoecious]. Inflorescences axillary, irregularly cymose, the rachises generally long in plants with mostly staminate flowers, or short in plants with mostly carpellate or perfect flowers. Flowers short-pedicellate, regular. Sepals 5, minute, united below, free above, alternate with the petals (corolla lobes). Petals 5: in staminate flowers united into a long tube, but lobes free above and contorted [or valvate] in bud; in carpellate flowers free nearly to base; in perfect flowers united into either a long or a short tube. Stamens 10 or 5 in one whorl; filaments \pm free, pilose; anthers 2-locular, with dehiscence introrse, longitudinal, the connective massive, short [or long-extended] or absent. Stamens in staminate and some perfect flowers in 2 dimorphic groups of 5 each, those of one group opposite the corolla lobes, with filaments short and anthers long, those of other group opposite the sepals, filaments longer and anthers shorter; in another kind of perfect flower, stamens 5, opposite sepals, filaments long. Gynoecium syncarpous, carpels 5, style short, stigmas 5, variously lobed [or filamentous and branched], ovary globose to elongate in carpellate and perfect flowers, rudimentary but with style prolonged and subulate in staminate flowers. Ovary 1- [or partly 5-]locular, superior or slightly inferior; placentation parietal, the placentae often dividing the locule into 5 parts; ovules numerous, in 2 rows on the placentae, funiculi long. Fruit a large [to small] berry, smooth or \pm 5-angled [or with 5 (rarely 10) longitudinal ridges], short or long pedunculate; seeds with a fleshy, translucent



FIGURE 1. *Carica*. a-l, *C. Papaya*: a, leaf, $\times \frac{1}{4}$; b, pear gland from abaxial surface of vein, $\times 25$; c, portion of staminate inflorescence, $\times 1$; d, staminate flower with corolla laid open (note rudimentary gynoecium), $\times 2$; e, vertical section of upper part of staminate flower, showing spatial relationships of stamens, $\times 5$; f, carpellate inflorescence with flower, three buds, and two bracteoles, $\times 1$; g, carpellate flower with two petals removed to show gynoecium, $\times 1$; h, gynoecium in vertical section, $\times 2$; i, diagrammatic cross section of ovary, showing five parietal placentae, $\times 2$; j, ovule (position of micropyle indicated), $\times 15$; k, fruit, $\times \frac{1}{4}$; l, seed with fleshy outer coat removed, $\times 5$.

sarcotesta outside a hard layer of irregular outgrowths (both from the outer integument) [or smooth]; embryo straight, cotyledons broadly elliptic; endosperm fleshy. LECTOTYPE SPECIES: *C. Papaya* L.; see Britton, Fl. Bermuda, 250, 1918. (Name probably from a supposed resemblance to the fig, *Ficus Carica* L.; the generic name *Papaya* rejected by Linnaeus because it lacked either a Greek or a Latin root.) — PAPAYA, PAPAW (British), FRUTA DE BOMBA (Cuban).

A small but taxonomically challenging genus of 22 species (Badillo, 1971), native to portions of Mexico and Central and South America, with *Carica Papaya* L., $2n = 18$, widespread throughout the tropics, long naturalized in southern Peninsular Florida, but also grown in the lower Rio Grande region of Texas and, with protection, in climatically appropriate areas of southern California. I have seen herbarium specimens collected during the last century from Brevard, Dade, Lee, Manatee, Martin, Monroe, and Palm Beach counties in Florida, all located south of about 28°N lat. (roughly a line between St. Petersburg and Cape Canaveral). Label data indicate a correlation with disturbed, open or semi-open habitats.

William Bartram observed fruiting specimens of papaya in 1773 or 1774 in northeastern Florida (e.g., along the St. Johns River near Palatka) considerably north of its present distributional area in the state. While Sargent included *Carica Papaya* in his *Silva of North America* on the authority of Robert Ridgway, who found papaya growing in a remote hammock in the Everglades and therefore considered it "indigenous to this part of south Florida," there is no compelling evidence that papaya was ever native to Florida or to any other part of our area.

Carica Papaya is generally regarded as having been introduced into Florida by the Spanish in the late 1500's, fairly soon after the establishment of their settlements. Its presence near St. Augustine during Bartram's visit may relate to those supposed introductions. Indians may have had a role in the spread of the papaya to or in Florida. There is good evidence that the Spanish took papaya to the Philippines and that the Spanish and/or Portuguese carried it elsewhere in the Old World Tropics at an early date (Burkill).

The original New World distribution of *Carica Papaya* is unknown. Spruce (in Mello & Spruce) considered it indigenous to the West Indies, although statements of G. F. de Oviedo, a Spaniard who was stationed on Hispaniola between 1514 and 1525, show that the papaya was brought to Santo Domingo and taken elsewhere in the West Indies from Darién (now a part of Panama). De Candolle indicated that the species was native to the shores of the Gulf of Mexico and the West Indies. On the other hand, Badillo (1971), on the basis of the distribution of related species, concluded that *C. Papaya* reached Central America from northwestern South America, its place of origin. Solms (1889), in an analysis of data then available, suggested that *C. Papaya* arose in pre-Columbian times by interspecific hybridization and selection. He based this hypothesis upon the ease of cross pollination and supposed hybridization between certain species of *Carica*, the likelihood of the selection

of hybrids over parentals, and the ancient cultivation of papaya (evidently no truly indigenous plants are known anywhere). Although one natural interspecific hybrid is known (it has also been produced experimentally—plants of *C. × Heilbornii* Badillo and hybrids of *C. pubescens* Lenné & K. Koch in Braun & Bouché and *C. stipulata* Badillo are identical) and other species have been successfully hybridized under artificial conditions, the cytological evidence does not support the hypothesis that *C. Papaya* arose as an interspecific hybrid of unknown parentage (Storey, 1976). The qualities of its fruit as food doubtless resulted in the extensive transport of the papaya prior to European contact. Archaeological and paleoethnobotanical studies may eventually help to determine where the papaya originated and the path of its dispersal through the New World tropics.

Badillo (1971) divided *Carica* into sect. *CARICA* (ovary 1-locular), containing only *C. Papaya*, and sect. *VASCONCELLEA* (St.-Hil.) Hooker in Benth & Hooker (ovary in large part 5-locular), possibly an artificial division. *Cylicomorpha* and *Carica* are very close morphologically, and it may prove reasonable to combine the two genera when more information (e.g., chromosome numbers) about *Cylicomorpha* has been gathered. Other authors have divided *Carica* into three units based on the character of the aestivation, the form of the stigma (lobes linear to flabellate, divided or undivided), and whether the ovary is one- or five-locular (Solms). The infrageneric classification of *Carica* deserves renewed attention.

Although stems of *Carica Papaya* attain the height of a small tree, they are basically herbaceous in organization. Their strength is provided by isolated strands of phloem fibers. Vascular bundles separated by wide parenchyma rays occupy a narrow circle outside a massive pith. Wood fibers are absent. Vessel elements are reticulately thickened, and the perforations are simple and horizontal (Metcalf & Chalk). Articulated laticifers occur throughout the ground tissue in all parts of the plant. Clavate glandular hairs with multicellular heads are reported from leaves, and translucent to whitish, nearly sessile pearl glands (largest seen ca. 1.25 mm) occur on leaf, petiole, and stem surfaces (Specher), usually in association with veins. Their function is uncertain, but they might serve to attract ants that may drive away potentially injurious insects. Stomata are abaxial and anomocytic. Stipules have been reported for *C. stipulata* Badillo but are otherwise absent from other species of *Carica*. The morphology of these structures has not been elucidated. Seeds of *C. Papaya* have been studied in detail (Singh, Corner). The sarcotesta develops from the outer epidermis of the outer integument, while the firm, irregularly tuberculate "seed coat" is derived from subepidermal cells of the outer integument, which become elaborated periclinally. Lignified fibers develop from cells of the outer epidermis of the inner integument. Other tissues of both the outer and inner integuments become variously differentiated. A funicular aril is reported as sometimes present but vestigial in *Carica* (Corner). Early, postzygotic cell divisions of the embryo are irregular in *C. Papaya*; its embryogeny does not conform to a specific type.

Chromosome numbers of five species and two hybrids (*C. × Heilbornii* nm. *chrysopetala* and nm. *pentagona*) are known; all are $2n = 18$. Aga-

mospermy has been reported (Badillo, 1971), and seedless, parthenocarpic fruits are occasional (Pope).

The flowers of *Carica Papaya* are of varied form, and although at least 40 types exist (Storey, 1958), four of these are convenient descriptive markers along what is really a continuum of morphological gradation from one type to another. The floral diversity of *C. Papaya* is evidently unique in the Caricaceae. Staminate flowers are decandrous (stamens organized in two dimorphic series of five each) and are sympetalous except for the free corolla lobes. Flowers of the "elongata" type are perfect and decandrous; the petals are fused for one fourth to three fourths the length of the corolla. The gynoecium is elongated. Flowers of the "pentandria" type are pentandrous and perfect. However, the corolla tube is short (ca. one fourth as long as the corolla), and the gynoecium is globose. The androecium consists of five antepetalous stamens. In carpellate flowers the petals are free except for a narrow basal zone of fusion, and the gynoecium is \pm globose. Some plants bear only carpellate flowers; others produce only staminate flowers or only mixtures of staminate, carpellate, and perfect flowers at the same time. Some principally staminate and polygamous plants (both andromonoecious and gynodioecious plants are reported) can also be phenotypically ambivalent (Storey, 1976) (i.e., the proportions of flower types produced vary throughout the year). Environmental factors such as photoperiod and climate appear to have a role in these changes.

The genetic basis of the inheritance of flower type (which is generally, though poorly, termed "sex expression") is explained by three hypotheses (Storey, 1976), which account for a considerable body of empirical data. That of Hofmeyr involves the balance between genes on "sex chromosomes" governing "femaleness" and zygotic lethality and other genes on autosomes controlling "maleness." The hypothesis of Horovitz and Jiménez assumes that dioecism is primitive in the Caricaceae and that flower type determination is basically of the XX (carpellate) and XY (staminate) type, but with YY and some XY combinations lethal to the zygote. Modification of the Y chromosomes produced the new, nonlethal andromonoecious genotype XY₂. Storey's hypothesis states that the genetic basis of dioecism in the family developed progressively from an unknown ancestor with perfect flowers. Staminate flowers (Storey, 1969) were derived by suppression (or elimination) of a functional gynoecium, while formation of carpellate flowers passed through successive stages: first, abortion of the original whorl of carpels and their replacement by new carpels homologous to the upper group of stamens (to give flowers of the pentandria type), and then abortion of the carpels of the pentandria flower and their replacement by another set of new carpels homologous to the lower group of stamens (to give flowers of the carpellate type). Expressed genetically (Storey, 1976), inheritance of flower type is under the control of factors involved in 1) transmuting the androecium into the gynoecium, 2) suppressing the gynoecium, and 3) enforcing heterozygosity in staminate and polygamous plants. Item 3 is a sex-linked lethal factor that is prevented from crossing over by another factor on the same chromosome.

Carpellate flowers of *Carica Papaya* produce no nectar, whereas staminate flowers are not only nectariferous but sweetly fragrant in the evening. This absence of nectar-producing tissue in carpellate flowers of *C. Papaya* is accounted for by Storey's explanation of the origin of the carpellate flower, whereby nectar-secreting tissue between the androecium and gynoecium is lost during ontogenetic conversion of stamens into carpels. Insects are not attracted to carpellate flowers for a nectar-reward, although in Costa Rica hawk moths have been observed visiting both staminate and carpellate flowers. The system has been termed "mistake pollination" (Baker). Other insects (mosquitoes, midges, thrips) may also act as pollinators. Baker noted that such an inefficient system of pollination requires a fairly dense plant population for reproductive success. In Costa Rica plants of *C. cauliflora* Jacq. grow in groups, and Baker speculated that this results from seeds being distributed *en masse* by frugivores. The stickiness of seeds of *C. Papaya* may also play a role in this.

Chemical data about *Carica Papaya* are varied but incomplete. The occurrence of glucosinolates and myrosin was early established. Whether myrosin is localized in special cells (idioblasts) as it is in most other families characterized by the glucosinolate-myrosinase system is evidently not known (Rodman). The presence of glucosinolates has been accorded phylogenetic significance. Other compounds (flavonoids, alkaloids) are reported, but these as yet have been of little use in taxonomic studies.

In cultivation throughout the tropics, *Carica Papaya* yields a widely praised fruit that is of considerable commercial importance. The crop is sufficiently large in Hawaii to allow shipment to the mainland U. S. A. and Japan. The Hawaiian papaya of commerce is the cultivar 'Solo', which was introduced into Hawaii from Barbados. Its rather small fruits are pyriform and are the products of an inbred gynodioecious strain in which trees with perfect flowers are selected by partial elimination of plants destined to produce carpellate flowers (Storey, 1976). The principal cultivar in South Africa, 'Hortus Gold', is a dioecious strain. In the papaya seed germination provides the main method of propagation for agricultural purposes. Edible fruits are also produced by *C. chilensis* (Planchon) Solms, of Chile; *C. Goudotiana* (Triana & Planchon) Solms, of Colombia and Panama; *C. monoica* Desf., of Ecuador, Peru, and Bolivia; and *C. pubescens*, mountain papaya, $2n = 18$, of Panama, Venezuela, Colombia, Ecuador, Peru, and Bolivia, and also in cultivation. The fruit of *C. Papaya* varies greatly in size and shape.

Carica Papaya is also the source of papain, a proteolytic enzyme used principally in the production of commercial meat tenderizers and also in the manufacture of chewing gum and cosmetics, in degumming silk and imparting shrink-resistance to wool, in the treatment of hides during tanning, and as a drug to counter dyspepsia. Papain in association with a second proteolytic enzyme, chymopapain, is refined from the latex of papaya; it is a white powder when more or less pure. Laticifers in the fruits are severed, and the latex exudate is collected on trays suspended below the infructescences. Although the papaya is a perennial, latex production is greatly reduced after a plant is three years old. Papain is or has been produced mainly

in Tanzania, Uganda, and Sri Lanka, with most of the yield being imported into the United States.

The papaya, a common feature of the tropical landscape, is often grown as an ornamental.

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THE GENERA OF MELASTOMATACEAE IN THE
SOUTHEASTERN UNITED STATES¹

JOHN J. WURDACK AND ROBERT KRAL

MELASTOMATACEAE A. L. de Jussieu, Gen. Pl. 328. 1789,
"Melastomae," nom. cons.

(MELASTOME FAMILY)

Herbaceous or woody plants (rarely trees) with simple, usually exstipulate, opposite (usually decussate) leaves, characteristically with 3-5 palmately arranged longitudinal veins tending to parallel the leaf margins and with horizontal cross-veins between. Inflorescences usually cymose, the flowers complete, actinomorphic (but usually zygomorphic with respect to the orientation of stamens and style), usually 4- or 5-merous, with a well-developed, urn-shaped floral tube (hypanthium) bearing sepals, petals, and stamens at its summit. Petals free, usually white to purple (rarely orange or yellow), dorsally imbricate, usually spreading. Stamens isomorphic [or heteromorphic], usually twice the number of petals, often with sterile appendages at base of connective; stamens bright yellow [purple or other colors], usually opening by a single pore at or near the apex. Gynoecium syncarpous, with a single style and stigma, the ovary (1- to 4- or 5- (to 11-)loculate, with axile placentation, often adnate to the floral tube (except near the apex) [or free from the floral tube], maturing into a many-seeded capsule or berrylike fruit. Seeds small, lacking endosperm. TYPE GENUS: *Melastoma* L.

A large, primarily tropical group of about 200 genera and 4500 species, most of which are easily recognized as belonging to the family by both leaf venation and stamen morphology. No genus is common to both the New and Old Worlds, but several Neotropical species have become noxious weeds in

¹Prepared for the Generic Flora of the Southeastern United States, a project of the Arnold Arboretum currently made possible through the support of the National Science Foundation under Grant DEB-81-11520 (Carroll E. Wood, Jr., and Norton G. Miller, principal investigators). This treatment, the 94th in the series, follows the format established in the first paper (Jour. Arnold Arb. 39: 296-346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets [].

The illustration of *Rhexia* was drawn by Virginia Savage from dissections by Carroll Wood; that of *Tetrazygia* is by Karen Stoutsenberger from dissections by Kenneth R. Robertson. Liquid-preserved specimens for illustration were collected by R. B. Channell, H. F. L. Rock, Alice Tryon, Carroll Wood, and John Wurdack; other materials were from the Gray Herbarium.

the Paleotropics. The stamens can be dimorphic, and they frequently bear highly modified appendages. (C. L. Wilson, however, cited these peculiar stamens as corroborating the "telome theory.") The family is represented in the continental United States only by *Rhexia* (of tribe Rhexieae), all species of which occur in the southeastern United States (and one of which is also in the West Indies), and by a single species of *Tetrazygia* (of tribe Miconieae), a predominantly West Indian genus.

Species of some 18 other genera are grown "as ornamentals either in greenhouses or outdoors in warm climates" in the United States (see *Hortus Third*). Among the most widely cultivated is the showy, purple-flowered *Tibouchina Urvilleana* (DC.) Cogn. (*T. semidecandra* Hort.) (see Wurdack, 1967; *Hortus Third*); at least eight other species of this large tropical American genus (ca. 350 spp.) are in cultivation in the United States.

Pollination is usually by insects, especially bumblebees, rarely (in tropical America) by hummingbirds, bats, or rats. The pollen of most Melastomataceae is 3-colporate. Wood anatomy includes the features of fiber-tracheids, included phloem, and usually solitary tracheids. The diversity and complexity of hair types are the greatest in any family of flowering plants.

Chromosome numbers are known in only about one third of the genera of melastomes and less than 10 percent of the species. The commonest base numbers are 9 and 17. Fossils (leaves) are known from widely scattered parts of the Northern Hemisphere, with very few Southern Hemisphere records. Ages are mostly Tertiary (Miocene), with a few Quaternary; data are found in the U. S. Geological Survey Compendium Index to Paleobotany.

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KEY TO THE GENERA OF MELASTOMATACEAE IN THE SOUTHEASTERN UNITED STATES

- Plants herbaceous; flowers 4-merous; fruits capsular; seeds usually cochleate. 1. *Rhexia*.
Plants woody; flowers 5-merous; fruits berrylike; seeds cuneate. . . . 2. *Tetrazygia*.

Subfamily MELASTOMATOIDEAE [Seringe ex DC., "Subordo Melastomeae"]

Tribe RHEXIEAE DC. Prodr. 3: 114. 1828.

1. *Rhexia* Linnaeus, Sp. Pl. 1: 346. 1753; Gen. Pl. ed. 5. 163. 1754.

Erect, sometimes suffrutescent perennial herbs, mostly of seasonally wet acidic soils of the Atlantic and Gulf Coastal Plain of the United States. Root

buds on rhizomelike roots, or from tubers, stems usually erect, arising from woody caudices, mostly glandular-hirsute, more or less quadrangular, with faces subequal or with one opposing set broader and convex, the other narrower and concave, often subligneous toward the base and with a thin, exfoliating bark. Flowers in simple or compound bracteate dichasia (sometimes a bostryx), 4-merous, showy, the petals fugacious, lavender to purple, rose, or white (yellow in *R. lutea*). Stamens 8, more or less isomorphic, the filaments exserted, the anthers linear or linear-lanceolate, mostly curved, at anthesis unilocular and subapically poricidal, the connective base appendaged. Ovary adnate to floral tube (except at apex), 4-locular, the ovules numerous on massive placentae; style linear, curved, exserted; stigma capitate. Fruit a loculicidal capsule retained in the lower, globose part of the flask-shaped, variously necked floral tube (hypanthium). Seeds cochleate (cuneate-prismatic in *R. alifanus* Walter). Chromosomes $2n = 22, 44, 66$. LECTOTYPE SPECIES: *R. virginica* L.; see Britton & Brown, Illus. Fl. No. U. S. Canada, ed. 2, 2: 582. 1913. (Name derived from Greek, *rhēxis*, a breaking or bursting forth. According to Barton, Pliny used the name for a plant thought to be a species of *Anchusa* or *Echium* [Boraginaceae].)—MEADOW-BEAUTY, DEERGRASS.

The genus includes eleven clearly marked species and three varieties, all represented in the southeastern United States, but with *R. cubensis* Griseb. extending into the West Indies (Cuba, Hispaniola, and Puerto Rico) and *R. virginica* L. into eastern Canada. The greatest concentration of species and the most morphological variation within species occur in northwestern Florida.

Four natural entities are evident (see Kral & Bostick). *Rhexia alifanus* Walter stands alone as the only species with essentially glabrous, isofacial, subentire, and glaucous leaves, caducous bracts, and seeds fully twice the size of those of other species and (unique in the Rhexieae) oblong-cuneate and subprismatic in shape, much like small corn grains. The yellow-petaled *R. lutea* Walter, a bushy subshrub with short, straight anthers opening by large, oblique pores, represents the second unit. This species is distinct enough anatomically and chromatographically to be placed in a section of its own (see Kral & Bostick). Both members of the third group, *R. petiolata* Walter and *R. Nuttallii* James, are low plants with woody, caudiciform rootstocks; flowers and fruit bases hidden by broad, persistent bracts; short, straight, large-pored anthers (as in *R. lutea*); and ascending-liguliform (rather than plane and spreading) petals. This pair of species is the least variable morphologically, while the fourth and largest group (seven species) is the most plastic genetically and phenotypically. These last species have elongate, small-pored anthers (as in *R. alifanus*) but produce the conventional small, cochleate seed of the other rhexias. Perennation is either by buds that form along shallow, elongate, rhizomelike roots, by fusiform tubers, or by a combination of both. Many of these species are weedy in character.

Several authors (Leggett; James; Kral & Bostick) have observed pollination of various species of *Rhexia* by bees. Other insects may also be involved because *Rhexia* buds usually open in late evening or at night (the petals

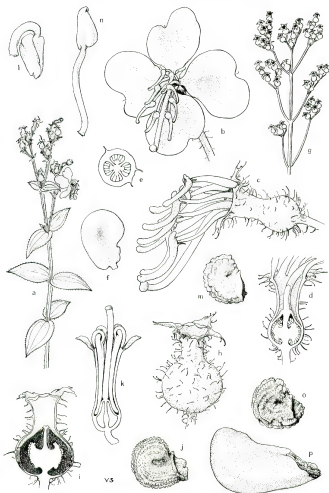


FIGURE 1. *Rhexia*. a-j, *R. virginica*: a, tip of flowering plant, $\times \frac{1}{2}$; b, flower, $\times 2$; c, same, side view with petals removed to show floral tube and arrangement of stamens (note pore at tip of anther), $\times 4$; d, floral tube and gynoecium in vertical section (note partly inferior ovary and placentation), $\times 4$; e, diagrammatic cross sec-

usually are shed around midday), but no observations have been made of insect visitors during this period. (For an account of pollination in *R. virginica* see Leggett; in *R. mariana* L., see James.) Because flowering times of all species overlap and several species may be found in the same site, and because outcrossing appears to be the common mode, it is reasonable to rule out pollen availability as a limiting factor in hybridization.

Natural F_1 hybrids have been recognized by several observers (Bostick, James, Kral): *Rhexia mariana* \times *R. virginica*, *R. aristosa* Britton \times *R. virginica*, *R. mariana* \times *R. salicifolia* Kral & Bostick, *R. virginica* \times *R. salicifolia* (Kral, previously unreported), *R. mariana* \times *R. Nashii* Small (hybrid swarms reported by Kral), *R. Nashii* \times *R. virginica*, and *R. Nashii* \times *R. cubensis*. In these hybrids, except in the case of observed backcrosses, there is early abscission of most fruit, and few seeds mature in capsules that remain attached. Only *R. Nuttallii*, *R. petiolata*, *R. lutea*, and *R. alifanus* seem not to hybridize with other species.

Test crosses made by James (1956) and a rather extensive series made by Bostick (see Kral & Bostick, 1969) showed that self-pollination resulted in germinable seed only in *Rhexia petiolata* and *R. lutea*, and in no seed whatever in *R. alifanus*. Germinable seeds were formed in crosses between *R. Nuttallii* and *R. petiolata* Walter; between *R. aristosa* and both *R. virginica* and *R. salicifolia*; between *R. Nashii* tetraploids and tetraploids of *R. mariana* and *R. virginica*, and between the tetraploid varieties *ventricosa* (Fern. & Griscom) Kral & Bostick and *interior* (Penn.) Kral & Bostick of *R. mariana*. Some seed was produced in crosses involving equal ploidy levels of most of the species (*R. parviflora* \times *R. mariana*; *R. cubensis* \times *R. Nashii*; *R. cubensis* \times *R. mariana*; *R. mariana* \times *R. salicifolia*; *R. mariana* \times its varieties, and *R. mariana* vars. \times *R. virginica*), but these seeds were not germinable, presumably because of some postzygotic isolating mechanism. The frequent occurrence of natural hybrids in the field can best be explained as a result of occasional bypassing of the isolating mechanism in parts of the ranges of such weedy species as *R. mariana*, *R. virginica*, *R. Nashii*, and *R. cubensis*.

Characteristics of the rootstock, stem faces, trichomes, staminal appendages and anther shape, hypanthial configurations, and seed sculpture have all been used in taxonomic treatments, with seed sculpture being the most variable and therefore the least reliable feature. Comparative studies of epidermis may have a higher diagnostic value than has yet been realized.

tion of ovary, $\times 4$; f, ovule, side view, $\times 50$; g, semidiagrammatic view of infructescence with leaves and bracts removed, hairs omitted, to show cymose arrangement of flowers, $\times \frac{1}{2}$; h, floral tube enclosing mature fruit, $\times 4$; i, same in vertical section, seeds removed from placentae, $\times 4$; j, seed, $\times 30$; k, *R. Nashii*: bud immediately before anthesis, in vertical section, petals removed, to show position of anthers within floral tube, $\times 3$. l, m, *R. Nuttallii*: l, stamen from flower bud, $\times 12$; m, seed, $\times 30$. n, *R. petiolata*: stamen from open flower, $\times 12$. o, *R. cubensis*: seed, $\times 30$. p, *R. alifanus*: seed, $\times 30$.

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Tribe MICONIEAE DC. Prodr. **3**: 152. 1828.

2. *Tetrazygia* L. C. Richard ex DC. Prodr. **3**: 172. 1828.

Shrubs or small trees. Young branches silvery-scaly or becoming glabrous. Leaves with 3 main veins, silvery-scaly beneath, the margins entire. Inflorescences terminal; flowers (4- or 5- (or 6-)merous. Calyx lobes rounded and inconspicuous; petals cuneate, white (to pink), often turning yellow in drying. Stamens (8 or 10 (or 12), isomorphic, the connective without appendages, the anthers linear. Ovary 3-locular; fruit berrylike, turning blue-black, with many cuneate seeds. Chromosomes, $2n = 34$. LECTOTYPE SPECIES: *T. discolor* (L.) DC.; see Britton & Wilson, Sci. Survey Porto Rico Virgin Is. **6**(1): 4. 1925.² (Name from Greek, *tetra*, four, and *zygon*, yoke, from the four-merous flowers of the species known to De Candolle; adopted by him from collection data in Richard's herbarium.)

The genus includes about 25 species, primarily of the West Indies. Only *Tetrazygia bicolor* (Miller) Cogniaux, of Cuba, the Bahamas, and subtropical Florida, occurs in our area. In the pinelands of the Miami area of Florida and the Everglade Keys the plant is usually a shrub, but in the denser hammocks it can be a small tree up to 10 m tall and 6-10 cm in diameter. This species is usually placed in Cogniaux's sect. MICONIASTRUM on the basis of its 5-merous (vs. 4-merous) flowers, but the taxonomic discreteness of the section, as well as that of the several species placed in it, is questionable. The diversity in stamen morphology, number of floral parts, and shape of the calyx lobes suggests the desirability of further investigations, especially in defining the limits of the genus and in determining its affinities within the tribe Miconieae.

²Britton and Millspaugh (Bahama Fl. 298. 1920) designated *Tetrazygia tetrandra* (Sw.) DC. as type species, but apparently discovered later that Swartz's *Melastoma tetrandra* is *Miconia tetrandra* (Sw.) D. Don (see Adams, Fl. Jamaica), hence the switch of the type to *T. discolor*. In establishing the genus *Tetrazygia* De Candolle himself expressed doubts about the relationship of *T. tetrandra* to the four other species he placed in the genus: "An genus proprium?"



FIGURE 2. *Tetrazygia*. a-o, *T. bicolor*: a, branchlet with flowers and immature fruit, $\times \frac{1}{4}$; b, leaf, $\times \frac{1}{2}$; c, flower bud, $\times 3$; d, side view of flower, $\times 3$; e, flower in section, $\times 3$; f, stamen, $\times 5$; g, tip of anther, showing pore, $\times 25$; h, semidiagrammatic cross section of ovary, $\times 10$; i, flower, from above, after fall of stamens and style (note rim of floral cup and disc on top of ovary), $\times 2$; j, mature fruit, $\times 2$; k, same, in vertical section, $\times 3$; l, semidiagrammatic cross section of fruit, $\times 3$; m, seed, $\times 12$; n, o, two views of embryo oriented as in seed, $\times 12$.

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THE GENERA OF GENTIANACEAE IN THE SOUTHEASTERN UNITED STATES¹

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GENTIANACEAE A. L. de Jussieu, Gen. Pl. 141. 1789,
"Gentianae," nom. cons.

(GENTIAN FAMILY)

Mostly glabrous annual, biennial, or perennial herbs [vines, shrubs, or even small trees], rarely parasitic or saprophytic. Leaves simple, opposite

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It is difficult to know where to begin to acknowledge the help of the many friends who have contributed to the preparation of this paper, for there are so many. If we can be forgiven for using a botanical figure of speech, they are all the root sources for this particular interpretation of the Gentianaceae. Although he may be appalled by this designation, the taproot of it all is Charles W. James, whose study, some 25 years ago in the very early years of the Generic Flora, produced a preliminary treatment of this family. Much information has accumulated since then. It has been possible to produce illustrations, to write and rewrite treatments of the genera, to do field work, and most gratifyingly, to see others going on to solve various taxonomic problems. In presenting this work, it has been necessary to omit a huge number of references that are connected primarily with the chemistry of compounds found in various species of *Gentiana* and of related genera of Europe or Asia.

We are most immediately indebted to Barbara Nimblett, Margaret van Montfrans, Norton Miller, and George Rogers for their multifarious help in the preparation and review of this manuscript and for various modifications of both manuscript and illustrations. We are also much indebted to Elizabeth Schmidt and Stephen Spongberg for their careful reviews and editorial help.

The initials on the illustrations will identify the artists: DHM, Dorothy H. Marsh, who was our first illustrator and who, through her special abilities, set the general style of the drawings; VS, Virginia Savage, of the thoroughly cultivated Savages of South Carolina; and KS, Karen Stoutsenberger, who worked at the Arboretum on the Generic Flora project for seven years, producing during that time more illustrations than any other artist.

The contributors of plant materials (we hope that we have not inadvertently omitted anyone) are George Avery, R. B. Channell, George R. Cooley, the late Richard J. Eaton, R. A. Howard, Robert Kral, Norton Miller, Kenneth R. Robertson, the late H. F. L. Rock, H. K. Svenson, and ourselves. Of course, the collections (both herbarium and library) of the Arnold Arboretum and the Gray Herbarium have been indispensable.

(subopposite or verticillate), sessile, entire (rarely reduced to chlorophyllous or achlorophyllous scales), estipulate, the bases joined by a transverse line around the stem (rarely not joined but decurrent). Flowers actinomorphic [or weakly zygomorphic], perfect, mostly proterandrous. Calyx persistent, synsepalous, with 4 or 5(-14) lobes (or in *Obolaria* of 2 free, foliaceous sepals). Corolla marcescent, sympetalous, 4 or 5(-14)-parted, rotate, salverform, cylindrical, funnellform, or campanulate, frequently bearing scales or glands [or spurs], contorted (imbricate in *Bartonia* and *Obolaria*) in bud. Stamens the same number as corolla lobes and alternate with them, epipetalous; filaments distinct; anthers versatile or almost basifixed, introrse, dehiscing longitudinally [rarely apically], distinct or rarely connate. Gynoecium bicarpellate, syncarpous; style distinct or absent; stigma generally 2-lobed or 2-branched, the segments linear to orbicular or decurrent [or rarely the stigma capitate and the lobes obscure]; ovary superior, sessile or stipitate, frequently bearing glands at the base, unilocular [or rarely bilocular] with intruding, parietal [rarely axile or very rarely free-central] placentae bearing numerous anatropous ovules with one integument (the ovules straight, with the integument indistinguishable in some species of *Voyria*), less commonly with placental intrusions absent and the ovules scattered over the locule wall. Fruit a bivalvate capsule [rarely fleshy and somewhat baccate], dehiscing septicidally or rarely irregularly. Seeds with a small embryo and fleshy, nuclear (or rarely cellular) endosperm (endosperm reduced to a few cells in some species of *Voyria*). Megagametophyte (embryo sac) of Polygonum type. (Excluding Menyanthaceae Dumortier, Anal. Fam. 20, 25, 1829, nom. cons.) TYPE GENUS: *Gentiana* L.

A family of approximately 80 genera and 1100 species, essentially world-wide in distribution, but most numerous in the mountainous areas of the Northern Hemisphere and in the Andes of South America. Of the genera found in the United States, only four are not encountered in our area: *Halenia* Borkh., a genus of temperate Eurasia and North America, with one of the species, *H. deflexa* (Sm.) Griseb., widely distributed in the northern United States and southern Canada, and another, *H. recurva* (Sm.) Allen, reaching into New Mexico and Arizona; *Lomatogonium* A. Br. (*Pleurogyne* Esch.), of the North Temperate Zone, with one of the species, *L. rotatum* (L.) Fries, widely distributed in Canada and Alaska and known from a single area in Colorado; *Microcala* Hoffm. & Link, a genus of two species in the Mediterranean-type climatic areas of Europe, Africa, and the Americas, with *M. quadrangularis* (Lam.) Griseb. distributed in western Oregon and California, and disjunctively in Peru and Chile; and *Swertia* L. (*sensu stricto*), a widely distributed genus with a single species, *S. perennis* L., in North America along the Pacific coast of Alaska and Canada and in a few scattered localities in the mountains of the western United States (also Eurasia). Although never forming the dominant element, many members of the Gentianaceae are conspicuous in various vegetation types around the world, from arctic tundras to tropical savannas. Several species are among our most beautiful wildflowers, but relatively few are cultivated.

The Gentianaceae have traditionally been associated with the Loganiaceae (and segregate families), Apocynaceae, and Asclepiadaceae (and sometimes the Oleaceae, Rubiaceae, and several small families) in the orders Contortae or Gentianales. Gilg and others have considered the Gentianaceae to be most closely related to the Loganiaceae, and indeed these two families are similar morphologically. Hutchinson, however, placed the Loganiaceae, as well as the Apocynaceae and the Asclepiadaceae, in his Lignosae subphylum, far distant from the Gentianales, which in his system included only the Gentianaceae and the Menyanthaceae. Most phylogenists have agreed that the origin of the Gentianales lies in the Caryophyllales or perhaps the Saxifragales, and that they are ancestral to most of the higher, sympetalous dicots.

The family is a difficult one taxonomically. Generic limits are often poorly defined, and intergeneric relationships are not well understood. Two subfamilies have often been recognized. The Gentianoideae, by far the larger, are terrestrial (rarely saprophytic or possibly parasitic) herbs or shrubs with mostly opposite, sessile (rarely alternate or petiolate) leaves, contorted or rarely imbricated aestivation, mostly nuclear (rarely cellular) endosperm, bicollateral vascular bundles, distinct lateral corolla traces, and a radially symmetrical vascular plan in the flowers. The Menyanthoideae, a small group of five genera and perhaps 40 species, on the other hand, are aquatic or palustrine herbs with alternate, petiolate leaves, induplicate-valvate aestivation, cellular endosperm, collateral vascular bundles, fused lateral corolla traces, and a more or less bilaterally symmetrical vascular plan in the flowers.

More recent authors have considered the differences between these subfamilies to be of sufficient magnitude to warrant their separation as distinct families, and we are adopting this view. The Menyanthaceae are represented in our area by *Menyanthes* L. (*M. trifoliata* L. var. *minor* Raf. barely reaches the mountains of northwesternmost North Carolina) and by *Nymphoides* Hill (two indigenous and one naturalized species).

Chromosome numbers have been reported for approximately 250 species in 35 genera. The base numbers appear to be $x = 5, 6, 7, 9, 11$, and 13. Chromosome number is often quite variable within a genus, and certain genera as presently circumscribed include elements apparently widely disparate cytologically. Change in chromosome number appears to have played a major role in the evolution of the family. Doris Löve contended that "... the family Gentianaceae can be regarded as one of the most interesting cytotaxonomical objects hitherto known. Its evolution at the species level seems to have been based on the formation of abrupt species by aid of polyploidy as well as on the gradual evolution of species with the same chromosome number. The generic diversification, however, has been based in a high degree on allopolyploidy, as shown in the great variation in the basic numbers of chromosomes between the different groups."

Floral anatomy in the Gentianaceae has been studied by several workers. The basic vascular plan appears to be one in which the traces to the three lower series of floral organs originate in whorls, with one trace to each organ. Each of the calyx and corolla traces branches into three. The vascular cyl-

inder ultimately splits into three traces that supply the gynoecium, with one dorsal and two ventrals to each carpel. Specialization has generally tended toward fusion of traces, both within the same whorl and between whorls. Thus, in some groups the lateral traces of adjacent calyx lobes arise as single fused bundles (distinct from the median bundles); the same is sometimes true for both adjacent corolla laterals and carpel ventrals. Extreme fusion is found in certain advanced members. In these the vascular cylinder breaks up below the receptacle into a dictyostele consisting of five bicollateral bundles, each one made up of traces to each of the floral whorls.

The placentation of the gentianaceous ovary has also received considerable attention. According to Lindsey, the primitive form is unilocular, with a single row of ovules along each of the four carpel edges (the placentation parietal). Specialization seems to have been in two directions: 1) the placental zone spreading laterally, with ovules borne over most of the locule wall; and 2) placental outgrowths from the carpel edges protruding in varying degrees into the locule, in extreme cases forming bilocular ovaries with essentially axile placentation or, very rarely, unilocular ovaries with at least partly free-central placentation. Gopal Krishna and Puri argue, however, that the bilocular condition, with axile placentation, is the primitive type, and that specialization has tended in one direction toward unilocular ovaries with free-central placentation and toward parietal placentation in the other. However, Lindsey warned against attaching too much taxonomic importance to the unilocular *vs.* bilocular condition of gentianaceous ovaries. "From the morphological standpoint it is apparent that a phylogenetic or even ontogenetic change from unilocular to bilocular or *vice versa* is by no means drastic in view of the highly plastic placentae in the Gentianaceae."

Gilg's monograph (1895), the most recent of the family, was based largely on characters of the pollen grain. Tribes, subtribes, and some genera were delimited primarily on this basis. Although some of Gilg's suprageneric groups appear to be natural, many—particularly the more advanced ones—are not. Pollen morphology in the family is diverse, particularly in exine ornamentation, and is difficult to correlate with gross morphological trends. Most genera have pollen produced as single grains, but some have pollen in tetrads, and a very few have tetrads held together in polyads. Genera with pollen in tetrads or polyads, an otherwise diverse group restricted to the New World Tropics, were assembled by Gilg into a separate tribe, *Helieae*; other genera, which have single pollen grains but are closely related morphologically, were placed in the *Gentianeae* or *Rusbyanthae* (*Rusbyanthus*, the only genus in the *Rusbyanthae*, has recently been included in *Macrocarpaea* by Weaver, thus eliminating the tribe). Recent palynological studies with larger samples and more advanced techniques have suggested that a review of the alignment or the circumscription of certain genera is in order. The presence or absence of floral glands and their position and morphology have been largely ignored as important characters above the generic level. Five distinct generic groups based on glandular characteristics appear to be present in the family: 1) genera in which glands are completely absent (*Centaureum*,

Sabatia); 2) genera in which the base of the ovary is glandular, but the glands are not well developed (*Gentiana*, *Eustoma*, *Obolaria*); 3) genera in which the glands are epipetalous (*Gentianella*, *Gentianopsis*, *Fraseria*, and *Swerfia*); 4) genera with a well-developed glandular disc at the base of the ovary (Gilg's Gentianeae subtribes Tachiinae and Helieae, mostly woody genera of the American tropics); and 5) *Voyria*, with a number of species having two stalked glands at the base of the ovary. The trend in the Gentianales appears to be from glandless flowers to flowers with a well-developed glandular disc (except for the highly specialized Asclepiadaceae). The Gentianaceae appear to represent an intermediate stage in the evolution of glands within the order.

Growth form in the family varies from delicate ephemeral annual herbs to substantial shrubs and even weak-wooded, small trees. The woody condition appears to be a derived one. Except for the South African *Orphium frutescens* (L.) E. Meyer, all the woody members are neotropical and on the basis of other characters appear to represent a natural group. They were placed in two tribes by Gilg (1895): Gentianeae (only subtribe Tachiinae) and Helieae, but these probably should be merged. Several herbaceous genera were included here as well, and the genus *Lisianthus* P. Br. alone contains the whole range from annual plants to small trees.

All of the plants in the primarily woody groups have a well-developed glandular disc at the base of the ovary, a specialized condition in the family. The presence of pollen grains in tetrads or polyads, again an apparently specialized condition in this family, is found in most members of these groups and is restricted to them. The vascular anatomy of the flowers is the most advanced type in the family. Finally, although chromosome counts in these groups are relatively few, the chromosome numbers are uniformly high.

A meaningful classification of the Gentianaceae must take into account the gradually accumulating evidence from all sources. Since none of the existing treatments of the family appears to be completely satisfactory, infrafamilial groupings will not be considered here.

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KEY TO THE GENERA OF GENTIANACEAE IN THE SOUTHEASTERN UNITED STATES

- A. Leaves mostly in whorls of 4 or 5; nectaries conspicuous, fringed, borne slightly below the middle of the corolla lobes. 6. *Fraseria*.
- A. Leaves opposite or rarely alternate; nectaries present or absent—if present inconspicuous, not fringed, borne at base of corolla or base of ovary.
- B. Calyx of 2 free, foliaceous sepals; corolla with inconspicuous scales below bases of filaments; petiole bases decurrent entire length of each internode. 7. *Obolaria*.
- B. Calyx of 4 or 5 (rarely to 14) nonfoliaceous segments united at least at base; corolla never with fimbriate scales; leaf or petiole bases joined, forming a green or scarious sheath around stem, very rarely weakly decurrent.
- C. Leaves well developed, never scalelike, always opposite; plants green and obviously autotrophic.
- D. Style filiform; ovary sessile.
- E. Corolla rotate, 5-12(-14)-parted; stigma lobes linear or spatulate, spirally twisted at anthesis but later uncoiling and spreading. 1. *Sabatia*.
- E. Corolla salverform or campanulate, 4- or 5-parted; stigma lobes elliptic or orbicular, never spirally twisted.
- F. Corolla salverform, tube longer than calyx; anthers becoming spirally twisted upon dehiscence. 2. *Centaureum*.
- F. Corolla campanulate, tube shorter than calyx; anthers remaining straight after dehiscence. 9. *Eustoma*.
- D. Style short and stout, sometimes barely discernible; ovary stipitate.

- G. Corolla 5-parted, with plicate appendages in sinuses of lobes; nectaries on base of gynophore. 3. *Gentiana*.
- G. Corolla 4- or 5-parted, without plicate appendages in sinuses of lobes; nectaries on base of corolla, alternating with the stamens.
 - H. Corolla 5-parted, lobes entire, erect; flowers sessile or short-pedicellate. 4. *Gentianella*.
 - H. Corolla 4-parted, lobes ciliate, spreading; flowers long-pedicellate. 5. *Gentianopsis*.
- C. Leaves scalelike, alternate or opposite; plants slender, green to colorless, semisaprophytic or semiparasitic.
 - I. Flowers 4-merous; plants with chlorophyll; aestivation of corolla imbricate; stigmas decurrent along style to top of ovary. ... 8. *Bartonia*.
 - I. Flowers 5-merous; plants without chlorophyll; aestivation of corolla convolute; stigmas capitate or peltate. 10. *Voyria*.

1. **Sabatia** Adanson, Fam. Pl. 2: 503. 1763.

Erect, glabrous, annual, biennial, or perennial herbs (the perennials sometimes stoloniferous), arising from branched rhizomes or rarely from a short, erect caudex. Roots fibrous, fleshy, or wiry, or some annual species with a slender taproot. Leaves decussate, cauline (but also in a basal rosette in some species), sessile and sometimes clasping, membranaceous to fleshy. Flowers large to quite small, sessile or long-pedicellate, subtended by scalelike or rarely foliaceous bracts, solitary or more commonly in few-flowered monochasia or conical, flat-topped, or subcapitate clusters of dichasia. Calyx 5-12(-14)-lobed, persistent, the tube campanulate to somewhat turbinate, the lobes minute to foliaceous. Corolla rotate, marcescent, often showy, white or various shades of pink to purple, often with a conspicuous yellow "eye" or "star" in the throat, the 5-12(-14) lobes much longer than the tube, dextrorsely convoluted in bud. Stamens 5-12; filaments slender, adnate to the upper edge of the short corolla tube; anthers basifixed, linear to oblong, dehiscent laterally by longitudinal slits, becoming circinate coiled or rarely only recurved or slightly twisted laterally after pollen discharge. Stigma 2-branched, the branches linear or slightly spatulate, tightly spirally twisted and bent to one side at anthesis, but later untwisting and becoming erect or recurved; style slender, ovary unilocular, the slightly intruded carpel margins forming 4 parietal placental lobes with numerous ovules. Capsule subglobose to cylindrical; seeds numerous, globose or somewhat flattened, densely pitted. (Including *Lapitheia* Griseb.) TYPE SPECIES: *Chironia dodecandra* L. = *Sabatia dodecandra* (L.) BSP. (Name commemorating Liberato Sabbati, eighteenth-century Italian botanist who published on the plants of Rome.)

A North American genus, primarily of the Atlantic and Gulf coastal plains of the southeastern United States, but extending northward into Nova Scotia and westward to Michigan, Kansas, Oklahoma, and central Texas, and southward into central Mexico (on the west) and from southernmost Florida to the Bahamas, Cuba, and Hispaniola (on the east). All of the eighteen species (two composed of two varieties) occur in the Southeast; four are not found outside this area.

Infrageneric groups in *Sabatia* appear to be well defined in most cases,

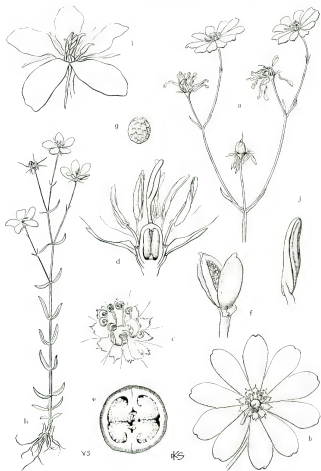


FIGURE 1. *Sabatia*. a-g, *S. Kennedyana*: a, inflorescence with flowers and partly mature fruit, $\times \frac{1}{2}$; b, flower, pollen shed, stigmas not yet expanded, $\times 1$; c, detail of flower, showing recurved anthers and receptive stigmas, $\times 2$; d, off-center vertical section of flower at anthesis, the ovary cut to show numerous ovules on two parietal placentae, $\times 3$; e, cross section of ovary, showing placentation, $\times 6$; f, dehiscing

but the rank of a few of these has been debated. Members of sects. *SABATIA* (13 species) and *CAMPESTRIA* J. D. Perry (three species) have in common pedicellate flowers borne either singly or in loose cymes and subtended by scalelike bracts, with the anthers becoming circinate-coiled as the pollen is discharged. Within sect. *SABATIA*, Wilbur (1955) recognized five subsections, one of which (*Campestres* Blake) was later raised to sectional rank by Perry (1971) on the basis of both morphological and crossing data. A third section, *PSEUDOCHIRONIA* Griseb., composed of two well-marked species, has been generally recognized and sometimes raised to the rank of genus (*Lapitheia* Griseb.).

Annuals, biennials, and perennials with alternate to opposite branching and with affinities to a wide variety of habitats (dry to wet, fresh to salt water) are represented in sect. *SABATIA*. Various species have 5–12(–14) corolla lobes, and haploid chromosome numbers of 13, 14, 16, 17, 18, 19, 20, 32, and 38 are known (along with two aneuploid races in *S. quadrangula* [$2n = 32, 34$]). The anthers are either recurved or circinate-coiled after pollen release, and the stigmatic branches are usually coiled when receptive. *Sabatia angularis* (L.) Pursh, $2n = 38$, of subsect. *Angulares*, is the most widespread and familiar species of the genus. Subsection *Dodecandrae* Wilbur (four species of rhizomatous perennials with pink, mostly plurimerous flowers and alternate branching) was considered by Blake to be worthy of sectional rank (sect. *Pleienta* (Raf.) Blake). Both *S. dodecandra* (type species of the genus) and *S. Kennedyana* Fern. (widely disjunct between Nova Scotia, eastern Massachusetts and Rhode Island, and southeastern North Carolina and northeastern South Carolina) belong here.

In Wilbur's excellent revision of *Sabatia*, *S. campestris* Nutt., $2n = 26$, and *S. arenicola* Greenman (including *S. carnosa* Small), $2n = 28$, constitute subsect. *Campestres* Blake. Both species, which have more westerly distributions than others in the genus, are annuals with pink, pentamerous flowers, a predominantly five-veined and thinly winged calyx tube, and alternate branching. In an extensive biosystematic study of the genus, Perry (1967, 1971) found that all artificial crosses between the two species were unsuccessful, as were all crosses between them and other species of the genus. The lack of crossability suggested to Perry greater divergence than would be implicit in only subsectional status. He concluded that the closest relatives appear to be the species of subsect. *Angulares*. More recently, Bell and Lester (1978, 1980) presented morphological and allozymic evidence for recognition of a third species in the section, *S. formosa* Buckley (first recognized in 1862), which is very similar to *S. campestris* and which had been merged with it. They also discovered a cline of variation between *S. arenicola* and *S. formosa* that they attributed to introgressive hybridization resulting from "hybridization of the habitat."

capsule, the marcescent perianth and androecium removed, $\times 3$; g, seed, $\times 25$. h, *S. campanulata*, flowering plant, $\times \frac{1}{2}$. i, *S. difformis*, flower showing recurved (rather than coiled) anthers, $\times 2$. j, *S. gentianoides*, dehiscing anther, $\times 6$.

Section PSEUDOCHIRONIA Griseb. (*Lapitheia* Griseb.) includes only two very distinctive species, both perennials (see Perry) with pink, 7-12-lobed corollas. Both differ from species of sects. SABATIA and CAMPESTRIA in their nearly sessile solitary or capitate flowers subtended by foliaceous bracts, and in their anthers that become only slightly twisted laterally upon pollen discharge. Geographically the most restricted of all the species of *Sabatia*, and the only one that is not found on the Coastal Plain, *S. capitata* (Raf.) Blake, $2n = 76$, is a rare plant of open hardwood forests on hillsides and ridges in the Appalachians of northwestern Georgia, southeastern Tennessee, and northern Alabama.

Easily distinguished from the preceding species by its dimorphic leaves, subulate (rather than linear) calyx lobes, and distribution, *Sabatia gentianoides* Ell., $2n = 28$, is found in pinelands and savannas on the Coastal Plain from northern North Carolina south and west to eastern Texas (rare in peninsular Florida). The chromosome numbers of these species represent extremes in the genus, and repeated artificial crosses between them have failed. However, seed-set was high when both were crossed with various species in sect. SABATIA subsect. *Dodecandrae*; *S. gentianoides* also crossed with several species of sect. SABATIA subsect. *Campanulatae*, although only the cross with *S. grandiflora* produced a high seed-set. Progeny from only one of the crosses (*S. gentianoides* \times *S. Bartramii*) were grown to maturity, and in those pollen viability was very low. The crossing experiments suggest that the species of this section are most closely related to those of sect. SABATIA subsect. *Dodecandrae*.

The basic chromosome number in *Sabatia* is thought to be $x = 7$, the present array of numbers resulting from a remote and now concealed polyploidy, with subsequent aneuploid reduction and secondary polyploidy. Although not necessarily operating at the level of initial crossability, difference in chromosome number is a barrier to hybridization in the genus. "While heteroploid crosses do not give a true indication of genetic relationship, they show that aneuploidy has been an effective source of cytological variation leading to reproductive isolation among closely related species and, presumably, to species formation" (Perry, 1971). Corresponding to a decrease in chromosome number are tendencies toward an annual or biennial habit and simplification of morphology (including decrease in floral size, number of floral parts, and prominence of leaves).

The breeding system is primarily allogamous. The flowers of most species are proterandrous, the anthers twisting or recurving as the pollen is shed. The two stigmatic branches are "tightly spirally twisted at anthesis and bent to one side, later becoming erect, untwisting and exposing the densely papillate stigmatic surface" (Wilbur). In the proterandrous species, the anthers and stigmas of a single flower are not brought into direct contact. However, in the relatively unrelated *Sabatia calycina* and *S. arenicola* (both species of unstable habitats), the stigmatic surfaces are receptive on the same day that the pollen is released. In addition, the anthers and stigmas are brought into direct contact, assuring autogamy in these two species. The latest-ma-

turing flowers of *S. difformis* and *S. macrophylla* are frequently staminate due to arrested development of the gynoecium, but the effect of this staminate expression on out-crossing is thought to be negligible. Polylectic bees have been shown to be the primary pollinators of *Sabatia* species: *Bombus* (Apidae) in the case of the large-flowered ones, and smaller bees (usually Halictidae) in the others.

Although vigorous (but usually sterile) first-generation hybrids between many of the species have been produced artificially, instances of natural hybridization in *Sabatia* are unknown, even though as many as five species have been found in the same general area. In nearly all cases involving sympatry, however, the species concerned are not intercrossable. (See Perry.)

Although most of the species of *Sabatia*, particularly the plurimerous ones, have attractive and colorful flowers, none seems to be cultivated. The genus has been placed most often near *Centaurium* Hill (*q.v.*), from which it is distinguished by the rotate corolla and characters of the stigma and anthers.

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2. *Centaurium* Hill, *Brit. Herbal*, 62. 1756; Adanson, *Fam. Pl.* **2**: 502. 1763, "Centaurion."

Annual or biennial [rarely perennial] herbs. Roots fibrous [or rarely forming a slender taproot]. Stems sparingly to profusely branched from above or below, terete or quadrangular [or 4-winged] in cross section. Leaves cauline or the lower ones arranged in a basal rosette in the biennial species, sessile, opposite, often clasping, with 1-3 veins from the base. Flowers (4- or) 5-merous, rose, pink, or rarely white [or very rarely yellow], without obvious

glands, [solitary or] borne in loose or congested cymes. Calyx persistent, deeply divided into (4 or) 5 slender, carinate lobes. Corolla marcescent, salverform, with an elongate tube [to subrotate, with a short tube, or rarely funnelliform], the (4 or) 5 lobes patent, dextrorsely contorted in bud. Stamens (4 or) 5, inserted on the upper part of the corolla tube; filaments filiform; anthers often exserted, introrse, erect, oblong to linear, spirally twisted after anthesis. Stigmas 2, [linear to] oblong, reniform, or flabelliform, sometimes the stigma solitary, with 2 distinct lobes [or rarely the lobes confluent and the stigma subcapitate]; style filiform, bifid at apex or simple, deciduous; ovary unilocular, the 2 bilobed placentae often much intruded, each lobe with several rows of ovules. Capsule oblong to fusiform, the placentiferous margins of the valves often intruded and involute. Seeds numerous, minute, subpyramidal to suborbicular, brown or pale brown [or sometimes nearly black], finely foveolate-reticulate. (*Erythraea* Borkh.) TYPE SPECIES: *Gentiana Centaurium* L. (see Britton & Brown, Illus. Fl. No. U. S. Canada 3: 1, 1913) = *Centaurium littorale* (D. Turner) Gilmour (see Gillett, The gentians of Canada, Alaska, and Greenland, 78, 79, 1963). (Name from Latin *centaureum* [Greek, *kentaurion*], the ancient name of a red-flowered plant, possibly *Centaurium Erythraea*, the medicinal properties of which were supposed to have been discovered by Chiron, the centaur who tutored Achilles, Hercules, and Asclepius.)—CENTAURY.

A taxonomically difficult genus of approximately 100 described species, nearly cosmopolitan in distribution except for tropical and southern Africa. Four sections have been recognized by Grisebach, Gilg, and others, and two of these include species native to North America. Most of the 25 or so North American species are distributed in Central America, Mexico, and the western United States. Two or three of these barely reach the western part of our area, and two or possibly three more introduced European species are sporadic in the eastern portion. All except the adventive *Centaurium spicatum* (L.) Fern. are referable to section CENTAURIUM.

The typical variety of *Centaurium Beyrichii* (Torrey & Gray) Robinson is a plant of calcareous slopes and granitic rocks in Texas, Oklahoma, and Arkansas; var. *glanduliferum* Correll is restricted to western Texas. Another calciphile, *C. texense* (Griseb.) Fern. is recorded from central and southwestern Missouri, northern Arkansas, western Louisiana, and Texas. The widespread typical variety of *C. calycosum* (Buckley) Fern. is common from Texas throughout the Southwest. It has been recorded from Jackson County, Missouri (where it is possibly introduced), and is to be looked for in Arkansas; var. *breviflorum* Shinnery is restricted to central and southern Texas.

Centaurium Erythraea Rafn (*Gentiana Centaurium* of authors, not L.; *Erythraea Centaurium* of authors, not (L.) Borkh.; *C. minus* of authors, not Moench; *C. umbellatum* of authors), $2n = 20, 40, 42$, is indigenous to all but the northernmost parts of Europe. It is a variable plant, and six subspecies have been recognized on the basis of various morphological features, as well as chromosome number. It has been reported as adventive in a number of

localities in the United States and Canada. Within our area it has been reported from North Carolina and doubtfully from Georgia and is to be looked for elsewhere.

There is considerable confusion as to the application of Linnaeus's name *Gentiana Centaurium*, and therefore the typification of the genus. The name has most commonly been applied to this species. We are following Dandy, who (as reported by Gillett) pointed out that the type of *Gentiana Centaurium* L. is actually the plant now known as *C. littorale* (D. Turner) Gilmour. Dandy rejected the name *C. minus* Moench (which until that time was widely accepted as the correct name for this species, but based on *Gentiana Centaurium* L.) under Article 65 of the *International Code of Botanical Nomenclature* as having been consistently misapplied.

Another widespread European species, *Centaurium pulchellum* (Sw.) Druce, $2n = 20, 36, 40, 42, 54, 56$, has been recorded from southern Virginia, Mississippi, and Louisiana. *Centaurium spicatum* (L.) Fritsch, $2n = 22$, distinctive in its spiciform inflorescence, is native to southern Europe. It has been collected beyond our range from Virginia to Massachusetts and should be looked for in the Southeast.

Many of the species are quite variable. Taxonomic characters include inflorescence type; proportions and sizes of corolla lobes and tubes, insertion of stamens, shape of stigmas, and shape of leaves. Although various regional treatments exist, a modern monograph of the genus is much needed.

Centaurium is presumably most closely related to *Sabatia*, from which it is readily distinguished by the salverform (as opposed to rotate) corollas and the spirally twisted (rather than coiled) or recurved anthers.

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3. *Gentiana* Linnaeus, Sp. Pl. **1**: 227. 1753; Gen. Pl. ed. 5. 107. 1754.

Glabrous or puberulent perennial [annual or biennial] herbs, with 1 to several [to many] simple or sparsely branched stems and stout, often yellowish roots from a short caudex [or plants rhizomatous with fibrous roots, or annual species with stems often branched from base and with fibrous roots or weak taproots]. Leaves opposite [very rarely verticillate], cauline, often gradually reduced below, the lowermost scalelike [or the lower ones in a loose to dense rosette and either similar to or quite different in shape from the cauline ones], the upper pairs often congested and appearing involucrate about the flowers. Flowers sessile or pedicellate, solitary or in simple dichasia, these often congested in dense terminal and/or axillary clusters. Calyx [4 or] 5 [or 6]-lobed, the lobes minute and toothlike to subfoliaceous, connected by a membrane continuous around the inner rim of calyx tube [or the intracalyxine membrane very rarely absent], [tube occasionally split down 1 side and calyx then spatheform, or split down 2 sides and calyx 2-lipped]. Corolla marcescent, [4 or] 5 [or 6]-lobed, funnelform to broadly cylindrical or fusiform [or rotate, campanulate, salverform, or obconical]; the lobes spreading to erect or incurved, large to obsolescent; the tube with plicate appendages (plaits, pleats) between the lobes, these asymmetric [or symmetrical], [entire or] variously toothed or divided, retuse to lacerate, shorter (rarely longer) than corolla lobes [or rarely obsolescent]. Stamens [4 or] 5 [or 6]; filaments often winged, adnate to corolla tube, the adnate portions decurrent; anthers free at anthesis or connate, introrse, or becoming pendent and then extrorse. Gynoecium stalked [or sessile], the gynophore glandular at base [or if sessile, glands at base of ovary], glands as many as corolla lobes; ovary bilocular, fusiform to ovoid or ellipsoid, the numerous ovules scattered over most of inner surface of ovary [or organized into 4 distinct vertical zones]; styles short and stout [or slender] or stigma sessile; stigma deeply bilobed [or lobes connate into a roundish disc], the lobes subulate [or roundish]. Capsule stalked [or sessile], protruding from or enclosed by the marcescent corolla, 2-beaked. Seeds numerous, roundish [or elongate], smooth [or striate or alveolate], broadly or narrowly winged all around [or wingless]. LECTOTYPE SPECIES: *Gentiana lutea* L.; see Adanson, Fam. Pl. **2**: 503. 1763. (Name from Gentius, King of Illyria, who supposedly discovered medicinal properties in the plants.)—GENTIAN.



FIGURE 2. *Gentiana*. a-h, *G. villosa*: a, flowering stem, $\times \frac{1}{2}$; b, flower with subtending bracts, $\times 1$; c, opened calyx (abaxial lobe longest) seen from within, showing intracalcine membrane, $\times 1$; d, opened corolla, showing stamens and plaits, $\times 1$; e, gynoecium with nectariferous lobes at base of ovary, $\times 2$; f, cross section of ovary, showing placentation, $\times 6$; g, nearly mature capsule, $\times 1$; h, seed (wingless), $\times 12$. i-k, *G. clausa*: i, tip of flowering stem, $\times 1$; j, mature fruit with marcescent corolla (note plait between corolla lobes—two lobes of plait unequal), $\times 1$; k, seed (winged),

Gentiana is here accepted in its restricted sense; that is, the group corresponding basically to Kusnezow's subgenus *EUGENTIANA* and distinguished from *Gentianella* Moench (subgen. *GENTIANELLA* Kusn.) by the presence of nectaries around the base of the ovary or on the gynophore (rather than on the corolla tube), plaited appendages between the corolla lobes (these occasionally greatly reduced, or absent in *G. lutea*, the type of the genus), and (usually) a rim or membrane extending completely around the interior of the calyx tube. Even in this restricted sense, *Gentiana* is a large, polymorphic, and taxonomically difficult genus. Kusnezow, the most recent monographer, recognized 161 species, but Marquand later listed 184 species for China alone. The genus occurs primarily in arctic and montane areas of the Northern Hemisphere, with one to three species crossing the Equator in Andean South America and a few in the large islands of Indonesia.

All of the species of *Gentiana* in our area belong to section *PNEUMONANTHAE* Bunge, a group of 40 to 50 species widespread in Eurasia and North America. The plants of this section are perennials with one to several stems arising from a short rootstock; a well-developed intracalycine membrane; conspicuous, symmetrical or asymmetric, more or less bifid corolla plicae with erose or laciniate apices; flattened seeds completely surrounded by a membranaceous wing; and a diploid chromosome number of 26 (except for the European *G. asclepiadea* L., which is probably misplaced here). About 25 species are found in North America, with two more or less distinct areas of distribution, one in the western mountains from Alaska to Mexico, the other in the eastern woodlands and prairies. The species of eastern North America have been treated most recently by Pringle, who recognizes 11 species in our area. Only one of these is restricted to the Southeast, but seven others are primarily Southeastern in distribution.

Two distinct groups are recognizable within the Southeastern species of sect. *PNEUMONANTHAE*. *Gentiana autumnalis* L. (*G. Porphyrio* J. F. Gmelin), $2n = 26$, a plant of sandy meadows and pine woods on the Atlantic Coastal Plain from central New Jersey to south-central South Carolina, and *G. Pennelliana* Fern., an endangered species restricted to open sandy sites in western Florida (Bay, Gadsden, and Wakulla counties), are distinctive in their narrow, often linear leaves, solitary pedicellate flowers, and open, campanulate corollas with spreading lobes that far exceed the plicae (plaits or pleats). The two were segregated by Clausen as subsect. *Angustifoliae*, a taxon that has not commonly been accepted. As Pringle (1967) pointed out, the subsection was based solely on a consideration of American species; moreover, these species are "much more similar to *G. pneumonanthe* [the type of sect. *PNEUMONANTHAE*] than are most of the North American species left in the nominate subsection."

× 12. 1, m, *G. austromontana*: 1, flower with upper part of corolla removed to show connivent stamens, × 2; m, three corolla lobes (corolla opened out flat, the corolla lobes with veins) and plaits between (plaits with two equal lobes), × 2. n, *G. autumnalis*, flower, × 1.

The remaining species are characterized by broader leaves; clustered, involucrate, sessile or subsessile flowers; and broadly funnellform or cylindrical corollas that are closed at anthesis or occasionally have spreading lobes. The "bottle gentians" belong here. One of the most widespread and familiar of the Southeastern species, *Gentiana Saponaria* L. (*G. latifolia* (Chapman) Britton and including *G. cherokeeensis* (Lemmon) Fern.), $2n = 26$, is a plant of moist or seasonally wet thickets, open woods, and roadsides from eastern Long Island, south along the Atlantic Coastal Plain to northeastern North Carolina, then through the Piedmont of the Gulf States from northwestern Florida to southeastern Texas, north to southeastern Oklahoma and northwestern Illinois (mostly absent from the Appalachians). According to Pringle (1967), *G. Saponaria* var. *latidens* House, from the mountains of western North Carolina, is a hybrid between *G. clausa* and *G. decora*.

Similar to the preceding but more coastal in distribution, *Gentiana Catesbaei* Walter (*G. Elliottii* Chapman, *G. parvifolia* (Chapman) Britton) is found in open woodlands, clearings, and roadsides on the Atlantic Coastal Plain from northern New Jersey to northern Florida. It differs from *G. Saponaria* in its broader leaves, longer calyx lobes, and longer and more spreading corolla lobes. Although these species are sympatric to some degree, and their habitats are apparently similar, clear-cut instances of hybridization are rare.

The montane counterpart of *Gentiana Saponaria*, *G. decora* Pollard, $2n = 26$, is distributed in mesic woodlands at higher elevations from northeastern Georgia through western North and South Carolina and eastern Tennessee, to southwestern Virginia, with an outlier in northeastern West Virginia. This species differs from *G. Saponaria* in its smaller, paler, and more open flowers, its asymmetric corolla plicae, and its shorter, subulate calyx lobes. Hybridization between *G. decora* and *G. Saponaria* has been suspected in at least one instance.

Primarily a prairie species, *Gentiana puberulenta* Pringle (*G. puberula* of authors), $2n = 26$, barely enters our area. Its distribution is in a roughly triangular area from southern Manitoba to western New York and extreme northwestern Arkansas. An outlying locality in central Louisiana (Rapides Parish) is several hundred miles distant from the nearest known populations (northwestern Arkansas). With its rather open flowers, relatively large corolla lobes, and anthers free at anthesis, this is one of the most distinctive eastern species. Until recently *G. puberulenta* has been known as *G. puberula* Michaux, but Pringle (1966) found that Michaux's type is really *G. Saponaria*.

A plant primarily of the northeastern United States, *Gentiana clausa* Raf., $2n = 26$, extends southward along the Appalachians to northeastern Tennessee and western North Carolina. It is similar to and has often been confused with the extralimital *G. Andrewsii* Griseb. It differs from all of the preceding species in that its corolla lobes are shorter than or equal to the appendages (plicae). Some specimens from the mountains of western North Carolina appear to be hybrids between *G. clausa* and the sympatric *G. decora*.

Similar to *Gentiana clausa*, but with a more slender corolla, shorter filaments, and puberulous stems and calyx lobes, the recently described *G. austromontana* Pringle & Sharp is a plant of higher elevations in the mountains of southern Virginia, northeastern Tennessee, and western North Carolina. A few collections appear to be intermediate between this and *G. decora*.

Gentiana linearis Froel., $2n = 26$, very rare in our area, is primarily a plant of boreal and subarctic areas, from southern Labrador and the eastern shore of James Bay, south to northern West Virginia and central New Jersey, with outlying populations around Lake Superior and in eastern Tennessee (Sevier County). It can be distinguished from other gentians of our area by its narrow involucre leaves and its obliquely triangular corolla plicae. The extralimital subsp. *rubricaulis* (Schwein.) Gillett is sometimes treated as a distinct species, *G. rubricaulis* Schwein.

The last two species differ from the others in their whitish or green-veined (rather than blue or purple, or blue- or purple-veined) corollas. Primarily a prairie species, *Gentiana alba* Muhl. (*G. flavida* A. Gray) barely enters our area. It is distributed from eastern Pennsylvania and southern Ontario, west to central Minnesota, and south to northwestern Arkansas, with a few populations in the southern Appalachians to Watauga County, North Carolina. Numerous hybrids (*G.* \times *Curtisii* Pringle) between this species and the largely sympatric but quite different *G. puberulenta* have been reported. Hybrids between *G. alba* and *G. Andrewsii* have been named *G.* \times *pallidocyanea* Pringle.

Widespread and familiar in the southeastern United States, *Gentiana villosa* L., $2n = 26$, is a plant of mesic woodlands throughout the area south of the Ohio River and east of the Mississippi, except for peninsular Florida. It can be distinguished from *G. alba* by its ecarinate calyx lobes and its dark green leaves. A specimen from Gadsden County, Florida, appears to be a hybrid between this and *G. Catesbaei*.

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4. **Gentianella** Moench, *Methodus* Pl. 482. 1794, nom. cons.

Mostly glabrous, annual [biennial or perennial] herbs [or rarely subshrubs]. Stems simple below and sparsely branched above [or several to many stems from the base in some perennials], [terete or] quadrangular and the angles winged at least below. Lower leaves [sessile or] tapering to an indistinct petiole and forming a loose rosette [or the rosette dense to absent], often withering before anthesis [but persistent in some perennial species]; principal cauline leaves opposite, sessile and [often] somewhat clasping, prominently [3 or] 5–7-veined [or the venation indistinct]. Flowers [4- or] 5-merous, borne in terminal and axillary umbelliform cymes [or in dichasia, or the flowers solitary, or the plants rarely subscapose]. Calyx persistent, [4- or] 5-lobed, the lobes imbricate in bud, subequal [or unequal or rarely reduced to teeth but then the calyx splitting down 1 side to form a spatheiform sheath], the tube well developed, without an inner membrane, the squamellae borne at the very base in sparse tufts opposite the lobes [or in a \pm continuous uniseriate ring]. Corolla funnellform [or cylindrical, salverform, rotate, or rarely campanulate], the lobes dextrorsely convolute in bud, erect [or spreading] at anthesis, the tube unornamented in the throat [or with vascularized filiform appendages, or fimbriae, these scattered, united into a continuous ring, or arranged in a row along the base of each corolla lobe; occasionally the lower part of the tube pilose inside] but with glands alternate with the stamens near the base, these glands cushionlike, crescent shaped [to deeply bifid]. Stamens included, inserted on the corolla tube at the middle or below; filaments filiform [or subulate], glabrous [or with minute papillae, or occasionally barbate below]; anthers \pm versatile, introrse, but reflexing and becoming pendent and extrorse upon dehiscence [or basifixed and remaining erect in a few species]. Gynoecium stipitate [or sessile]; stigma 2-lobed, sessile [or nearly so]; ovary cylindrical [or fusiform], unilocular, the numerous ovules borne on weakly intruded placentae, these in pairs along each suture. Seeds smooth, globose [or slightly flattened], wingless. (*Gentiana* L. subg. *Gentianella* Kusn.; *Amarella* Gilib., nom. rejic.) TYPE SPECIES: *Gentianella tetrandra* Moench = *Gentianella campestris* (L.) Borner (*Gentiana campestris* L.). (Name a diminutive of *Gentiana*.)

A genus of perhaps 250 species, nearly worldwide in distribution (absent from Africa) with concentrations in the North Temperate and Arctic zones of Eurasia and North America, and in the Andes of South America (where Gilg recognized 182 species, and Macbride 97 species in Peru alone). Of the several species in the United States, only *Gentianella quinquefolia* (L.) Small, stiff gentian, ague-weed, $2n = 36$, of sect. ARCTOPHILA (Griseb.) J. Holub is found in our area. Two allopatric subspecies (or varieties) of *G. quinque-*

folia have generally been recognized: subsp. *quinquefolia* (with narrowly triangular, hyaline-margined, distinctly keeled calyx lobes 2–2.5 mm long), distributed from southern Maine to western New York, then southward along the Appalachians to northern Georgia; and subsp. *occidentalis* (A. Gray) Gillett (with elliptic-lanceolate to oblanceolate, thick-margined, indistinctly keeled calyx lobes 5–6 mm long), distributed from extreme southern Ontario and northern Ohio, west to south-central Minnesota, and south to northwestern Arkansas and southeastern Kentucky.

Gentianella has been included in *Gentiana* L. by most authors, usually as subg. GENTIANELLA Kusn. However, its relatively large number of distinctive characters, in this portion of the family where generic limits are particularly fuzzy, argue strongly for maintaining it as a distinct genus. The most obvious difference separating *Gentianella* from *Gentiana* is the absence of plicae or folds (plaits, pleats) in the sinuses of the corolla (these are greatly reduced in a few species of *Gentiana*, and generally absent in *G. lutea*, the type of *Gentiana sensu stricto*). In addition, the species of *Gentiana* are characterized by a membranaceous ring of tissue extending completely around the inner rim of the calyx tube (except in *G. Douglasiana* Bong., from western North America), while in *Gentianella* this intracalyxine membrane is completely absent. Finally, the nectariferous glands are borne on the base of the ovary or the gynophore in *Gentiana*, and on the corolla tube in *Gentianella*. This last character is perhaps the most significant one. It is the only one that is entirely constant, and as pointed out by both Gillett and Toyokuni, it suggests that *Gentianella* is more closely related to *Swertia*, *Halenia*, and *Lomatogonium*, all of which have epipetalous glands or spurs, than to *Gentiana*.

Kusnezow (in Gilg, 1895) recognized nine sections in his subg. GENTIANELLA. Of these, sects. IMACOLA Griseb. and CROSSOPETALUM Froel. ex Griseb. are now referable to *Gentianopsis* Ma, and sects. MEGACODON Hemsley and STYLOPHORA Clarke to *Megacodon* (Hemsley) H. Sm. The remaining five sections constitute *Gentianella* in its strictest sense, still a large and complex group that has never been monographed in its entirety. The typical section, GENTIANELLA (sect. *Amarella* (Griseb.) Gillett), contains most of the species of the North Temperate Zone as well as a few in the mountains of tropical America. These are annuals with salverform corollas that are usually fimbriate in the throat. The much smaller, but still primarily North Temperate, sect. ARCTOPHILA (Griseb.) J. Holub (to which *G. quinquefolia* belongs) also contains annual species, but those with salverform or funnellform corollas are not fimbriate in the throat. Gillett, in his treatment of the North American species of *Gentianella*, reduced these sections to series of sect. *Amarella* (GENTIANELLA). The fimbriae in the throat of the corolla are not constant, and corollas of *G. Wislizenii* (Engelm.) Gillett (which Gillett placed in his series *Arctophilae*) vary from efimbriate to densely fimbriate at the base of each corolla lobe, even on the same plant.

By far the largest and most diverse group, sect. ANDICOLA (Griseb.) J. Holub includes most of the Andean species as well as several of Australia and New Zealand. These plants are perennials (occasionally even subglabrous

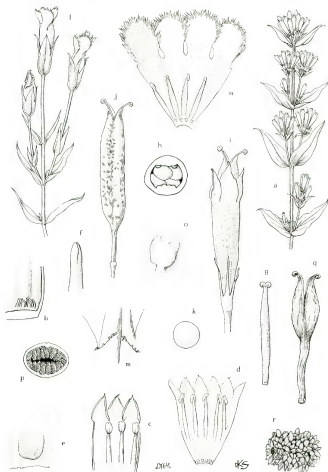


FIGURE 3. *Gentianella* and *Gentianopsis*. a-k, *Gentianella quinquefolia* var. *quinquefolia*: a, upper part of flowering plant, $\times \frac{1}{2}$; b, interior of calyx at base of one lobe, showing intracalyxine squamellae, $\times 25$; c, three corolla lobes and stamens at anthesis, showing position of anthers, $\times 3$; d, opened corolla, showing glands at base and position of anthers after pollen is shed (cf. "c"), $\times 2$; e, detail of gland at base

ones) or rarely biennials with rotate or salverform corollas. The bases of the filaments and/or the base of the corolla tube is occasionally pilose or barbate. Section ANTARCTOPHILA (Griseb.) J. Holub contains a relatively small number of species restricted to temperate South America, Australia, and New Zealand. These plants are supposedly annuals with rotate, glabrous, effimbriate corollas. These last two sections appear to be heterogeneous and should be reevaluated. The distinction of annual vs. perennial habit does not hold, and even *Gentianella montana* (Forster) J. Holub, which was selected by Holub as the lectotype of sect. ANTARCTOPHILA, is a perennial species. The barbate corolla tube and the pilose filaments, used by both Grisebach and Kusnezow to characterize sect. ANDICOLA (although both admitted that neither is constant), are found in relatively few species. Section DASYSYEPHANA Griseb. (not *Dasysephana* Adanson, a genus; see *Gentiana*) contains only *G. thyrsoidea* (Hooker) Fabris, a coarse Peruvian perennial that differs from the above plants principally in that the anthers are basifixed and erect after dehiscence, rather than versatile and pendent. However, several species referable to sect. ANDICOLA in other respects also have erect anthers; this helps to cast doubt on the distinctness of sect. DASYSYEPHANA.

More recently, *Comastoma* (Wettst.) Toyokuni has been segregated from sect. GENTIANELLA—apparently on good evidence. The ten or so species, including the circumboreal *C. tenellum* (Rottb.) Toyokuni, differ from those of *Gentianella* in that there are two epipetalous nectaries per corolla lobe (rather than one) and the fimbriae in the throat of the corolla are united into two nonvascularized scales per corolla lobe (rather than being vascularized, and scattered or united into a continuous ring, if present at all). In addition, those species investigated are $2n = 10$, rather than $2n = 36$, the diploid number characteristic of *Gentianella*. *Comastoma* forms a connecting link between *Gentianella* and *Lomatogonium* A. Br., also with $2n = 10$, and has been united with the latter by several workers.

Chromosome numbers are known for about 30 species in sects. GENTIANELLA, ARCTOPHILA, and ANDICOLA, and all—as pointed out by Weaver and Rüdénberg—are $2n = 36$, with the exception of *G. Moorcroftiana* (Wallich ex Griseb.) Airy Shaw, $2n = 18$ (Mehra & Vasudevan, 1972) and $2n = 26$ (Wada, 1966); *G. auriculata* (Pallas) Gillett, $2n = 48$ (Sokolovskaya, 1968);

of corolla, $\times 20$; f, stigmatic lobes at anthesis (same stage as in "c"), the lobes not yet receptive to pollen, $\times 12$; g, gynoeceum with receptive stigmas, $\times 3$; h, cross section of ovary, showing two placentae, each with two rows of ovules, the two upper ovules visible, $\times 12$; i, mature capsule with marcescent calyx and corolla, $\times 3$; j, open fruit with calyx and corolla removed, $\times 3$; k, seed, $\times 12$. l-r, *Gentianopsis crinita*: l, top of flowering stem (note calyx of two large and two small sepals), $\times \frac{1}{2}$; m, interior (adaxial) side of base of one of small sepals, showing intracalyceine membrane with squamellae, $\times 6$; n, opened corolla, showing glands at base and stamens, $\times 1$; o, detail of gland from corolla, $\times 10$; p, cross section of ovary, showing placentation, $\times 6$; q, mature capsule, calyx and corolla removed, $\times 1$; r, seed, $\times 40$.

and *G. uliginosa* (Willd.) Borner, $2n = ca. 54$ (Holmen in Löve & Löve, 1961). The base number is clearly $x = 9$ for the great majority of the species investigated.

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5. *Gentianopsis* Ma, *Acta Phytotax. Sinica* **1**: 7. 1951.

Annual or biennial [rarely perennial], glabrous [or minutely pubescent], taprooted herbs. Lower leaves arranged in a loose rosette [or rosette dense to absent], attenuate into an indistinct petiole, often withering before anthesis; cauline leaves opposite, sessile, the bases of each pair connected by a transverse line. Flowers 4-merous, large and showy [rarely small], blue or rarely white, long-pedicellate [rarely short-pedicellate to nearly sessile], in few-flowered monochasia or solitary [rarely the plants subscapose], the buds large, ellipsoid, flattened. Calyx persistent, shorter than or equal to the corolla tube, the tube well developed, the lobes [usually] carinate, hyaline margined, the 2 outer ones [usually] plicate, longer and narrower than the inner ones [rarely the lobes nearly equal], each sinus with a thin inner membrane bearing few to many blunt squamellae. Corolla marcescent, broadly funnel-form, the tube with 4 cushionlike glands near the base and alternate with the stamens, the lobes dextrorsely contorted in bud, spreading at anthesis, about as long as the tube [or shorter], oblong to spatulate [or orbicular], the margins ciliate in the upper two thirds [more rarely the tips denticulate or the lobes nearly entire]. Stamens included, inserted in the lower half of the corolla tube; filaments with broad [to narrow], lateral, membranaceous wings; anthers distinctly longer than broad, versatile, introrse before dehiscence but bending backward upon dehiscence and appearing extrorse. Stigma with 2 broad, reniform [suborbicular or oblong] lobes; style very short but distinct [rarely absent]; ovary stalked, fusiform, 1-locular, with the numerous ovules covering most of the inner surface. Seeds numerous, oblong [rarely ellipsoid], covered with elongate papillae [rarely seeds reticulate, caudate]. (*Anthopogon* Necker; *Gentiana* L. sect. *Crossopetalum* Froel. ex Griseb.; *Gentianella*

Moench subg. *Eublephis* (Raf.) Gillett.) TYPE SPECIES: *Gentiana crinita* Froel. = *Gentianopsis crinita* (Froel.) Ma.

A genus of 16–25 species distributed throughout most of the boreal and north temperate regions of Eurasia and North America with extensions into the arctic and mountainous areas of the tropics (central Mexico). Although several species are found in the United States, only *Gentianopsis crinita*, $2n = 78$, enters our area. Typical *G. crinita* ranges from central Manitoba, south through the Dakotas and Iowa, and east through the Great Lakes States and southern Quebec to the Atlantic Coast from southern Maine to Maryland and New Jersey, with a few localities along the Appalachians into southwestern North Carolina. Gillett, who included the fringed gentians in *Gentianella* Moench, treated *Gentianopsis Victorinii* (Fern.) Ilitis, of the Saint Lawrence Valley, *G. procera* (T. Holm) Ma, of the Great Lakes States, and *G. Macounii* (T. Holm) Ilitis, of the prairie areas of the northern United States and Canada, as subspecies of *G. crinita*, but most other authors have considered them to be distinct species.

The fringed gentians form a seemingly natural group, but their proper taxonomic rank has been much debated. Most authors have regarded them as a section of the large, inclusive genus *Gentiana* L. Others have segregated *Gentianella* Moench from *Gentiana* and have included the fringed gentians as a section of that genus. The arguments of Ma and, more recently, Ilitis for treating *Gentianopsis* as a distinct genus seem convincing and are accepted here.

Gentianopsis can be separated from *Gentianella*, its closest ally, by a number of characteristics: constant tetramery (vs. tetramery or pentamery); squamellate intracalyxine membranes at the base of and alternate with the calyx lobes (vs. absent); seeds distinctly papillate and generally oblong or angular (vs. smooth and globose or slightly flattened); ovules borne over practically the entire inner surface of the ovary (vs. borne in two rows along the margins of each suture or rarely in a third row between the sutures); and surface of pollen grains reticulate, with relatively large, angular lumina and adjacent smaller ones (heterobrochate) (vs. surface pattern uniformly reticulate, striate, or striate-reticulate).

In addition, the floral vasculature of three species of *Gentianopsis* (*G. crinita*, *G. detonsa* (Rottb.) Ma, and *G. thermalis* (O. Kuntze) Ilitis) has been shown to differ from that of the several species of *Gentianella* studied. In *Gentianopsis* the lateral traces of adjacent calyx segments are fused, as are the ventral traces of adjacent carpels at their origin, although the latter soon become free. In *Gentianella* the adjacent calyx laterals are free, while the adjacent carpel ventrals are fused throughout most of the ovary.

Two widely different chromosome numbers have been reported in *Gentianopsis*: $2n = 44$ for the European *G. ciliata* (L.) Ma and the circumboreal *G. detonsa*, and $2n = 78$ for *G. crinita* and *G. procera*. Doris Löve mentioned, without elaboration, that these groups are "morphologically very well distinguishable" and maintained that "from an evolutionary standpoint it is

very unlikely that both these groups represent the same ancestral line." She therefore suggested that these groups, if segregated from *Gentianella*, be placed in separate genera. Gillett, on the other hand, maintained that *G. crinita* and *G. detonsa* are very close morphologically and that they form a single large species or else two rather weak ones. (He chose the latter alternative in his treatment.) As pointed out by Iltis, very few of the taxa of *Gentianopsis* have been investigated cytologically, and to segregate the *G. ciliata*-*G. detonsa* and the *G. crinita*-*G. procera* groups into separate genera on the basis of chromosome number would be premature.

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6. *Frasera* Walter, Fl. Caroliniana, 87. 1788.

Coarse, long-lived monocarpic perennials from a thick taproot [or rather delicate, nonmonocarpic perennials from a woody, horizontal rhizome]. Stems simple, erect, hollow, to 3 m tall [or much shorter in many western American species]. Leaves [opposite or] in whorls of 4 (or 5) [conspicuously white margined], the lower ones tapering to a winged petiole and arranged in a basal rosette, the cauline ones sessile, weakly connate at the base, not decurrent [or the plants subscapose with only a basal rosette]. Inflorescence paniculate, composed of long-pedunculate, modified dichasia arranged in whorls from the upper leaf axils [or dichasia nearly sessile, or rarely the inflorescence a simple terminal raceme or panicle]. Flowers tetramerous. Calyx persistent, deeply divided, the 4 lobes in 2 unequal pairs. Corolla rotate, the 4 lobes united only at the base, greenish-white [bluish], with numerous purplish, blackish, or dark green spots or streaks, each lobe bearing below its middle a large, circular gland conspicuously fringed along its margin [or the gland lunate, linear, deeply bilobed, or tubular] and at its base an inconspicuous, short-fringed coronal scale [or the scale conspicuous and long-fringed or petaloid, or absent]. Stamens inserted in the sinuses of the corolla lobes; filaments subulate-filiform; anthers oblong, reflexing upon dehiscence. Ovary ovate-fusiform, sessile; style filiform, persistent; stigma bilobed, the lobes minute, ovate-orbicular. Capsule flattened parallel to [or rarely opposite] the valves, surrounded by the marcescent corolla and persistent calyx. Seeds dark brown, crescent shaped, finely pitted [or nearly smooth], completely encircled by a membranaceous wing. TYPE SPECIES: *F. caroliniensis* Walter. (Name commemorating John Fraser, 1750–1811, Scottish plant collector and traveler in North America, who published Walter's *Flora Caroliniana*.)—COLUMBO, GREEN GENTIAN.

A genus of about 15 species, with all but one in the mountainous areas of the western United States, often at high elevations. A single species, *Frasera caroliniensis* (*Swertia caroliniensis* (Walter) Kuntze), $2n = 78$, occurs widely in eastern North America. Its distribution is centered in the lower Ohio River valley but extends from Michigan, southern Ontario, and western New York, south to Alabama and Louisiana, and west to eastern Oklahoma. It has been collected in every state in our area except Florida, but only in Tennessee can it be said to be at all common and widespread. It is typically a plant of upland deciduous forests, particularly around their margins and in clearings.

Frasera caroliniensis, as well as several other species, has usually been described as a biennial or triennial. However, Threadgill, Baskin, and Baskin (1981b) recently reported that the plants mature slowly and remain in a rosette stage for an undetermined, but probably prolonged, period. Inouye and Taylor have postulated that in the closely related western American *F. speciosa* Douglas, the minimum age before flowering is 25 to 30 years. Plants of both species die after flowering; most of the species, however, are not monocarpic.

The conspicuous glands on the corolla lobes of all species produce copious nectar. At least *Frasera caroliniensis* appears to be pollinated by several species of bumblebees (*Bombus* spp.). Strong proterandry and the movement of the stamens away from the stigma after dehiscence are adaptations that promote outcrossing.

Frasera is often included in *Swertia* L., the circumscription of which is perhaps the most controversial in the Gentianaceae. It is typified by *S. perennis* L., a plant widespread in alpine areas across much of the Northern Hemisphere, including those in western North America. Perhaps 15 closely related and certainly congeneric species are native to Eurasia. Most modern authors interpret *Swertia* to include *Ophelia* Don, *Stellera* Turcz., and *Anagallidium* Griseb., all restricted to the Old World, and some go so far as to include *Lomatogonium* A. Br. and *Veratrilla* Baillon. The critical characters within the group are plant duration and habit, number of flower parts, number of glands per corolla lobe and morphology of these glands, presence or absence of a style, seed morphology, pollen grain morphology, nodal anatomy, and chromosome number. These groups have not been studied and compared on a world-wide basis since Grisebach's monograph of the family (1845), so overall patterns in the variation or expression of the above characters are not well understood.

Plants of *Frasera* differ most consistently from the other swertoid Gentianaceae in having a distinct, filiform style. In all of the others, the stigma is sessile or nearly so. In addition, the bases of the cauline leaves in *Frasera* are weakly connate and not decurrent, rather than free and decurrent along the length of an internode. The flowers of *Frasera* are always tetramerous, with a single gland per corolla lobe, while those of *Swertia* are usually pentamerous with two glands per corolla lobe. However, several species of *Swertia* are either tetramerous or have a single gland on each corolla lobe.

Nilsson found the pollen of *Frasera* to be morphologically distinct from that of *Swertia*, except for the northern Asian *S. tetrapetala* Pallas. Toyokuni recently transferred this and several other Japanese species to *Frasera*, but this alignment is contradicted by other characters.

Chromosome numbers (all based on 13) have been reported for several *Frasera* species, but only a few species of *Swertia* have been investigated cytologically. The perennial species of *Swertia* (sensu stricto) have numbers mostly based on 14, but 9, 12, and 13 have been reported. *Swertia perennis* itself is variable, with $2n = 18, 24$, and 28 . The annual species, sometimes treated in *Ophelia*, have chromosome numbers based on 10, 12, and 13.

The species included in *Frasera* by Card and others form an undoubtedly natural group. In the absence of a modern, comprehensive investigation of the swertoid Gentianaceae, we prefer to maintain them as a distinct genus.

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7. **Obolaria** Linnaeus, *Sp. Pl.* **2**: 632. 1753; *Gen. Pl.* ed. 5. 280. 1754,
"Obularia."

Low, fleshy, perennial herbs; glabrous except for a few glandular hairs in
the axils of the leaves and the sinuses of the corolla; the roots coralloid my-
corrhizae. Leaves sessile, purplish, the lower scalelike, the upper spatulate
to obdeltoid, the bases decurrent the entire length of the internode, the vena-
tion distinct. Flowers sessile or short-pedicellate, usually in 3's or solitary
by abortion of the lateral flowers, each group of flowers subtended by a pair
of foliaceous bracts. Calyx of 2 free, foliaceous sepals, with a few squa-
mellae on the adaxial side near the base. Corolla imbricate, narrowly cam-
panulate, marcescent, divided nearly to the middle into 4 lobes; tube with
inconspicuous, fimbriate scales below the base of each stamen; lobes acute,
crose. Stamens 4, inserted at the sinuses of the corolla, equal in length; an-

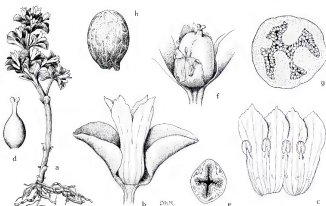


FIGURE 4. *Obolaria*. a–h, *O. virginica*: a, plant with flowers, $\times \frac{1}{2}$; b, flower, $\times 3$; c, corolla laid open to show minute fimbriate scales, introrse anthers, $\times 3$; d, gynoeceium, nectariferous tissue not shown, $\times 3$; e, cross section of ovary, $\times 6$; f, nearly mature fruit with marcescent corolla, $\times 3$; g, cross section of nearly mature fruit, $\times 6$; h, seed, $\times 100$.

thers nearly square, dorsifixed, introrse. Ovary sessile, glandular at base, somewhat flattened, 1-locular, the minute ovules very numerous, borne over practically the entire surface of the locule; style short; stigma bilobed, the lobes orbicular, erect, apparently receptive only along the edges. Capsule plump, 1-locular, thin walled, rupturing irregularly. Seeds minute, very numerous, ovoid, minutely striate. (*Shultzia* Raf., 1808; not *Obolaria* Siegesb. ex Kuntze, 1891, = *Linnaea* Gronov. ex L.) TYPE SPECIES: *O. virginica* L. (Name from *obolos*, a small Greek coin, from the fleshy, rounded leaves.)—PENNYWORT.

A single species, *Obolaria virginica* L. (*Shultzia virginica* (L.) Kuntze, *S. obolarioides* Raf.), $2n = 56$, a plant chiefly of moist, shady sites in deciduous forest, distributed from northern New Jersey, west to northern Ohio, southern Indiana, southern Illinois, western Tennessee, southeastern Missouri, and easternmost Arkansas, and south to central Alabama and Georgia and eastern North Carolina, with outlying stations in northern Florida (Jefferson County) and eastern Louisiana (East Feliciana Parish); also reported from Texas. The proterandrous flowers are produced in spring (early March to late May); the seldom-collected fruits mature from late May to early June. The plants are inconspicuous, often barely protruding from the litter on the forest floor, and are easily overlooked.

The generally reduced size of the plants, the purple coloration, and especially the mycorrhizae (which lack root hairs) have led to the suggestion of various degrees of saprophytism or parasitism. However, no haustorial connections with other plants have been found and much chlorophyll is present in the leaves; the plant is thus "able to provide its own starch" (Holm). The physiology has not been studied, and nothing seems to be known of embryology or other details of the life history.

The calyx of *Obolaria*, consisting of two free, foliaceous sepals, is unique among Gentianaceae. The resemblance of the sepals, both in shape and venation, to the leaves and bracts has led some investigators to conclude that *Obolaria* lacks a calyx.

Holm considered the fimbriate scales near the base of the corolla to be nectariferous. However, Lindsey, in his survey of the floral anatomy of the family, found glandular material at the base of the ovary. These macroscopically visible glands are more likely the nectaries.

Decurrent leaf bases are unusual among Gentianaceae. The common condition is for the bases of each pair of leaves (or the petiole bases) to be united, forming a sheath around the stem. The exceptional condition has been noted only in *Obolaria*, *Bartonia*, and *Swertia*.

The relationships of this well-marked genus are somewhat obscure. *Obolaria* has consistently been most closely associated with *Bartonia*, a genus also characterized by mycorrhizae, the presence of glandular hairs in the axils of the leaves (these also in the corolla sinuses of *Obolaria*), the imbricate veneration of the corolla (in contrast with the usual convolute veneration in other Gentianaceae), and the decurrent (rather than connate) leaf bases. It differs conspicuously, however, in its relatively robust stature, as well as in

having well-developed, characteristic leaves, a calyx of two free, leaflike sepals, inconspicuous fringed scales within the corolla tube, and nectaries at the base of the ovary.

Holm presumed the presence of fimbriate scales on the corolla tube to indicate a relationship with *Swertia*. Nilsson and Skvarla suggested a relationship with the same genus on the basis of pollen-grain morphology, although both Gilg and Kohler had considered the pollen of *Obolaria* to resemble more closely that of *Sabatia*, *Centaurium*, and *Enicostema* Blume.

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8. *Bartonia* Muhlenberg ex Willdenow, Ges. Naturf. Freunde Berlin Neue Schr. **3**: 444. 1801, nom. cons.²

Low, erect (rarely twining) annuals with reduced mycorrhizae, lacking root hairs, presumably partially saprophytic or parasitic. Stems very slender, quadrangular, green to purple, the leaves reduced to minute, opposite to alternate subulate scales with a few glandular hairs at base on adaxial surface. Inflorescence basically of pedunculate dichasia, these terminal and axillary from the upper nodes, sometimes appearing to be racemose by reduction of the lateral dichasia or sometimes reduced to a single flower (especially in *Bartonia verna*). Flowers 4-merous, long-pedicellate. Calyx with a short tube or the 4 lobes nearly free, the 2 outer overlapping the 2 inner. Corolla campanulate, deeply 4-lobed, the lobes imbricate (2 lobes without, 2 within) in bud, each lobe with 1 (in *B. verna*) or 3 veins, greenish yellow, white, or

²Conservation superfluous; see Rickett and Stafleu, *Taxon* **9**: 79. 1960.

pinkish to purplish, marcescent. Stamens 4, alternate with the corolla lobes; filaments short, somewhat dilated, attached at sinuses of corolla lobes; anthers ovate to oblong, mucronate, rounded or emarginate, introrse, frequently deciduous after anthesis, yellow or purple. Gynoecium sessile or somewhat stipitate, the stout style hardly differentiated from the ovary, the 2 stigmas decurrent, usually to top of ovary; ovary oval to elliptic in outline, compressed to quadrangular, unilocular, with numerous minute, 1-integumented ovules covering the entire inner surface on branched, protruding ridges. Fruit a thin-walled, 2-valved capsule, dehiscent along the sutures from the tip or from below the style (thus opening only in the middle). Seeds very numerous, minute, ellipsoid, smooth to minutely reticulate. (*Centaurella* Michaux, 1803; *Centaureum* Pers., 1805, not Hill, 1756; *Agina* Necker ex Post & Kuntze, 1903; not *Bartonia* Sims, 1812, = *Mentzelia* (L.) BSP.) TYPE SPECIES: *B. tenella* Muhl. ex Willd. = *B. virginica* (L.) BSP. (Named for Professor Benjamin Smith Barton, 1766–1815, physician and botanist of Philadelphia, one of the earliest teachers of botany in the United States.)

Three (or possibly four) species, entirely eastern North American in distribution, often of sporadic occurrence, all plants of usually moist, acid soils in peaty, sandy, or sphagnum habitats. The species can be divided into two remarkably distinct groups. Characterized by the combination of early flowering period (November in the south to mid-April in the north), white, one-veined corolla lobes that are three times the length of the calyx, and a capsule opening septicidally below the persistent "style," *Bartonia verna* (Michaux) Raf. ex Barton, $2n = 44$, ranges northward from Broward and Lee counties, Florida, westward on the Gulf Coastal Plain to eastern Louisiana and northward on the outer Atlantic Coastal Plain to southeastern North Carolina (Carteret County).

Both *Bartonia paniculata* (Michaux) Muhl., $2n = 52$, and *B. virginica* (L.) BSP., $2n = 52$, are summer-flowering species (July to late September) with smaller, three-veined corolla lobes up to twice as long as the calyx. Characterized by essentially alternate scale leaves; whitish to purplish, oblong, acute corolla lobes; and a completely two-valved capsule, *B. paniculata* occurs from northern Florida to eastern Texas, northward to Oklahoma, Arkansas, and Kentucky, and especially along the Atlantic Coastal Plain to New England, Nova Scotia, and Newfoundland. It has a single disjunct population in southern Ontario. The southern representative is the more slender, frequently twining, yellow-anthered subsp. *paniculata* (*B. lanceolata* Small), while northward, especially from Rhode Island and Massachusetts to Newfoundland, occurs subsp. *iodandra* (Robinson) Gillett (including vars. *iodandra* (Robinson) Fern., *sabulonensis* (Fern.) Fern., and *intermedia* Fern.), characterized by stouter habit, generally purplish color, and somewhat larger (0.5–1 mm vs. ca. 0.5 mm long), usually purple anthers. Gillett noted free intergradation between the subspecies and mapped intermediates from Mississippi, Alabama, and eastern North Carolina, northward to southern Maine and Nova Scotia.

Bartonia virginica, differing in the mostly opposite scale leaves, the greenish yellow, oblong corolla lobes with an apiculate, erose, or entire apex, and

the capsule opening as in *B. verna*, is distributed from central Florida and southern Louisiana, northward to eastern Tennessee, Wisconsin, Michigan, southern Ontario, southern Quebec, and Nova Scotia. The ranges of *B. paniculata* and *B. virginica* overlap in large part; the two sometimes grow together, but usually remain distinct, although putative intermediates have been reported from Mississippi, Alabama, and eastern Virginia, northward to Nova Scotia. Further studies of variation are desirable. (See Gillett.)

Recently an additional species, *Bartonia texana* Correll, has been described from southeastern Texas. This plant reputedly differs from *B. paniculata* in its shorter calyx and corolla, its elliptic and obtuse to obtuse-apiculate (rather than lanceolate and acute or acuminate) corolla lobes, and its capsule usually exceeding (rather than shorter than) the corolla. An isotype, however, suggests that "*B. texana*" may represent merely slightly abnormal populations of *B. paniculata*.

The genus is well marked by the greatly reduced vegetative parts, the tetramerous flowers with imbricate vexillum, the peculiar decurrent stigmas, and the numerous minute ovules over the entire surface of the single locule. It is presumably most closely related to *Obolaria* but represents a further stage in specialization. The presence of two types of capsular dehiscence in *Bartonia* is of interest in connection with the distinctions made between *Leiphaimos* and *Voyria*.

All three species are said to be annuals, but little has been recorded of their life histories. On the basis of the coralloid mycorrhizae and greatly reduced leaves, partial saprophytism or partial parasitism has been supposed, although the plants are green and the habitat is a peculiar one for a saprophytic existence. No haustorial connections with other vascular plants have been found, but the possibility of parasitism via a fungal "bridge" (as demonstrated in *Monotropa*; see Furman & Trappe) should be investigated.

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9. *Eustoma* Salisbury, *Paradisus Londinensis* **1**: pl. 34. 1806.

Glaucous, erect, annual or perennial, taprooted herbs, usually of somewhat calcareous or alkaline open habitats. Leaves opposite, sessile, more or less clasping, palmately veined. Flowers large, long-pedicellate, in few-flowered monochasia. Calyx persistent, longer than the corolla tube, the tube short, the 5 (or 6) lobes long-acuminate, keeled abaxially. Corolla showy, blue-purple, rose-purple, violet, pink, white, or rarely yellow, campanulate-fun-

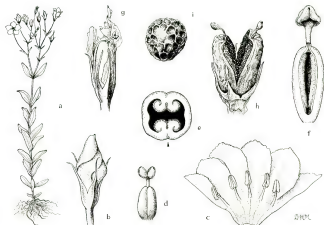


FIGURE 5. *Eustoma*. a-i, *E. exaltatum*: a, small plant in flower, $\times \frac{1}{4}$; b, flower bud, $\times 1$; c, corolla laid open to show contorted imbrication and epipetalous stamens, $\times 1$; d, gynoecium, $\times 1$; e, cross section at middle of ovary, $\times 3$; f, gynoecium, the ovary in vertical section, position indicated by arrow in "e," $\times 2$; g, nearly mature capsule with marcescent corolla, $\times 1$; h, mature fruit, showing dehiscence and numerous seeds on four placentae, $\times 2$; i, seed, $\times 50$.

nelform, marcescent, dextrorsely contorted in bud, the 5 (or 6) lobes ascending, longer to much longer than the broadly campanulate tube. Stamens 5 (or 6), inserted in the throat of the corolla below the sinuses; filaments slender; anthers versatile, oblong, longitudinally dehiscent, extrorse, straight, not recurving. Stigma with 2 broad, oval to suborbicular lobes; style slender, shorter than to as long as the ovary, the base persistent; ovary 1-locular with 2 bilamellate, parietal, weakly projecting placenta with very numerous ovules, glandular at base, but the glands not macroscopically discernible. Capsule oblong or ovoid, 1-locular, 2-valved, dehiscent through the placenta. Seeds minute, very numerous, globose, densely pitted, detaching from the persistent funiculi on the placenta. (*Dupratzia* Raf.) TYPE SPECIES: *E. silenifolium* Salisb. = *E. exaltatum* (L.) Salisb. ex G. Don. (Name from Greek, *eustomos*, "a beautiful mouth," or "of good countenance," alluding to the beautiful throat of the corolla).

Three species, two partly in our region, the third, *Eustoma Barkleyi* Standley ex Shinnars, apparently known only from a limited area in Coahuila, Mexico. *Eustoma exaltatum*, catch-fly gentian, ranges from the Greater Antilles to the Bahamas and into coastal areas, open pinelands, coastal sand dunes, and openings in hammocks of southern and central Florida, southern Mississippi, and southern Louisiana; thence across southern Texas, and sporadically inland in calcareous or alkaline soils through New Mexico to southern California, and south through Mexico and Central America into Venezuela. *Eustoma grandiflorum* (Raf.) Shinnars (*E. Russellianum* (Hooker) G. Don ex Sweet), Texas bluebell, prairie gentian, is a showier, larger-flowered plant (corolla lobes 2.5–5 cm long vs. 1.4–2.6 cm), of more inland range, from southern Texas and northern Mexico to New Mexico, Utah, Wyoming, Colorado, Nebraska, Kansas, and Oklahoma. A single collection has been reported by Moore from Arkansas (Arkansas County). Shinnars suggested "very extensive introgression between the[se] two most wide-ranging species where their ranges overlap in southern Texas," as well as between *E. grandiflorum* and *E. Barkleyi*, and pointed to the desirability of a detailed genetic and biometric study of the genus. A number of color forms (see Shinnars) have been distinguished in *E. grandiflorum*, which merits more frequent cultivation. Both single- and double-flowered forms of this species are grown in Japan for cut flowers.

The affinities of *Eustoma* have been the subject of some debate. Grisebach did not treat the genus at all in his *Genera et Species Gentianearum* (1839) but later (1845) included it in his tribe Chloreae, next to *Sabatia*. The basic character used in delimiting the Chloreae was the presence of a completely deciduous style, even though the base of the style in *Eustoma* is persistent. Bentham and Hooker placed *Eustoma* in the tribe Chironeae, subtribe Lisantheae, with five other genera, all restricted to the American tropics. Characters used to delimit this subtribe included the presence of a bilamellate stigma and a persistent style. Gilg treated the genus in his tribe Gentianeae, subtribe Tachiinae, with six neotropical genera (including several associated with it by Bentham and Hooker) in addition to the Malagasyan genus *Tach-*

ladenus Griseb. Gilg's tribes and subtribes were delimited primarily on the characters of the pollen grains, and Gentianeae-Tachiinae were characterized by having single grains (monads) with a reticulate exine pattern.

Work since Gilg's time has more or less supported his placement of *Eustoma*. Chromosome numbers reported for *E. exaltatum*, $2n = \text{ca. } 72$, and *E. grandiflorum*, $2n = 72$, support a relationship with *Lisianthus* P. Br. (nine species with $2n = 36$), one of its closest relatives in Gilg's system. According to Lindsey, the vascular anatomy of the flowers of *Eustoma* supports its inclusion in the Gentianeae-Tachiinae, but he noted that it appears to be the least specialized member of the group. Lindsey also reported the presence of glandular tissue at the base of the ovary. These glands, however, are not macroscopically discernible, whereas other genera in Gilg's Gentianeae-Tachiinae have a well-developed glandular disc at the base of the ovary. It seems that *Eustoma* is somewhat transitional between *Gentiana* and its relatives in Gilg's Gentianeae subtribe Gentianinae, and *Lisianthus* and other genera associated with it in the Gentianeae subtribe Tachiinae.

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10. *Voyria* Aublet, Hist. Pl. Guiane Fr. 1: 208. 1775.

Small, erect, presumably saprophytic herbs with mycorrhizae, lacking chlorophyll. Leaves opposite, scalelike, usually small and inconspicuous. Flowers in terminal cymose inflorescences [or solitary], ebracteate or 1[-3]-bracteate, usually 5-merous. Calyx of 5 [rarely 4 or 6] lobes, persistent [or deciduous], much shorter than the corolla tube, often with 5 glandlike structures within, these probably representing fused masses of calycine squamellae. Corolla white or pinkish [yellow, orange, blue, rose, or reddish purple], usually salverform [or rarely clavate], with a long tube, [4 or] 5 [or 6]-lobed [the lobes rarely reduced to teeth], lobes contorted in aestivation, corolla marcescent. Anthers nearly sessile [or filamented], introrse, sometimes connate, the base of each half [obtuse, acute, or] more or less elongated into a subplumose bristle; pollen very small, [circular to oval or irregular in polar view, in lateral view convexo-concave, or convexo-plane to ovate-flattened], 1-3-porate. Stigma peltate [or capitate], bilobed; style usually distinct, filiform, short [or long], persistent; ovary spindle shaped [or ovoid and sometimes with 2 stalked nectaries at the base], 1-locular, the 2-lobed placenta parietal along the sutures, the ovules very numerous, [anatropous, 1-integumented] to much reduced, straight, and without a distinguishable integument. Capsule surrounded by the persistent membranaceous corolla, 2-valved, fenestrate (dehiscing in the middle, not at base and apex) [or completely 2-valved from the apex]. Seeds numerous, small, spindle shaped with threadlike tails [or globose, sometimes winged], with a few endosperm cells and rudimentary embryo; in ours, sterile ovules developing into scattered hairlike structures ("paraphyses") persistent on the placenta. (Including *Leiphaimos* Schlecht. & Cham. Linnaea 6: 387. 1831. Type species: *L. parasitica* Schlecht. & Cham.) LECTOTYPE SPECIES: *V. rosea* Aublet.³ (Local name for these plants in French Guiana; "elle est nommée *Voyria* par les Garipons.")

About 30 species (placed in six sections by Progel), centered in the lowland forests of tropical Central and South America, but also in the West Indies, with one (*Voyria primuloides* Baker) in West Africa. The northernmost, and one of the most widespread species, *V. parasitica* (Schlecht. & Cham.) Ruyters & Maas (*Leiphaimos parasitica* Schlecht. & Cham., *V. mexicana* Griseb.), of sect. LEIPHAIMOS Griseb., is primarily of the Bahamas, Cuba, Hispaniola, Jamaica, southeastern Mexico, and Honduras, but reaches the extreme south of our area in hammocks of subtropical Florida (Dade and Monroe counties). The species is easily recognizable by the small, whitish flowers arranged in open cymose inflorescences.

³Although the general practice in these treatments has been to avoid the designation of lectotype species, which are more appropriately chosen by monographers, in this instance the choice seems clear: Aublet's genus is based largely on *Voyria rosea*, which is much more fully described and is illustrated in greater detail than *V. caerulea* Aublet (noted as "altera species"). In this we disagree with Raynal (*Adamsonia* II. 7: 64. 1967), who instead chose *V. caerulea* without discussion.

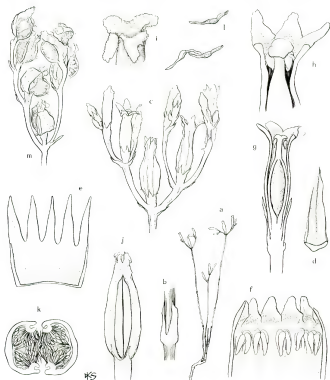


FIGURE 6. *Voyria* (*Leiphaimos*). a-m, *V. parasitica*: a, plant with flowers and immature capsules, $\times \frac{1}{2}$; b, stem node, showing perfoliate leaf-pairs, $\times 6$; c, inflorescence with buds, flowers, and developing fruits, showing cymose arrangement, $\times 3$; d, adaxial surface of inflorescence bract, showing position of basal gland (densely stippled area), $\times 12$; e, calyx laid open to show glandlike structures (probably representing fused masses of squamellae), $\times 24$; f, upper part of corolla laid open to show reflexed anther halves, $\times 12$; g, flower in vertical section, $\times 12$; h, detail of upper part of flower (part of corolla removed), showing relationship of anthers to stigma, $\times 12$; i, stigmas with two adherent, flaplike pollen masses below, $\times 25$; j, mature but undehiscent capsule partly enclosed by persistent corolla, $\times 6$; k, cross section of dehiscent capsule, showing parietal placentation, dehiscence occurring between the placentae (many seeds and paraphysislike hairs omitted), $\times 12$; l, seeds, membranaceous seed coat elongated as wings (or tails), $\times 25$; m, infructescence of dehiscent capsules, showing hairs along suture margins, $\times 3$.

Members of this curious genus, all of which have mycorrhizae and lack chlorophyll, have been supposed to be saprophytes dwelling in humus, fallen leaves, and decaying wood, but parasitism has also been suggested, and it is most likely that members of *Voyria* (and *Voyriella* Miq.) are parasites of the *Monotropa* type (see Furman & Trappe). The species of *Voyria* are notable for their wide range in corolla size, color, and shape; diversity in anther shape, appendages, filaments, and connation; variation in inflorescences, calyx, and nectar glands at the base of the ovary and within the calyx; and extreme reduction of embryo and endosperm.

The genus is here maintained in the sense of Progel (its most recent monographer) and of Bentham and Hooker, rather than that of Gilg, who restricted *Voyria* to a group of about six species, mostly with thick, fleshy mycorrhizae, relatively large flowers, completely bivalved capsules that open from the top, and slightly convexo-concave pollen with two "polar" germ pores. Gilg maintained *Leiphaimos*, of which ours is the type species, for those species with more delicate mycorrhizae, smaller flowers, capsules that open only in the middle (the valves above and below remaining united), and ovoid pollen with a single apical pore. Badly overemphasizing incompletely studied pollen characteristics, he even assigned the two genera to different tribes.

The supposed differences, however, appear to be inconsistent. There seems to be no discontinuity in the degree of vegetative development or in the size of the flower (corolla length 3.5–11 cm in *Voyria* vs. 1–4.5 cm in *Leiphaimos*). The number of bracts (used by Jonker, 1936b) varies from three to none, often depending upon the position of a flower in the inflorescence. Although the manner of dehiscence of the capsule is often characteristic, it should be noted that the capsules of many species are unknown, and Splitgerber described and illustrated that of a *Leiphaimos* (his *V. aurantiaca*) with a completely 2-valved capsule. Both types of dehiscence occur in *Bartonia*, the species of which are likewise much reduced vegetatively. Both "bent" and "straight" pollen sometimes occur in the same flower (Jonker, 1936a; however, cf. Nilsson & Skvarla), and the number and size of pores vary. Erdtman commented, "Pollen morphology does not argue in favor of \pm pronounced differences (cf. Svedelius 1902) between *Leiphaimos* and *Voyria*. A parallel to the partial aperture reduction in (these) genera is found in Apocynaceae (*Landolphia* sect. *Saba*)." Nilsson and Skvarla agreed that neither the pollen shape nor the number of apertures is stable enough to differentiate *Leiphaimos* as a genus distinct from *Voyria*.

More recently, Raynal has suggested that *Leiphaimos* be restricted to the type species, *L. parasitica*. The supposedly unique characteristics of this species are its scorpioid inflorescence and its peculiar stigma, which Raynal described as bilobed with a pendent, glandlike flap on both sides between the lobes. However, our own observations have shown that the inflorescences of *Voyria parasitica* are commonly normal compound dichasia, rather than scorpioid ones. In addition, the anthers dehisce directly against the stigma, and the stigmatic flaps reported by Raynal are merely coalesced masses of germinated pollen grains (FIGURE 6, i).

Williams divided the Central American saprophytic gentians between *Lei-*

phaimos and *Voyria*, using characters of the capsule and seeds to distinguish the two. According to him, species with wingless ovoid or trigonous seeds and no elaterlike hairs (paraphyses) within the capsule belong to *Voyria*, while those with flattened, winged or appendaged seeds, and elaterlike hairs within the capsule belong to *Leiphaimos*. Although these characters may yet prove to be important, the South American species were not included in Williams's study. Elias and Robyns found the conclusions of Raynal and of Williams contradictory and combined *Voyria* and *Leiphaimos* in the *Flora of Panama*.

Altogether, the combinations of characters are reticulate, and in the absence of a modern and balanced monograph, the generic treatment of these imperfectly known plants followed by most authors previous to Gilg seems the most reasonable. The relationships of *Voyria* to other Gentianaceae are not clear. Most authors have considered the genus to be closely allied to *Voyriella* Miq., a bitypic, achlorophyllous, mycotrophic South American genus, but recent evidence, particularly palynological, argues against such a relationship (Nilsson & Skvarla).

Few species have been studied embryologically. A variety of seed types occur, and a reduction series from anatropous, one-integumented ovules to apparently straight ovules with no distinguishable integument is indicated. The megagametophyte appears to be of the Polygonum type. Both endosperm and embryo are much reduced, reaching an extreme of three and two cells, respectively. The chromosome number of "*Leiphaimos azurea*" (*L. azurea* (Karsten) Gilg = *V. tenella* Hooker, according to Jonker, 1936b) has been reported as $2n = 36$.

Aublet said that the fleshy rhizomes of *Voyria rosea* and *V. caerulea* were eaten by the Indians of French Guiana.

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THE GENERA OF VERNONIEAE (COMPOSITAE) IN THE
SOUTHEASTERN UNITED STATES¹

SAMUEL B. JONES, JR.

VERNONIEAE Cassini, Jour. Phys. Chim. Hist. Nat. Arts **88**: 203. 1819.²

Perennial or annual herbs, [shrubs, rarely trees or vines]. Leaves alternate, rarely opposite or whorled, sessile or petiolate. Heads homogamous, 1- to many-flowered, sometimes syncephalous, the receptacles flat or subconvex, usually smooth or pitted, rarely hairy, bristly, or chaffy. Flowers usually perfect; phyllaries many, in several series, closely or loosely imbricate, or rarely few and not imbricate. Pappus in one or more series, usually setose, the bristles in some genera flattened or rarely reduced or lacking. Corollas tubular (subligulate in *Stokesia*), tube elongate, limb with 5 narrow lobes, rarely (3- or) 4-lobed and slightly bilabiate, deep purplish-red, white, or blue [rarely yellow to orange in some Old World species], frequently glandular. Anthers with or without auriculate basal appendages; pollen grains echinate to lophate. Style branches slender, acute or slightly obtuse, uniformly and shortly hirsute, the stigmatic papillae on the inner surface toward the base (see Solbrig, 1963, fig. 2c). Achenes variable, terete to subterete, 3- to 10- (to 20-)ribbed or 4- or 5-angled. TYPE GENUS: *Vernonia* Schreber, Gen. **2**: 541. 1791.

A tribe of about 70 genera and 1500 species grouped into two to eight

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I am grateful to Drs. Wood and Miller for their editorial assistance, and to my associates at the University of Georgia, Nancy C. Coile and Anna Baker, as well as to my past and present graduate students who have worked toward developing a better understanding of this fascinating tribe. This research was supported by the University of Georgia and by several research grants from the National Science Foundation.

The illustration of *Stokesia* was drawn by the late Dorothy H. Marsh from plants sent from Mississippi by Dr. R. B. Channell and grown by Dr. Wood for the Generic Flora.

²The tribes of Compositae have been treated previously by O. T. Solbrig (The tribes of Compositae in the Southeastern United States. Jour. Arnold Arb. **44**: 436-461. 1963). The reader should consult this work for additional information (e.g., familial and tribal descriptions, notes, and references) not included here.

subtribes with two centers of diversity: south-central Brazil and south-central Africa. About 21 species in *Vernonia*, *Stokesia*, *Elephantopus*, and *Pseudo-elephantopus* occur in the southeastern United States. Nineteen species are indigenous, while *Vernonia cinerea* (L.) Less. and *Pseudo-elephantopus spinatus* (B. Juss. ex Aublet) C. F. Baker are pantropical weeds. *Centratherum punctatum* Cass. is occasionally grown as an ornamental in the Southeast but probably has not become naturalized.

Members of the tribe can be distinguished by their generally alternate leaves; homogamous heads with one to many, usually perfect flowers (florets); tubular corollas (subligulate in *Stokesia*) that are deep purplish-red to blue or rarely white; and semicylindrical, long, slender, acutely tipped style branches that bear the stigmatic surface on their flattened inner surfaces. This type of style is found in all genera of the tribe.

One of the less well known tribes taxonomically, the Vernoniaceae have been recognized as a unit since 1817 (Cassini). Lessing's organization of the group formed the basis for De Candolle's classification of the tribe. Bentham and Hooker provided the next major revision, which was essentially followed by Hoffmann. Both Bentham and Hoffmann recognized two subtribes: Vernoniinae (Euvernoniinae), with separate heads and distinct involucre, and Lychnophorinae (Lychnophoreae), with few-flowered heads aggregated into secondary heads as glomerules. Bentham also noted that subtribe Vernoniinae consists principally of one large genus, *Vernonia*, with a number of smaller genera closely connected and clustered about it. Philipson expressed dissatisfaction with the subtribal arrangement of Bentham, noting that retaining subtribe Elephantopodinae Cass. (1817) (maintained by both Lessing and De Candolle) was preferable to placing *Elephantopus* in subtribe Lychnophorinae. Philipson argued also for the separation of subtribe Rolandrinae. Jones (1977) concluded that Bentham's two subtribes, which are based on the presence or absence of the secondary aggregation of heads, was artificial and far from satisfactory.

More recently, Robinson *et al.* published a revised classification of the subdivisions of the tribe Vernoniaceae, emphasizing the value of chemical, cytological, and structural data that had previously been unavailable. They agreed with Philipson's separation of the subtribes Elephantopodinae and Rolandrinae. However, in the opinion of Gerald Smith (pers. comm.), a student of *Piptocarpha*, their delimitation of subtribe Piptocarphinae is probably unwarranted. The separation of subtribe Centratherinae is also unnecessary (Kay Kirkman, pers. comm.). For the present, these latter subtribes are better included in the Vernoniinae.

I agree with Robinson *et al.* in the exclusion of the Liabeae from tribe Vernoniaceae (see Jansen & Stuessy). The tribe Liabeae is a distinct group that is related to the Vernoniaceae but with significant differences.

Although delimitation of taxa above the rank of species in the Vernoniaceae is often difficult, series, sections, genera, and subtribes can usually be circumscribed due to significant discontinuities. For the most part, these groupings appear to be biologically meaningful, even though difficult to characterize.

Among the tribes of the Compositae, the Vernoneae, with their largely tropical distribution, are one of the least known cytologically (Turner, 1977a). Jones (1979) reported that chromosome numbers are known for 16 of the 70 genera of the Vernoneae. Genera with $x = 10$ predominate (five genera); three have $x = 9$, and others $x = 7, 8, 11, 13, 15$, and 17.

The Vernoneae encompass an impressive array of form, habit, and geographic distribution. The tribe includes one of the largest woody composites, the polymorphic *Vernonia arborea* Buch.-Ham. of India, Indochina, Malaya, southern China, the Philippines, and Indonesia. It reaches a height of 36 m (see Koster). At the other extreme, in the repeatedly burned grasslands of Africa there are acaulescent perennial species of *Vernonia* that are only 3 to 4 cm tall. *Pacourina edulis* Aublet is an aquatic with edible leaves. Although most species in the tribe are herbaceous perennials, subshrubs, or shrubs, others may be annuals, lianas, or trees. There is considerable variation in vegetative morphology attending the extensive speciation and wide distribution of the tribe, and there are both convergent and divergent trends among species of various climatic regimes. In contrast, many of the reproductive characters have remained remarkably uniform.

A notable exception to the uniformity of reproductive characters is the pattern of pollen sculpture. As first noted by Wodehouse and recently studied by several workers (Kingham; Keeley & Jones; and Bolick), the surface patterns of pollen of the tribe are taxonomically useful. Relative to pollen of other Compositae, the multiplicity of surface configurations in the Vernoneae is unusual, being approached in variability only in the Lactuceae, and the various patterns often provide a powerful tool for resolving taxonomic problems (Keeley & Jones). Sculpturing varies from echinate to lophate. The wall structure as seen by transmission electron microscopy resembles the Anthemoid pattern and is considered to be a modification of it (Skvarla *et al.*).

A number of Vernoneae have been surveyed for chemical constituents (Harborne & Williams). Flavonoids appear to be useful in the arrangement and characterization of species, series, and sections. Among the more interesting constituents are the sesquiterpene lactones, which are taxonomically useful at the subgeneric and generic levels and which have provided evidence for relationship between Old and New World species of *Vernonia* (Turner, 1981).

Little work has been done on the comparative morphology and anatomy of the Vernoneae. Metcalfe and Chalk mentioned several anatomical features of the wood of *Lychnophora*, *Piptocarpha*, and *Vernonia*, and Carlquist found mostly uniseriate rays and relatively long vessel elements in six genera. Other workers have noted that trichomes, venation patterns, and epidermal features of cleared leaves of *Vernonia* can be useful in discovering relationships (Faust & Jones).

Muller noted that pollen of the Compositae has been verified in the Oligocene and may date back to the Eocene. However, he stated that pollen of the tribe Vernoneae has not yet been found as a fossil. The family is likely of Gondwanalandian origin, and the tribe may be as well (see Turner,

1977a). The Vernoniaceae are probably most closely related to tribes Mutisaceae, Cynareae, and Liabeae (Wagenitz; Robinson *et al.*).

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KEY TO THE GENERA OF VERNONIEAE IN THE SOUTHEASTERN UNITED STATES

- A. Corollas of outer flowers subligulate. 2. *Stokesia*.
- A. Corollas all tubular.
- B. Heads free from one another, not syncephalous. 1. *Vernonia*.
- B. Heads united into glomerules, syncephalous.
- C. Pappus of straight bristles; glomerules broad. 3. *Elephantopus*.
- C. Pappus of bristles, at least two of which are spirally twisted or doubly bent; glomerules narrow. 4. *Pseudo-elephantopus*.

1. *Vernonia* Schreber, Gen. 2: 541. 1791, nom. cons.

Erect perennial (rarely annual) herbs [shrubs, trees, or lianas]. Leaves alternate [rarely whorled or opposite], pinnately veined, usually cauline or sometimes mostly basal, the margins generally entire but sometimes remotely crenulate [rarely lobed]. Heads relatively small [sometimes large and showy], with ca. 10 to 80 flowers cymosely or paniculately arranged [in scorpioid cymes, or heads solitary and terminal]. Involucre cylindrical to broadly hemispheric or campanulate, composed of loosely or closely imbricated phyllaries arranged in several series, the inner phyllaries progressively longer. Receptacles flat to subconvex, naked. Flowers perfect; pappus in 2 series [sometimes 1], the outer pappus short, of scales or bristles [sometimes absent], the inner pappus of capillary, terete or slightly flattened, purple to straw-colored, often setose bristles. Corolla tube regular, elongate, with 5 narrow lobes, deep reddish-purple, rarely white or pink [blue, yellow to orange], often resinous dotted. Anthers exserted, sagittate at the base; pollen grains echinolphate to lophate. Style branches elongate, semicylindrical, apices acute, hispidulous with stigmatic papillae near the base on the inner surface. Achenes ribbed, usually resinous dotted. (Including *Seneciodes* Post & Kuntze, nom. superfl.; *Eremosis* (DC.) Gleason; *Leiboldia* Schlect.; *Monosis* DC.; *Lepidaploa* Cass.; *Suprago* Gaertner; *Behen* Hill; *Critoniopsis* Schultz Bip.). TYPE SPECIES: *Vernonia noveboracensis* (L.) Willd. Sp. Pl. 3:

1632. 1803 (*Serratula noveboracensis* L.), typ. cons.; see Int. Code Bot. Nomencl. 1978, p. 402. (Named for William Vernon, 1680's-1710's, an English botanist who collected plants with D. Krieg in Maryland in 1698 and who was a correspondent of H. Sloane, J. Petiver, and R. Uvedale, among others.) —IRONWEED.

A largely tropical genus of some 800 to 1000 species, with 15 in our area. Species of *Vernonia* are considered to fall into two subgenera, each with four sections: subgenus VERNONIA is confined to the New World, while subgenus ORBISVESTUS S. B. Jones occurs in Africa, Madagascar, and southeastern Asia (Jones, 1979, 1981). Subgenus ORBISVESTUS is dibasic with $x = 9, 10$. The base number for subgenus VERNONIA has generally been considered to be $x = 17$, but Turner (1981), as the result of his work on a group of primitive vernonias from Mexico and Central America, has recently proposed a base number of $x = 10$. The two subgenera differ in sesquiterpene lactones, but Turner's work has suggested that there may be a connecting link among these compounds. The corollas of a few species of subgenus ORBISVESTUS are yellow to orange, a coloration unknown in subgenus VERNONIA. Further distinctions, as well as connecting links, are apparent from the distribution of pollen types within *Vernonia* (Keeley & Jones).

All species of *Vernonia* native to the southeastern United States have a chromosome number of $n = 17$; the introduced *V. cinerea* (L.) Less. has $n = 9, 18$. On a worldwide basis, the most frequent reports are $n = 9, 10, 17, 18, 20, 34, 51, 68$ (Jones, 1979).

Species of *Vernonia* native to the southeastern United States are herbaceous perennials, with the exception of the pantropical *V. cinerea* (*Seneciodes cinerea* (L.) Kuntze), a weedy annual. Although best represented in the tropics, vernonias are found in a wide variety of habitats and climatic regimes ranging from subtropical cloud forests and other wet areas to xeric sites in deserts, seasonally dry grasslands and savannas, and the temperate regions of eastern North America. Many of the species have distinct habitat preferences. For example, in our area, *V. Lettermannii* Engelm. ex Gray grows only on chert rocks along rivers of the Ouachita drainage system; *V. Blodgettii* Small is found in low pinelands in South Florida; *V. angustifolia* Michaux occurs on high sandy pineland; and *V. flaccidifolia* Small is encountered only in upland deciduous woods. Several other species (e.g., *V. gigantea* (Walter) Trel. ex Branner & Cov.) seem to be less restricted ecologically. The most important reproductive isolating mechanism in our species appears to be habitat, and the settlement of eastern North America with the resulting disturbance of the vegetation seems to have increased the frequency of hybrids.

I have made artificial F_1 hybrids in all combinations among all of the species of eastern North America (Jones, 1976). The hybrids are highly fertile, although F_2 breakdown has been detected among some F_2 combinations. Vigorous hybrids were obtained when our species were crossed with closely related ones from the highlands of Mexico, but pollen fertility was low because of irregular chromosome pairing at meiosis. The introduced *Vernonia*

cinerea is self-compatible, but our native species are not. Self-incompatibility and an annual habit help to account for the weedy character of *V. cinerea*.

Pollinators from several orders of insects, primarily Lepidoptera and Hymenoptera, are attracted in relatively large numbers to the flowers of *Vernonia* in both tropical and temperate regions. A list of insects associated with *V. Baldwinii* Torrey in Kansas is given by Schwitzgebel and Wilbur. Rusts of the genus *Puccinia* parasitize *Vernonia* (see Urban).

One of the more useful taxonomic characters is external pollen morphology (Keeley & Jones). There are six basic pollen types, the distribution of which appears to be correlated with evolution within the genus. In general, pollen types have been found to correlate well with classification schemes based on other morphological characters in defining the subsections of *Vernonia*.

The usefulness of sesquiterpene lactones and flavonoids as aids in the classification of the genus has been demonstrated by Mabry and associates. Sesquiterpene lactones provide remarkable systematic markers at the subgeneric and sectional levels, while flavonoids show great promise at the ranks of species and series.

Selected taxa of *Vernonia* have been examined by a number of workers interested in anatomical or morphological characters, including trichomes (Hunter & Austin, Faust & Jones, and Wild), anatomy (Alencastro), micro- and megasporogenesis (Tiagi & Taimni), and gross morphology (Schaffner, Gleason, and Wagner). Aside from trichome characters, little of taxonomic value has been found.

Economically, *Vernonia* is of little importance. Several of our species (e.g., *V. noveboracensis*, *V. angustifolia*, and *V. arkansana* DC.) are used as ornamentals, as are a few African species. Some North American species (notably *V. Baldwinii*, *V. gigantea*, and *V. missurica* Raf.) can be weedy. Farmers in Alabama have told me that *V. gigantea* is a problem in pastures, and McCarty and Scifres have investigated many aspects of *V. Baldwinii*, which is a serious weed in Nebraska. Their reports provide information on the life history of this plant and its response to herbicides.

That the bitter sesquiterpene lactones of *Vernonia* are deterrents to herbivores was first demonstrated by Burnett *et al.*, who showed that rabbits and white-tail deer avoid *V. gigantea* and *V. noveboracensis*, both of which contain the sesquiterpene lactone glaucolide-A, but will eat *V. flaccidifolia*, which lacks sesquiterpene lactones. Glaucolide-A was also shown to deter the feeding of some but not all lepidopteran larvae.

Many *Vernonia* species have had wide use in folk medicine for treating a variety of diseases. The presence of active substances in these plants was demonstrated with the isolation of the sesquiterpene lactone vernolepin from the African species *V. hymenolepis* (Kupchan *et al.*). Vernolepin shows activity, both *in vitro* and *in vivo*, against carcinomas (see Kupchan *et al.*) and as an inhibitor of plant growth (Sequeira *et al.*). *Vernonia anthelmintica* (L.) Willd., from India, has been used as an anthelmintic and also has possible value as an industrial oil-seed crop. The achenes contain vernolic acid, which has potential as a stabilizer in plastics (Higgins). Work in connection with

developing this species as a crop plant has been reported by Berry *et al.* and Massey.

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2. *Stokesia* L'Héritier, Sertum Anglicum, 27. 1788.

Erect, somewhat branched, herbaceous perennials to 5 dm tall, stems glabrate below, pubescent above. Leaves alternate, minutely punctate; the upper reduced, sessile, and clasping; the basal larger. Heads large, showy, many flowered (with both ligulate and discoid perfect flowers), solitary or 1-7 in a corymb on terminal leafy peduncles; involucre hemispheric and composed of numerous pectinate-spinulose to foliaceous phyllaries (bracts) imbricate in several series, the outer phyllaries larger; receptacles flat, naked, somewhat fleshy. Pappus of 4 or 5 narrow paleaceous awns, soon deciduous from the achene but remaining enclosed in the head until corollas fall. Corollas blue (to purplish or white), resinous dotted, 5-lobed, the outer flowers ligulate, inner flowers tubular. Anthers included, appendages ovate; pollen grains echinolophate. Style branches long and slender. Achenes light brown, plump, 4-angled. TYPE SPECIES: *S. cyanea* L'Hér., nomen superfluum including *Carthamus laevis* J. Hill = *S. laevis* (J. Hill) Greene. (Named for Jonathan Stokes, M.D., 1755-1831, contributor to William Withering's *Botanical Arrangement of British Plants* and author of *Botanical Materia Medica* and *Botanical Commentaries*.)—STOKES' ASTER, STOKESIA, BLUE STOKESIA.

A monotypic genus endemic to the Coastal Plain of the southeastern United States. The range of *Stokesia laevis*, $2n = 14$, extends from Louisiana east of the Mississippi, across southern Mississippi and Alabama, into western Florida, northeastward across Georgia, and into southeastern South Carolina (see map in Gunn & White). *Stokesia* is frequently encountered in southern Mississippi and Alabama but is uncommon elsewhere. Its distribution across Georgia seems to be correlated with that of pitcher plant (*Sarracenia*) bogs with an underlying impermeable hardpan that holds moisture for at least part of the year. Elsewhere, this attractive plant grows on seasonally wet, sandy-peaty soil, in pine savannas and flat woods, and in hillside seepage bogs and adjacent sandy-peaty roadsides.

Stokesia, consistently regarded as a distinct genus, has always been placed

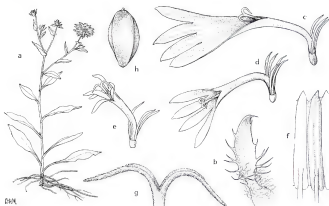


FIGURE 1. *Stokesia*. a-h, *S. laevis*: a, habit of flowering plant, $\times \frac{1}{2}$; b, involucral bract (phyllary), $\times 2$; c-e, outer, central, and inner flowers, respectively, $\times 2$; f, anther, abaxial side, $\times 10$; g, style branches and stigmas, $\times 10$; h, achene, $\times 10$.

in the tribe Vernonieae on the basis of the features of its style branches and stamens even though the outer ligulate corollas (described by J. Small as "five-lobed palmate") differ from the usual tubular corollas of the Vernonieae.

Wodehouse presented the first illustrations of the pollen, noting a resemblance to the pollen of *Barnadesia* Mutis, of the tribe Mutisieae. However, the pollen is echinolophate with greatly reduced spines, a type commonly found elsewhere in the Vernonieae.

Stokesia has been reported (Mabry *et al.*) to contain the sesquiterpene lactone glaucolide-A, a compound also found in several North American species of *Vernonia*, thus further suggesting that, in spite of the ligulate outer flowers, *Stokesia* is properly included in the Vernonieae. However, the haploid chromosome number of $n = 7$ is unique in the tribe (Jones, 1979), and the chromosomes of *Stokesia* are much larger than those usually seen in the Vernonieae (Gunn & White; pers. obs.)

Stokesia is often grown as an ornamental perennial, especially in the eastern United States and in England. A number of color forms have been recognized. Cultivars include 'Blue Danube', 'Blue Moon', 'Caerulea', 'Lilacina', 'Purpurea', 'Rosea', 'Alba', and 'Silver Moon' (see *Hortus Third* and Gunn & White). In the southeastern United States the plants are semi-evergreen in winter, quite hardy, and easily maintained in the garden. Propagation is by either seeds or division.

The oil content of the achene of *Stokesia* is about 40 percent, and of this 70 percent is epoxyoleic acid (White & Gunn). Since epoxidized products

are useful as stabilizers for vinyl plastics, the U. S. Department of Agriculture examined the possibility of using *Stokesia laevis* as a source of oil and conducted the initial phase of crop development research. This work provided an estimate of seed yield and a discussion of agronomic advantages and disadvantages. However, neither the mode of pollination nor the breeding system is known, and both will have to be determined prior to any serious attempts at breeding agronomically useful cultivars.

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18-22. 1934. [Seven soap bubbles blown together produce a geometric pattern similar to the pollen of *Stokesia*.]

3. **Elephantopus** Linnaeus, Sp. Pl. 2: 814. 1753; Gen. Pl. ed. 5. 355. 1754.

Erect perennial, simple or sparsely branched, pubescent-stemmed herbs from stout rootstocks. Leaves chiefly basal or cauline, the petioles usually indistinct, the blades elliptic to lanceolate or ovate, acute at the apex, attenuate at the base, margins entire to crenate or dentate. Inflorescences complex, composed of few-flowered heads arranged in bracteate glomerules; these, in turn, in terminal corymbose or somewhat paniculate groupings. Heads homogamous, with (1 or) 2-4 (or 5) perfect flowers; the involucre composed of 8 phyllaries in 4 decussate pairs; glomerules of heads subtended by bracts. Pappus composed of [scales or of 20-40 or] fewer than 15 straight bristles. Corollas blue or lavender to white, the tube slender, the limb unequally 5-cleft with a deeper fissure on the inner (adaxial) side. Anthers sagittate at base. Achenes ribbed or angled. (Including *Orthopappus* Gleason; excluding *Pseudo-elephantopus* Rohr. LECTOTYPE SPECIES: *E. scaber* L.; see C. F. Baker, Trans. Acad. Sci. St. Louis 12: 44. 1902. (Name from Greek *elephas*, elephant, and *pous*, foot. Included by Linnaeus in a list of names expressing resemblance in his *Critica Botanica* [1739, p. 99] and in a list in *Philosophia Botanica* [1751, p. 179] headed "Habitus indicat similitudinem, qua excitatur idea, & ex idea nomen." Resemblance to an elephant's foot not otherwise explained.)—ELEPHANT'S FOOT, DEVIL'S GRANDMOTHER, TOBACCO WEED.

A genus of about 30 species centered in the Neotropics but also found in the Old World, with nine species occurring in North America and four of these in the southeastern United States (see Clonts & McDaniel; Jones in Cronquist). Although the genus is easily recognized, the species (which are based on characters of pappus, leaves, bracts, branching patterns, pubescence, and glomerules) are not always sharply defined and require some experience to identify. *Elephantopus carolinianus* Raeuschel and *E. elatus* Bertol. are restricted to the southeastern United States, while *E. nudatus* A. Gray reaches northern South America and *E. tomentosus* is distributed from Virginia to Texas and into Mexico. The single species of *Orthopappus*, *O. angustifolius* (DC.) Gleason, a plant of southern Mexico, the West Indies, and South America (south to Argentina and Chile), characterized by its numerous pappus bristles, is generally treated as a species of *Elephantopus*, but the two species segregated as *Pseudo-elephantopus* (q.v.) on the basis of their twisted or folded bristles are still being shuffled between the two genera.

The morphology of the inflorescence and the glomerules of *Elephantopus scaber* L. was described in some detail by Kunze. The main axis of the inflorescence or panicle is determinate. Each glomerule is terminal on its own stem and forms a part of a larger paniclelike inflorescence. Kunze noted that the branching pattern evident in the inflorescence is similar to that found within the glomerules, but the latter are very strongly reduced into a compact, complicated mass.

Kunze described the glomerule as a branch of the paniculate inflorescence so greatly reduced that each head appears to be sessile within its subtending bract; the whole thus forms a glomerule or "synflorescence." The bracts and florets are arranged in a tightly spiraling aggregate, making it virtually impossible to distinguish between the phyllaries and the subtending bracts. Kunze noted that many workers have been mistaken in thinking that the glomerule is subtended by three foliaceous bracts when, in fact, each bract subtends a panicle branch of its own. Thus, three greatly reduced panicle branches in close association form a glomerule. Overall, the inflorescence of *Elephantopus* seems to have been derived from a scorpioid inflorescence such as that found in many Neotropical vernonias.

Several sesquiterpene lactones (germacranolide dilactones)—for example, elephantin, elephantopin, elephantol, deoxyelephantopin, isodeoxyelephantopin, and molephantin—have been found in *Elephantopus*. Elephantopin has been shown to have significant activity *in vitro* against cells derived from human carcinoma of the nasopharynx, and *in vivo* against rat carcinomas (Lee *et al.*, 1981). It is believed that the sesquiterpene lactones that exhibit antitumor properties have general cytotoxic effects (Burnett *et al.*).

Chromosome numbers of $2n = 22$ and 44 have been reported for species of *Elephantopus*. The four species of *Elephantopus* occurring in the southeastern United States all have a diploid number of 22 . James (1959) suggested that hybridization and introgression between *E. elatus* and either *E. tomentosus* or *E. nudatus* occur in Florida. The biology of the taxa is poorly known.

The genus has little economic importance, except for a few species that are weedy in some areas.

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4. **Pseudo-elephantopus** Rohr, *Skr. Naturhist.-Selsk. Kjøbenhavn* **2**(1): 214, 1792, "Pseudo-Elephantopus."³

Erect perennial herbs; stems solitary, branched. Leaves cauline, alternate, the lower larger, the others gradually reduced, pinnately veined, the petioles

³Although the spelling *Pseudelephantopus* has been widely used, the original spelling and hyphenation of the generic name must be retained. Article 73.9 of the *International Code of Botanical Nomenclature*, 1978, prescribes that "The use of a hyphen after a compounding form in an epithet is treated as an orthographic error to be corrected." In the paragraph of examples that follows, it is noted that "Art. 73.9 refers only to *epithets* (i.e., of species, of infraspecific taxa, or of subdivisions of a genus), not to *names* of genera or taxa of higher rank; a generic name published with a hyphen, e.g. *Pseudo-elephantopus* Rohr, can be changed only by conservation."

indistinct. Inflorescences terminal, bracteate, slender, racemose-spicate, with sessile glomerules of 1–5 heads on distal part of main stem and branches. Heads homogamous with 4 perfect flowers, the involucre of 4 pairs of decussate phyllaries (bracts), the 2 inner pairs almost equal, the 2 outer successively shorter. Pappus uniseriate, composed of 5–15 unequal or subequal bristles, some of the main ones doubly reverse-bent [or curled or loosely spiraled toward the tip]. Corollas bluish-purple to white, tubular-funnelform, the tube slender, the limb 5-cleft, deeply divided on one side, subligulate. Anthers sagittate at the base. Style branches slender, elongate, gradually pointed, minutely hispidulous, without conspicuous stigmatic lines. Achenes 10-ribbed. (Including *Distreptus* Cass., *Matamoria* La Llave & Lex., *Spirochaeta* Turcz., and *Chaetospora* S. F. Blake.) TYPE SPECIES: *Elephantopus spicatus* B. Juss. ex Aublet = *P. spicatus* (B. Juss. ex Aublet) C. F. Baker, Trans. Acad. Sci. St. Louis 12: 45. 1902.⁴ Name from Greek *pseudein*, false, and *Elephantopus*, elephant's foot.)—WHITE ELEPHANT'S FOOT, DOG'S TONGUE.

A neotropical genus of two closely related but quite distinct species, *Pseudo-elephantopus spiralis* (Less.) Cronq. and *P. spicatus*, $2n = 26$, the latter introduced into Florida some forty years ago.

Pseudo-elephantopus differs from *Elephantopus* in chromosome number ($2n = 26$ [$2n = 28$ also reported] vs. $2n = 22, 44$) and various morphological features (heads not held in a tight glomerule, subtending bracts leaflike, and pappus with at least two spirally twisted or doubly bent bristles vs. heads in tight glomerules with specialized subtending bracts and a pappus of straight bristles). Clonts, however, submerged *Pseudo-elephantopus* in *Elephantopus*, although others (e.g., Adams, Busey, Cronquist, Philipson, and Ward) have recognized it as distinct.

A number of authors have reported that *Pseudo-elephantopus spicatus* is a troublesome weed in tropical and subtropical areas. Fosberg first called attention to this species in Hillsborough County, Florida, and Blake warned that it is a potentially injurious weed that should be eliminated before it becomes thoroughly established. Ward, however, commented that "in no area of Florida has this plant yet given indication of the aggressive weedy nature manifested in other parts of its range." Widespread in the American tropics, *P. spicatus* is naturalized in Africa, eastern Asia, and Guam.

Little is recorded about the biology of the two species comprising this genus, but presumably the modified pappus bristles adhere to clothing and to the hair of animals, probably aiding in the spread of these plants. In Jamaica, the stalks and leaves of *Pseudo-elephantopus spicatus* have been used as brooms for sweeping houses.

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⁴Although Vahl (Skr. Naturhist.-Selsk. Kjøbenhavn 2(1): 216. 1792) gave a description of *P. spicatus* immediately after Rohr's generic description, he did not make the combination, because he referred to this plant as *Elephantopus*.

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