Flora of Barro Colorado Island

Introduction

Barro Colorado is an island in the Panama Canal Zone lying midway between the Atlantic and Pacific Oceans (9°09′N, 79°51′W). At about 15.6 km² (6 square miles), BCI is the largest island in Gatun Lake, the lake formed between 1911 and 1914 by the damming of the Río Chagres to form the Canal. Gatun Lake, by far the largest expanse of water in the Canal, covers 420 km² (164 square miles) at an elevation of about 25 m (85 feet) above sea level. The ship channel traversing the lake passes along the eastern and northeastern shores of the island, and waves from the passing ships cause substantial erosion along parts of these shores, especially during the dry season, when the trade winds are more forceful.

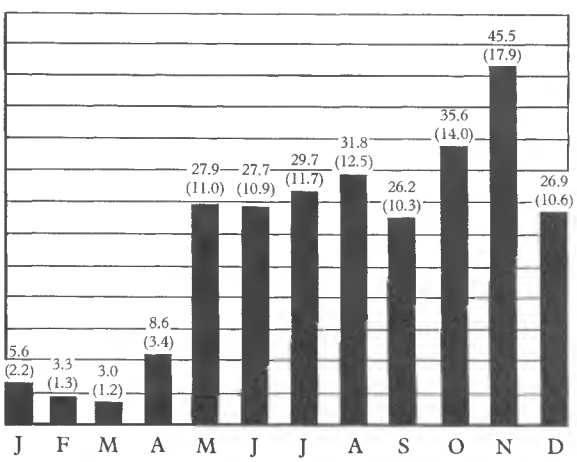
BCI was set aside as a biological preserve in 1923 and is currently supervised by the Smithsonian Tropical Research Institute, which operates a modern field station at the Laboratory Clearing, on the northeast shore. Aside from this modest little settlement, there is very little that interrupts the dense forest cover: a dozen-odd smaller clearings, some of them used for navigational beacons; a network of trails crossing most of the island; a scattering of tree falls; a few shoreline marshes and silted coves; and an occasional ravine or streambed. And except for a small plateau in the west-central part of the island, the terrain is hilly, the hills dissected by ravines and generally well-drained slopes. The highest point, the Tower Clearing, is 165 m (538 feet) above sea level, 140 m (453 feet) above the level of the lake.

The shoreline, deeply dissected by coves over much of its extent, is altogether about 65 km (40 miles) long, including the shores of its associated islands. The principal island associated with BCI (see the map on the endsheets) is Orchid Island, which is separated from Gross Point by a very narrow passage. Others that are considered part of the biological preserve are Slothia Isle, in Laboratory Bay; Ormosia Isle, near the Front Lighthouse Clearing; and Sal and Pimiento Islands, a pair of small islands northeast of Fairchild Point.

General Climatic Features

Under the Köppen system of climatic classifications, BCI's climate is Am, or Tropical Monsoon Climate. Annual rainfall on BCI (see Graph 1) ranges from 190 to 360 cm (76 to 143 inches); between 1924 and 1962 it averaged 275 cm (107.3 inches). This compares with an average 328 cm (128 inches) at Colón, on the Atlantic Coast of the Canal Zone, and 177 cm (68 inches) at Balboa, on the Pacific Coast, during the same period. The climate is markedly seasonal, with a sharp dry season usually starting in mid-December and continuing until about the beginning of May. During the dry season, only 18–26 cm (7–10 inches) of rain fall.

The dry season, in fact, sees considerable leaf litter accumulating on the forest floor, and a great deal more light reaches the forest floor than during the rainy season. Most of the steep, rapidly flowing streams dry up completely, but many form small pockets of water that can survive the dry season. What rain does fall during the dry season rapidly disappears, with very little or no runoff. Even after the rains begin, usually in May, less than 2% of the water may leave as runoff. However, by late in the rainy season, in December, nearly 85% of the water falling as rain leaves as runoff (Rubinoff, 1974).



Graph 1. Rainfall on BCI, in cm (and inches). (Source: Panama Canal Company)

View of Fairchild Point, from the canopy west of the Laboratory Clearing

The dock and laboratory

TABLE 1
Mean relative humidity by month, at 1200 hours, 1973, on BCI
(in percent)

Month	Mean relative humidity	
	Clearing	Forest floor
January	78.5%	85.6%
February	72.2	80.6
March	65.9	80.2
April	62.1	76.4
May	63.8	84.0
June	74.5	92.5
July	65.2	92.1
August	66.5	91.8
September	68.0	92.2
October	70.4	92.4
November	76.6	94.2
December	69.3	87.8

SOURCE: Rubinoff, 1974.

In any given month, average relative humidity is appreciably higher in the forest than in such open areas as the Laboratory Clearing. The drop in relative humidity at the onset of the dry season is also less rapid in the forest than in clearings (Rubinoff, 1974). The mean monthly relative humidity for 1973 is presented in Table 1.

Temperature measurements in the forest and in the Laboratory Clearing throughout a single year (1973) are shown in Table 2. The atmospheric temperature may vary from as low as 16.5°C (61.7°F) to as high as 35.5°C (95.9°F), with the lowest temperatures being recorded within the forest during the rainy season and the highest at the Laboratory Clearing in the dry season. With rare exceptions the temperature ranges between 21 and 32°C (70 and 90°F) throughout the year, and the average ambient temperature in the Laboratory Clearing is 27°C (77°F). The seasonal variation in monthly averages is just 2.2°C. In the dry season the range of the monthly averages of diurnal temperature is 9–11°C, and during the rainy season it is 8–9°C. Thus the diurnal temperature variation is greater than the variation between seasons. Temperature on the forest floor is especially constant, the range of the average diurnal temperature being about 6.1°C.

The first three months of the dry season offer the most hours of sunshine, July and August the least (Foster, 1974). During most of the rainy season, and particularly when skies are overcast, conditions are very dark on the forest floor and visibility is poor.

Winds are about twice as forceful at midday in the dry season as at the same time in the rainy season. Measurements of wind velocity for 1973 showed the rainy-season months having an average of about 4.9 km (3 miles) per hour, whereas for the dry season the average was about 9.8 km (6 miles) per hour (Rubinoff, 1974). Wind velocity is always substantially higher at midday than in the morning or evening.

Geology and Soil Types

Much of the present area of Central America was sea floor during early times, and land emerged only during the Oligocene, as a number of islands. In the middle Miocene there was a general uplifting as well as much volcanic activity in the central and western portions of Panama. The final retreat of the isthmus from the sea occurred in Darién during the upper Miocene and Pliocene, although there were later movements of the coastline in the west, in Chiriquí (Torre, 1965). The final uplift could have been in the late Pliocene, "and continuous land connections have existed for three to five million years" (Graham, 1972). Recent data (Emiliana et al., 1972) indicate that the final closing of the isthmus occurred 5.7 million years ago.

The important parent rocks in the Canal Zone are of two kinds—sedimentary rocks, including limestone,

TABLE 2
Atmospheric temperature on BCI, 1973
(degrees C)

Month	Clearing temperature						Forest floor temperature					
	Maximum			Minimum			Maximum			Minimum		
	Mean	High	Low	Mean	High	Low	Mean	High	Low	Mean	High	Low
January	31.7	33.0	30.0	23.2	24.5	21.5	28.3	30.0	27.5	22.9	24.5	20.5
February	32.2	33.5	31.0	22.2	24.5	21.0	28.7	29.8	26.5	22.3	24.8	21.2
March	32.5	34.5	29.5	23.2	25.0	21.2	29.4	30.5	29.0	23.2	24.8	21.0
April	33.8	35.5	30.0	22.9	21.5	21.5	30.8	32.5	28.0	22.8	25.0	21.0
May	32.0	34.0	28.5	23.1	25.0	21.0	29.1	30.8	26.0	21.4	24.8	16.8
June	30.1	32.5	26.5	22.6	23.5	21.5	27.1	29.5	25.2	21.8	23.2	16.5
July	30.8	32.0	28.0	22.3	23.5	21.0	27.6	30.0	25.8	20.9	23.2	17.0
August	31.1	33.0	28.5	22.4	24.5	20.0	27.4	29.8	26.0	22.0	24.2	18.5
September	31.5	32.5	29.5	22.3	23.5	21.5	27.4	29.0	26.2	22.0	23.2	20.5
October	30.8	32.0	27.5	22.7	24.0	22.0	27.5	28.8	25.5	22.3	23.2	20.5
November	30.4	31.5	25.5	22.5	23.0	21.5	26.5	29.0	25.0	21.8	23.2	18.0
December	30.2	31.5	29.5	21.8	23.0	21.0	26.1	27.4	25.2	21.5	22.5	20.4
Annual mean and extremes	31.4	35.5	25.5	22.6	25.0	20.0	28.0	32.5	29.0	22.1	25.0	16.5

SOURCE: Rubinoff, 1974.

claystone, shales, and tuffs, and igneous rocks, including basalt, andesite, granodiorite, diorite, metabreccia, and rhyolite (Bennett, 1929).

Bennett (1929) classified BCI soil as Frijoles Clay, which is characterized by its red or deep red color (slightly more brownish in the uppermost 5 cm) and by being well drained, well aerated, slightly acid to alkaline, and friable when moist. Kenoyer (1929) described the soils as "a chocolate brown alluvium underlain by a red subsoil arising from the decomposition of the Bohio sandstones and conglomerates." Soil maps by McDonald (1919) showed all of BCI being made up of Bohio sandstones and conglomerates. According to Woodring (1958), the parent rock is predominantly marine Caimito and non-marine Bohio sedimentary formations (late Oligocene); there is a cap of basalt at the central part of the island and some volcanic rock toward the east.

Knight (1975a) reported finding a second soil type in several areas of the island—a gley, which is an impervious clay subsoil appearing gray mottled with red—at a depth of 59–75 cm, and contrasts it with the Frijoles Clay. According to Foster (1974), the past history of human disturbances appears to have had a more pronounced influence on the soils than the parent material had: in most cases, those areas known to have been disturbed in the past 75 years have developed a hardpan beneath a grayish soil, whereas the less disturbed areas exhibit only a thin brown layer covering a very deep red clay that is almost devoid of humus.

General Characteristics of the Vegetation

The vegetation on Barro Colorado Island is semi-evergreen moist tropical forest (Knight, 1975a). In terms of the classification system devised by Beard (1944; 1955), the oldest forest on the island would appear to be intermediate between Evergreen Seasonal Forest and Semi-Evergreen Seasonal Forest (Bennett, 1963). And in the Holdridge Life-Zone System (Holdridge et al., 1971, discussed below, p. 60), the forest is *tropical moist forest*. The Holdridge system is used in this text as a means of delineating the ecological range of each species within Panama; though not universally accepted, it seems to work for Panama, and it is the only system for which a comprehensive map for Panama has been produced (see pp. 58–59).

Although no major disturbances have taken place on the island since it was set aside as a preserve in 1923, a major portion of the island lay deforested until 1905 (Enders, 1935; Knight, 1975a). This includes much of the eastern third of the island, major promontories on the north side of the island (including Orchid Island), and small portions of the western periphery. According to Enders (1935), most parts of the younger forest (on the east and north sides of the island) may date from as early as 1880, though a few small clearings persisted longer (i.e., the forest that has overtaken them is younger). He reported that the old cocoa plantations on Peña Blanca Peninsula date from 1905, and that much of the Burrunga Peninsula was cleared during 1920–23. One small area north of the present Laboratory Clearing (formerly a garden for workers) dates from about 1955 (Knight, 1975a). An aerial view of BCI taken in 1927, published by Knight (1975a), shows the approximate distribution of the young and old forest; one published by Hladik and Hladik (1969) shows the forest as it occurs today.

Types of Natural Vegetation

Forest. Most of BCI, then, is covered with forest, perhaps none of it climax forest. Superficially, the forest seems everywhere the same, but there are differences between the young and the old forests. Bennett (1963) described the young forest as having two strata and the old forest as having two or three strata. Though there are clearly differences in the average height of the canopy between the two forest types, I have never been able to distinguish any sharply defined stratification. My impression is one of trees forming a continuous and undifferentiated cover, their crowns fitting together like the pieces of a jigsaw puzzle.

The following are the more common trees, as determined by the density data compiled by Knight (1975a; see his Appendix 1). The list includes species from both young and old forests.

Acalypha diversifolia
Alseis blackiana
Anacardium excelsum
Andira inermis
Annona hayesii
Apeiba membranacea
A. tibourbou
Aspidosperma cruenta
Astronium graveolens
Bombacopsis quinata
Capparis frondosa
Casearia guianensis
Cecropia insignis
Cordia alliodora
C. lasiocalyx
Coussarea curvigemmia
Desmopsis panamensis
Didymopanax morototoni
Dipteryx panamensis
Erythroxylum multiflorum
Faramea occidentalis
Gustavia superba
Heisteria longipes
Hirtella americana
H. racemosa
H. triandra
Hura crepitans
Hybanthus prunifolius
Luehea seemannii
L. speciosa
Miconia argentea
Mouriri myrtilloides subsp. *parvifolia*
Nectandra purpurascens
Ochroma pyramidale
Oenocarpus panamanus
Ouratea lucens
Platymiscium pinnatum
Platypodium elegans
Poulsenia armata
Prioria copaifera
Protium panamense
Pseudobombax septenatum
Pterocarpus officinalis
P. rohrii
Quararibea asterolepis
Quassia amara
Randia armata
Rinorea sylvatica
Scheelea zonensis
Simarouba amara
Sorocea affinis
Spondias mombin
Swartzia simplex
Trattinnickia aspera
Trichilia cipo
Triplaris cumingiana
Virola surinamensis
Zanthoxylum panamense

The forest on BCI is rich in species. Lang et al. (1971) found that even in the areas where the composition of the forest appears to be most homogeneous, there are as many as 130 species of trees (more than 2.5 cm in diameter at

breast height, both adults and juveniles) in 1.5 hectares (3.7 acres). The species/area curve shows only moderate signs of leveling off in this case. These figures would be much higher if vines, lianas, shrubs, herbs, epiphytes, and hemiepiphytes were included.

Species diversity in the younger forest is about the same as that in the older forest, and is probably increasing very slowly where the forest has reached 50–60 years of age (Knight, 1975a). Knight indicated that the most rapid increase in species diversity occurs during the first 10–15 years of succession, and that after 65 years the increase is slow. So great is the species diversity that, despite several years of collecting on BCI, I discovered a new species for the flora almost every day of collecting, during even the most recent trips. More recently, of 200 collections made by Gene Montgomery in the canopy of the forest, three were species new to the island; and one of these was a species new to Central America. Four species new to the island were collected by Garwood and Foster as late as 1976, and one of these represents a family new to the flora (Humiriaceae). Many of the plants that are being collected for the first time are common on the island. Some are conspicuous but have nevertheless been overlooked: *Celtis schippii,* which was collected only a few years ago for the first time for Panama, is growing at the edge of the Laboratory Clearing; the plant is at least 40 years old and scores of botanists have no doubt walked past it. Many other plants on the island, especially the forest trees, are evidently rare; some are known from only a few individuals, some from only a single plant.

In the young forest, which appears more uniform than the old, the larger trees of the canopy average 18–24 m tall. The understory is usually moderately dense and tangled, and there are few disturbances from tree falls, perhaps because few of the trees are old enough to have been subject to dying or to windfall. Knight (1975a) found the following species of trees only in the young forest: *Annona hayesii, A. spraguei, Casearia guianensis, Didymopanax morototoni, Hymenaea courbaril, Inga mucuna,* and *Stemnadenia grandiflora.* Other species that I have seen only or mostly in areas of young forest include:

Aegiphila panamensis
Apodanthes casearіae (parasite)
Bombacopsis quinata
B. sessilis
Byrsonima spicata
Calycophyllum candidissimum
Cryosophila warscewiczii
Ficus perforata
Heisteria costaricensis
Nectandra purpurascens
Ocotea pyramidata
Psychotria carthagenensis
Tournefortia cuspidata
Trigonia floribunda
Vochysia ferruginea
Vriesia heliconioides

Knight (1975a) listed *Cordia alliodora, Luehea seemannii, Miconia argentea, Spondias mombin, Scheelea zonensis,* and *Zuelania guidonia* as being more abundant in the young forest.

The canopy trees in the old forest average 22–30 m tall (Bennett, 1963). Species composition is qualitatively similar to that of the young forest, and there is no strong correlation between the age of the forest and its floristic composition (Knight, 1975a, 1975b). Knight has shown that in both the young and the old forest about 15% of the species can be classified as infrequent reproducers—plants incapable of reproducing in the understory environment. The percentage of total species that are frequent reproducers is also about the same (39% in the old forest, 37% in the young forest). In the canopy, it is a different matter: only 7% of the canopy trees of the young forest are classified as frequent reproducers, whereas 73% are infrequent reproducers; by contrast, 48% of the canopy trees in the old forest are frequent reproducers, and only 40% (primarily pioneer species) are infrequent reproducers.

The old forest differs from the young principally in having larger lianas and trees. Several species that are represented in both the old and the young forest are two to five times larger in girth in the old forest than in the young; on this basis, Knight (1975a) has estimated that the old forest is at least twice as old as the young, or as much as 130 years old. But because of the relatively high density of infrequent reproducers, he believes that the vegetation of the old forest is still in a successional stage.

Among the species of trees that Knight found almost exclusively in the old forest are:

Acalypha diversifolia
Desmopsis panamensis
Erythrina costaricensis var. *panamensis*
Ficus tonduzii
Guarea multiflora
Heisteria longipes
Poulsenia arnata
Tovomitopsis nicaraguensis
Trattinnickia aspera
Virola surinamensis
V. sebifera

He also has the following occurring as large trees only in the old forest:

Andira inermis
Casearia arborea
Guarea glabra
Hirtella triandra
Hura crepitans
Inga marginata
Pouteria sapota
Prioria copaifera
Protium panamense
P. costaricense
P. tenuifolium subsp. *sessiliflorum*
Quararibea asterolepis
Rheedia acuminata
Tetragastris panamensis
Trattinnickia aspera

Other species that I have observed chiefly or only in the old forest include the following:

Epiphytes
Ludovia integrifolia
Peperomia macrostachya

Hemiepiphytes
Philodendron fragrantissimum

Herbs
Asplenium delitescens
Calathea micans
Dieffenbachia pittieri
Heliconia irrasa
Phaeosphaerion persicariifolium
Pharus parvifolius
Selaginella exaltata

Vines
Fevillea cordifolia
Gurania coccinea

Lianas
Acacia acanthophylla
Adelobotrys adscendens
Cynanchum recurvum
Macfadyena unguis-cati

Shrubs

Anaxagorea panamensis
Ardisia pellucida
Geonoma cuneata
Hamelia axillaris
Justicia graciliflora
Miconia nervosa
Picramnia latifolia
Psychotria granadensis
Solanum argenteum

Small trees

Bactris coloradonis
Coccoloba acapulcensis
Picramnia latifolia
Xylopia macrantha
Xylosma oligandrum

Trees

Astronium graveolens
Diospyros artanthifolia
Drypetes standleyi
Hampea appendiculata
Inga spectabilis
Laetia thamnia
Nectandra cissiflora
Ocotea oblonga
O. pyramidata
O. skutchii
Pouteria fossicola
Prioria copaifera
Protium costaricense
Psidium anglohondurense
Sloanea terniflora
Symphonia globulifera
Tabernaemontana arborea

Perhaps because of its age and its greater content of mature trees, the old forest appears to have more tree-fall gaps than the young forest does. One result of this difference is the somewhat higher incidence in the older forest of *Cecropia* trees, which establish themselves in the canopy gaps (Knight, 1975a; R. Foster, pers. comm.).

Although climax forest possibly does not exist on BCI, a number of potential climax species can be listed, on the basis of Knight's list of frequently reproducing tree species. The following, each often more than 30 m tall, are listed by Knight as frequent reproducers, and hence are potential climax-canopy species:

Alseis blackiana
Aspidosperma cruenta
Calophyllum longifolium
Guarea multiflora
Heisteria concinna
Licania platypus
Lonchocarpus pentaphyllus
Maquira costaricana
Poulsenia armata
Prioria copaifera
Protium panamense
Pterocarpus rohrii
Quararibea asterolepis
Simarouba amara
Socratea durissima
Tabernaemontana arborea
Tachigalia versicolor
Trichilia cipo
Triplaris cumingiana
Virola sebifera

The following smaller trees, which Knight also lists as frequent reproducers, are potentially a part of the climax flora of the island:

Casearia guianensis
C. sylvestris
Cordia lasiocalyx
Coussarea curvigemmia
Cupania rufescens
C. sylvatica
Desmopsis panamensis
Eugenia nesiotica
Faramea occidentalis
Guarea glabra
Guettarda foliacea
Heisteria longipes
Hirtella americana
H. triandra
Inga fagifolia
I. marginata
Mabea occidentalis
Mouriri myrtilloides subsp. *parvifolia*
Oenocarpus panamanus
Picramnia latifolia
Protium tenuifolium subsp. *sessiliflorum*
Quassia amara
Randia armata
Rheedia acuminata
Sorocea affinis
Spachea membranacea
Stemmadenia grandiflora
Swartzia simplex

Although more than 70 species of trees reach a height of about 30 m, relatively few grow appreciably taller and occur as emergents above the general level of the canopy. Among these taller trees are:

**Anacardium excelsum* (to 37 m)
Aspidosperma cruenta (35)
A. megalocarpon (40)
Astronium graveolens (35)
Beilschmiedia pendula (40)
Brosimum alicastrum (35)
Calophyllum longifolium (35)
**Cavanillesia platanifolia* (40)
**Cecropia insignis* (40)
Cedrela odorata (40)
Ceiba pentandra (40)
Couratari panamensis (40)
**Dipteryx panamensis* (40)
**Ficus insipida* (30)
F. obtusifolia (40)
F. yoponensis (40)
Guarea multiflora (40)
Guatteria dumetorum (35)
**Hyeronima laxiflora* (40)
Myroxylon balsamum var. *pereirae* (40)
Ormosia macrocalyx (40)
Peltogyne purpurea (50)
Pithecellobium macradenium (40)
Prioria copaifera (40)
Pterocarpus rohrii (50)
Simarouba amara (35)
Sterculia apetala (40)
**Tabebuia guayacan* (40)
**Terminalia amazonica* (35)
T. chiriquensis (35)
Tetragastris panamensis (35)
**Trattinnickia aspera* (50)
Schizolobium parahybum (40)
Vantanea occidentalis (40)

Those species marked by an asterisk are listed by Knight (1975a) as infrequent reproducers. Most of the species listed by Knight, then, are large, and some are emergent trees. In addition to those marked with an asterisk, Knight (1975a) lists the following species of large trees as infrequent reproducers:

Apeiba membranacea
A. tibourbou
Bombacopsis quinata
B. sessilis
Byrsonima crassifolia
Casearia arborea
Chrysophyllum cainito
Cordia panamensis
Dendropanax arboreus
Didymopanax morototoni
Enterolobium cyclocarpum
Guapira standleyanum
Hura crepitans
Hymenaea courbaril
Platypodium elegans
Pseudobombax septenatum
Sapium aucuparium
Socratea durissima
Trema micrantha
Turpinia occidentalis subsp. *breviflora*
Virola surinamensis
Zuelania guidonia
Zanthoxylum panamense

Clearings. Although man-made clearings constitute much less than 1% of the total area of the island, they contribute 7% to the total flora, representing 197 species. (This total does not include the 53 species of cultivated plants that occur in the Laboratory Clearing.) Most of the natural vegetation occurring in clearings consists of weedy plants, especially of the families Gramineae (37 species), Compositae (27), Leguminosae (17), Solanaceae (13), Cyperaceae (11), Euphorbiaceae (10), Melastomataceae (7), Cucurbitaceae (6), Convolvulaceae (5), Passifloraceae (4), Commelinaceae (3), Phytolaccaceae (3), Rubiaceae (3), and Polypodiaceae (2).

A number of different clearing types occur on the island. These include the Laboratory Clearing, the Tower Clearing (a small clearing at the center of the island), small clearings maintained at the ends of many of the trails, and some clearings along the north and east sides of the island that are maintained for navigational signs for ships in the Panama Canal (of these, the only sizable clearings are those around the Front and Rear #8 Lighthouses).

The large lighthouse clearings are cleared annually, most of the smaller clearings and the Laboratory Clearing more than once per year, and the debris is usually left to decompose. At the time of clearing, the growth is about 2–3 m tall. Regrowth is relatively rapid for those species that survive the cutting back. Since burning is not permitted anywhere on the island, the seeds and roots are not killed, and regrowth follows a similar pattern each year. Herbaceous or suffruticose plants that soon become reestablished include:

Abelmoschus moschatus
Aeschynomene americana var. *glandulosa*
Blechum brownei
Blepharodon mucronatum
Borreria densiflora
B. laevis
B. latifolia
B. ocimoides
Calapogonium mucunioides
Chamaesyce hyssopifolia
C. hypericifolia
Chelonanthus alatus
Chromolaena odorata
Cissampelos pareira
Clibadium surinamense
Clitoria rubiginosa
Costus guanaiensis var. *macrostrobilus*
Cuphea carthagenensis
Cyathula prostrata
Cyperus diffusus
Desmodium adscendens
D. canum
Diodea ocimifolia
Dioscorea alata
D. sapindoides
Elephantopus mollis
Fleischmannia sinclairii
Heliconia latispatha
Hyptis capitata
H. mutabilis
Indigofera mucronata
Ipomoea squamosa
Justicia pectoralis
Lasiacis oaxacensis
L. procerrima
Manettia reclinata
Melampodium divaricatum
Melanthera aspera
Melochia melissifolia
Melothria pendula
Mikania micrantha
Mimosa casta
M. pudica
Momordica charantia
Oplismenus burmanni
Panicum fasciculatum
P. maximum
P. pilosum
Paspalum conjugatum
P. virgatum
Phyllanthus urinaria
Rolandra fruticosa
Salvia occidentalis
Setaria paniculifera
Sida acuta
S. rhombifolia
Spilanthes alba
Spiracantha cornifolia
Synedrella nodiflora
Tibouchina longifolia
Tridax procumbens
Verbesina gigantea
Vernonia cinerea

These herbaceous species are accompanied or followed by the more dominant shrubby element of the clearing, which includes:

Cassia fruticosa
Cestrum latifolium
Conostegia speciosa
C. xalapensis
Cordia spinescens
Dioclea guianensis
Guazuma ulmifolia
Hamelia patens
Lantana camara
Mandevilla villosa
Melochia lupulina
Ochroma pyramidale
Piper auritum
P. dilatatum
Serjania mexicana
Solanum jamaicense
S. subinerme
Trema micrantha
Triumfetta lappula
Vernonia canescens
V. patens

Shorelines and marshes. The flora of the lakeshore contributes the next largest number of herbaceous plants, with 68 species more or less restricted to the shore. Since an additional 197 species are more or less restricted to clearings (excluding cultivated species), these two habitat classes contribute a total of 265 species to the flora. Thus the flora is considerably richer relative to the size of the island than it would be if the area were an undisturbed forest lacking clearings and not surrounded by water. Trees and shrubs may grow very near the edge of the lake where the banks are low, but even where they do there is usually adequate light near the ground for the development of an herbaceous flora along the bank. Most common here are species of Cyperaceae and Gramineae.

There are drastic differences between the shorelines of the northern and eastern sides of the island, on the one hand, and the western and southern shores, on the other. During most of the year, especially during the dry season, the trade winds generate waves that buffet the northern and eastern shores, a condition that is greatly exacerbated by the passing of ships close by the north and east on their way through the Canal. In such areas, and especially on the promontories, the resultant erosion has created high banks with an almost constantly changing shoreline. This pattern creates habitats for the more persistent invading herbs. Among the most common species found on steep eroded banks are the following:

Anthurium brownii
Carludovica palmata
Chelonanthus alatus
Gynerium sagittatum
Kohleria tubiflora
Setaria vulpiseta
Thelypteris serrata
Trichopteris microdonta

The aquatic flora of the wave-swept portion of the shore is poor, often consisting only of *Hydrilla.* But in the more sheltered coves in the north and east, and along the entire shore of the western and, especially, southern sides of the island, the aquatic flora is very rich, and often blends almost imperceptibly with the remainder of the herbaceous shoreline vegetation. Moreover, hydrarch or

Buttressed trunk of *Ceiba pentandra*, one of the largest trees on the island

The Laboratory Clearing, near the beginning of Snyder-Molino Trail, Kodak House at left center, the Animal House at right front

Ships in the Canal, the channel passing within 120 m (400 ft) of the island

Vegetation on silt deposits in Shannon Cove, on the southern shore

Annona-Acrostichum association, along the western shore

Epiphytes on a floating log: *Nephrolepis biserrata, Hibiscus sororius,* and *Fuirena umbellata*

shore-depositing succession is in evidence, and there is often no abrupt end of shore. Similar situations can be found in all of the deeper bays and coves surrounding the island wherever the deposition of silt is great. Many of the coves have silted almost completely shut since the formation of the island. Other large expanses of silt are sometimes exposed during the dry season, when the level of the lake may drop several feet. These are quickly populated with herbaceous plants such as:

Acroceras oryzoides
Boehmeria cylindrica
Cleome parviflora
Dennstaedtia cicutaria
Gynerium sagittatum
Hygrophylla guianensis
Ludwigia leptocarpa
L. octovalvis
Panicum grande
P. milliflorum
P. polygonatum
P. trichanthum
Polygonum punctatum
Scleria mitis
Thelypteris serrata

The floristic composition of the aquatic community of the island is usually very rich. Certain species are often found in associations that bear special mention. The most consistent of these associations is made up of *Annona glabra,* a small tree occurring near the shore, and *Acrostichum* spp., large aquatic ferns sometimes forming dense stands. These species may be associated with a wide variety of other aquatic species, but especially the following:

Aeschynomene ciliata
A. sensitiva
Andropogon bicornis
A. glomeratus
Begonia patula
Boehmeria cylindrica
Ceratopteris pteridoides
Cyperus haspan
C. odoratus
Eleocharis caribaea
E. plicarhachis
Fuirena umbellata
Habenaria repens
Hibiscus sororius
Hydrocotyle umbellata
Isachne polygonoides
Leersia hexandra
Ludwigia leptocarpa
L. octovalvis
Nephrolepis biserrata
Passiflora punctata
Phaseolus trichocarpus
Pontederia rotundifolia
Rhynchospora corymbosa
Sagittaria lancifolia
Sarcostemma clausum
Stigmaphyllon puberum
Thalia geniculata
Thelypteris serrata
T. totta
Typha domingensis
Utricularia foliosa
U. obtusa

These species may be found with or separate from the close *Annona-Acrostichum* associations. When not in these associations, the plants often join together to form a floating island of emerged vegetation very rich in species but dominated by *Rhynchospora, Sagittaria,* or *Thalia.* Such islands of vegetation, covering water usually 1–2 m deep, may be surrounded by large masses of *Hydrilla verticillata* or, to a lesser extent, by the free-floating aquatics such as *Salvinia radula, Eichhornia* spp., and *Pistia stratiotes.* Also present are the rooted but otherwise free-floating plants such as *Nymphaea ampla, Limnobium stoloniferum, Nymphoides indica,* and *Ludwigia helminthorrhiza.* Thus, the free-floating aquatics, the attached floaters, and the especially abundant *Hydrilla verticillata* begin the shore-depositing succession by quieting the water and accumulating debris on the lake bottom. *Ceratophyllum demersum,* though less abundant, performs the same function as *Hydrilla.* These two are followed by the emerged aquatic associations and especially by the species-rich floating-island associations. The latter are so floristically variable that no dominant species can be singled out.

Usually nearer the shore, and frequently indistinguishable from the emerged aquatic associations, is an association of shore plants termed the "sedge association" by Kenoyer (1929). This assemblage may be composed of some of the same species found in the floating associations, but the dominant elements include:

Acroceras oryzoides
Cyperus giganteus
C. odoratus
Fuirena umbellata
Gynerium sagittatum
Hymenachne amplexicaulis
Panicum grande
P. mertensii
Phragmites australis
Rhynchospora corymbosa
Scirpus cubensis

Crinum erubescens, Hymenachne amplexicaulis, Spathiphyllum friedrichsthalii, and *Montrichardia arborescens* usually occur along the edge of the lakeshore and adjacent to the forest. Here also are such water-tolerant arborescent plants as:

Coccoloba manzanillensis
Cynometra bauhiniifolia
Dalbergia brownei
D. monetaria
Erythrina fusca
Inga sapindoides
Hibiscus bifurcatus
Pachira aquatica
Pithecellobium hymeneaefolium
P. rufescens
Prioria copaifera
Rhabdadenia biflora
Swartzia simplex

Other species that have been seen mostly along the shore are:

Allophylus psilospermus
Andira inermis
Antirrhoea trichantha
Bursera simaruba
Byrsonima crassifolia
Cecropia obtusifolia
Cochlospermum vitifolium
Coussapoa panamensis
Eugenia galalonensis
Grias fendleri
Inga fagifolia
I. mucuna
Leucaena multicapitula
Machaerium kegelii
Malouetia guatemalensis
Miconia elata
Nectandra purpurascens
Ochroma pyramidale
Ocotea cernua
Pithecellobium macradenium
Quararibea pterocalyx
Swartzia panamensis
Syzygium jambos
Terminalia amazonica
Trichilia hirta
T. verrucosa
Vismia macrophylla
Xylopia frutescens

Tree stumps in the lake. A number of tree stumps still remain from the trees that were drowned when the lake waters first rose. These stumps are generally exposed to full sunlight and provide unique epiphytic habitats. At least two hemiepiphytic trees, *Ficus insipida* and *Coussapoa magnifolia,* occur on the tree stumps. The epiphytic herbs on the stumps include:

Tree-stump epiphytes: *Nephrolepis pendula, Polypodium crassifolium, Sobralia suaveolens,* and *Sarcostemma clausum*

Tree stumps in the lake, offshore between Colorado Point and the laboratory

Anthurium brownii
A. gracile
Catasetum viridiflavum
Nephrolepis pendula
Peperomia cordulata
Polypodium crassifolium
P. phyllitidis
Sobralia suaveolens
Trigonidium egertonianum
Vittaria lineata

Other nonepiphytic species that commonly occur on tree stumps but are probably always rooted into the debris that accumulates on the trunk are *Eleocharis caribaea, Fuirena umbellata, Paspalidium geminatum,* and *Sarcostemma clausum.*

Trails. There are about 37 km (22 miles) of trails leading to all parts of the island (see p. 61 and the BCI map on the front endsheet and pp. 56–57). Each trail is named, and marked at 100 m intervals by permanent signposts. With this well-marked trail system, BCI becomes a unique place for scientific study, for it is relatively easy to note a position and return later to the same spot.

These trails offer yet another microhabitat, some species of plants having been found principally along their edges. The trails are usually not exposed to full sunlight, but the amount of light reaching the ground along them is considerably greater than that in adjacent areas of the forest. Because the trails range so widely throughout the island and pass through so many different habitats, a large part of the flora of the island can be found within a few meters of the trails. Species that are found principally *along* the trails are the following:

Herbaceous plants
Adiantum humile
A. obliquum
A. petiolatum
Blechum costaricense
Calathea panamensis
Calyptrocarya glomerulata
Campelia zanonia
Costus pulverulentus
Cyathula prostrata
Cyperus simplex
Dalechampia tiliifolia
Desmodium axillare var. *stoloniferum*
D. wydlerianum
Dimerocostus strobilaceus (rare)
Diodia denudata
Geophila croatii
G. repens
Gibasis geniculata
Gurania makoyana
Ichnanthus brevivaginatus
I. pallens
I. tenuis
Lithachne pauciflora
Nautilocalyx panamensis
Oplismenus burmanni
O. hirtellus
Orthoclada laxa
Panicum pulchellum
P. pilosum
P. polygonatum
Paspalum decumbens
Petiveria alliacea
Phaeosphaerion persicariifolium
Pothomorphe peltata (rare)
Ruellia metallica
Selaginella arthritica
S. flagellata
S. haematodes
S. horizontalis
Sida acuta
Spathiphyllum phryniifolium
Spigelia anthelmia
S. humboldtiana
Teliostachya alopecuroidea
Thelypteris dentata
T. nicaraguensis
T. poiteana
Xanthosoma helleborifolium
Xiphidium caeruleum

Shrubs and trees
Acalypha macrostachya
Ardisia bartlettii
A. pellucida
Cephaelis ipecacuanha
Hamelia axillaris
Lycianthes maxonii
Pavonia dasypetala
Piper darienense
Psychotria carthagenensis
P. psychotriifolia
P. racemosa
Vismia billbergiana

Ravines. Ravines offer a unique habitat, because they are moister and darker than any other part of the forest. Streams are never very large, but they flow rapidly, and generally have flowing water throughout the rainy season. The following species are either restricted to or most common in ravines:

Epiphytes and hemiepiphytes
Asplenium auritum
A. laetum
Guzmania lingulata var. *minor*
Maxonia apiifolia
Polybotrya villosula
Sobralia panamensis

Other herbs
Anthurium ochranthum
Asplenium delitescens
Asplundia alata
Bolbitis cladorrhizans
Carludovica drudei
Ctenitis protensa
Cyclanthus bipartitus
Cyclopeltis semicordata
Danaea nodosa
Diastema raciferum
Dictyoxiphium panamense
Dieffenbachia oerstedii
Hemidictyum marginatum
Homalomena wendlandii
Hymenocallis pedalis
Philodendron grandipes
Pteris altissima
P. grandifolia
Rhodospatha moritziana
Saccoloma elegans
Selaginella exaltata
S. mollis
Tectaria euryloba
Thelypteris balbisii
T. extensa
T. torresiana
Trichomanes diversifrons
T. pinnatum

Shrubs and trees
Clidemia purpureo-violacea
Geonoma cuneata
G. procumbens
Leandra dichotoma
Miconia lateriflora
Myriocarpa yzabalensis
Piper arieianum
P. culebranum
P. imperiale
P. pseudo-garagaranum
P. pubistipulum
P. viridicaule

Tree ferns
Cnemidaria petiolata
Metaxya rostrata
Nephelea cuspidata

A few species, such as *Asplenium delitescens* and *Bolbitis cladorrhizans,* may occur directly in the streams on rocks. In a few of the streams there are small waterfalls, but none have developed any plant associations—unlike so many waterfalls and rapid streams elsewhere in Panama where members of the Podostemonaceae might be found. This circumstance is due perhaps to an inadequate amount of light, or more likely to the fact that most streams dry up in the dry season.

Forest floor. In addition to the herbs that grow principally in ravines or along forest trails, a number occur in other parts of the forest. Those that are associated principally with light-gaps created by tree falls include:

Calathea inocephala
C. latifolia
C. marantifolia
Costus allenii

Streambed on Balboa Trail, in the dry season

The forest near Barbour and Lathrop trails

Costus laevis — *Ischnosiphon leucophaeus*
C. scaber — *I. pruinosus*
Heliconia catheta — *Renealmia alpinia*
H. subulata — *Scleria pterota*

There are other forest-floor herbs not regularly associated with either trails, ravines, light-gaps, or forest edges. These include:

Ferns
Adiantum decoratum — *A. seemannii*
A. fructuosum — *Asplenium delitescens*
A. lunulatum — *Dictyoxiphium panamense*
A. pulverulentum — *Diplazium grandifolium*

Araceae
Dieffenbachia longispatha — *Dracontium dressleri*
D. pittieri

Gramineae
Chusquea simpliciflora — *Streptochaeta sodiroana*
Pharus latifolius — *S. spicata*
P. parvifolius — *Streptogyne americana*
Rhipidocladum racemiflorum

Other families
Aechmea magdalenae — *Palmorchis powellii*
Calathea inocephala — *Peperomia killipi*
Dichorisandra hexandra — *P. obtusifolia*
Neomarica gracilis — *Renealmia cernua*

Aechmea magdalenae is a large conspicuous herb that becomes dominant in some areas of the forest, forming close, virtually impenetrable stands. These are especially in evidence in some of the wet, moderately flat areas along Zetek Trail below the escarpment.

Despite the long lists of herbaceous ground species that do occur in the forest, most of the plants growing in most areas of the forest are not herbaceous. The principal vegetation of the shaded forest floor consists of seedlings of arborescent plants and herbaceous vines. Herbaceous ground plants of any kind are uncommon, except for:

Adiantum lucidum — *Homalomena wendlandii*
A. petiolatum — *Pharus parvifolius*
Anthurium ochranthum — *Renealmia cernua*
Carludovica drudei — *Rhipidocladum racemiflorum*
Chusquea simpliciflora — *Selaginella haematodes*
Cyclopeltis semicordata — *Tectaria incisa*
Dieffenbachia longispatha — *Thelypteris dentata*
D. oerstedii — *T. nicaraguensis*
Dictyoxiphium panamense — *T. poiteana*
Diplazium grandifolium

Habit-and-Habitat Classes

Habit diversity, like poor soils and species diversity, is a principal feature of tropical forests, and most habit types are exhibited on BCI. Table 3 lists the number of BCI species in each of a number of habit-and-habitat classes; these classes are employed in the discussions of growth forms that follow and in Table 4 (on geographical affinities, p. 27) and Table 5 (on flowering and fruiting periods, p. 37).

Growth Forms

Arborescent plants. Though shrubs and trees exhibit a continuous range of heights and cannot be easily classified into categories, I have placed them in artificial categories because of obvious ecological differences. For convenience, I have classified as a small tree any species that usually does not become a part of the canopy; usually, these trees are less than 10 m tall. Trees more than 10 m tall are classified as medium-sized or large.

There are 1,316 native or naturalized species of vascular plants on the island. A total of 53 are cultivated and are excluded from further consideration here. Of the native or naturalized species, 481 (36.5%) are arboreal. Of the arboreal species, 34 (7%) are trees that may be taller than 30 m and are known or possible emergents, whereas 177 (37%) are trees 10–30 m tall, 247 (51%) are trees or shrubs less than 10 m tall, 16 (3%) are hemiepiphytic shrubs, and 7 (1.4%) are parasitic shrubs. Of the

TABLE 3
Summary of BCI habit-and-habitat classes

Habit-and-habitat class	Number of species	Percent of native flora (total 1,316)
CRYPTOGAMS		
Epiphytes	41	3.1%
Hemiepiphytes	1	.1
Aquatics	6	.5
Vinelike plants	4	.3
Other terrestrials	47	3.6
Tree ferns	5	.4
TOTAL CRYPTOGAMS	104	7.9
PHANEROGAMS		
Trees more than 10 m tall	211	16.0
Small trees or shrubs (not including plants that are always shrubs)	154	11.7
Shrubs 2(3) m tall	93	7.1
Epiphytic or hemiepiphytic shrubs or trees	16	1.2
Parasitic shrubs	7	.5
TOTAL ARBORESCENT SPECIES	481	36.5
Lianas or climbing woody plants (including ten climbing trees or shrubs)	171	13.0
Vines	83	6.3
Hemiepiphytic or epiphytic vines	11	.8
TOTAL SCANDENT SPECIES	265	20.1
Epiphytic herbs	135	10.3
Primarily aquatic herbs	54	4.1
Primarily clearing herbs	197	15.0
Primarily forest herbs	75	5.7
Parasitic herbs	1	.1
Saprophytic herbs	4	.3
Suffruticose herbs (included in above habitat classes)	(18)	
TOTAL HERBACEOUS SPECIES (not including scandents)	466	35.4
All woody plants (arborescents and lianas)	652	49.5
All herbaceous plants (including scandents)	560	42.6
TOTAL NATIVE PHANEROGAMS	1,212	92.1
Cultivated phanerogams	53	
TOTAL PHANEROGAMS	1,265	
TOTAL VASCULAR PLANTS	1,369	

247 small trees and shrubs, 93 are strictly shrubs (usually less than 3 m tall).

Some of the large trees may extend above the canopy and be classified as possible emergent species (see the list on p. 8), though trees classified as emergents are not always raised above the canopy. (Some individuals flower when they are young and growing at subcanopy levels; others may be found among the emergent trees.)

In general, crown shape is determined by the conditions under which a plant grows. A species with a broad, spreading crown, such as *Enterolobium cyclocarpum,* will usually be found in an area that was once quite open, since such species will not do well as seedlings under closed-canopy conditions. Other species, with narrower crowns, are plants that develop under closed, highly competitive conditions. However, some species that appear to do quite well under crowded conditions, such as *Tachigalia versicolor,* have relatively broad, spreading crowns.

Degree of buttressing is another character often found to be species-diagnostic, though some conditions—such as poor supporting soil, a steep slope, or a stream or lakeshore—tend to accentuate buttressing in most species that develop in this fashion. Buttressing varies considerably both between and within species. Knight (1975a) reported that 22% of the trees less than 10 cm in diameter at breast height in the old forest have buttresses, and that 4% have individual buttresses with an area of more than 0.3 m^2 (on one face of buttress only). Among the species that usually exhibit buttressing on BCI are:

Acacia glomerosa
Anacardium excelsum
Apeiba membranacea
Aspidosperma cruenta
Beilschmiedia pendula
Bombacopsis quinata
B. sessilis
Calophyllum longifolium
Castilla elastica
Cedrela odorata
Ceiba pentandra
Celtis schippii
Cespedezia macrophylla
Cordia alliodora
Couratari panamensis
Dipteryx panamensis
Enterolobium schomburgkii
Ficus bullenei
F. costaricana
F. dugandii
F. insipida
F. obtusifolia
F. tonduzii
F. trigonata
F. yoponensis
Guapira standleyanum
Guatteria dumetorum
Hyeronima laxiflora
Jacaranda copaia
Licania platypus
Luehea seemannii
Maquira costaricana
Mosquitoxylon jamaicense
Ochroma pyramidale
Ocotea oblonga
Pachira aquatica
Poulsenia armata
Pterocarpus officinalis
P. rohrii
Quararibea asterolepis
Sapium caudatum
Schizolobium parahybum
Sloanea terniflora
S. zuliinensis
Tabernaemontana arborea
Tachigalia versicolor
Terminalia amazonica
T. chiriquensis
Tetragastris panamensis
Trattinnickia aspera
Virola surinamensis
Zanthoxylum panamense

In some of these species, the buttressing may be slight, or it may not always be present on all individuals. Some species typically produce stilt or adventitious roots, which may be effective in providing additional support to the plant. These include the following:

Cecropia spp.
Chamaedorea wendlandii
Ficus pertusa
Pourouma guianensis
Protium panamense
Socratea durissima
Tovomita longifolia
Trichanthera gigantea

The trunk height (above ground) of the lowermost branches is also quite variable. In some species, such as *Jacaranda copaia,* the branches may be restricted to the uppermost part of the trunk. Branching is irregular in most cases, but may be markedly regular in the case of *Virola surinamensis,* where the branches are spirally arranged in a more or less systematic manner.

A common feature of many tropical trees, particularly of small or medium-sized trees that are not buttressed, is the production of sucker shoots near the base of the trunk. Sometimes this produces small clumps of trunks, as in the case of *Coccoloba acapulcensis* and *coronata* (Polygonaceae) and *Cupania sylvatica* (Sapindaceae). In other cases, the sucker shoots are not produced until one trunk has become fairly tall, as in *Guettarda foliacea* (Rubiaceae), *Nectandra cissiflora* (Lauraceae), and *Macrocnemum glabrescens* (Rubiaceae). Ecologically, the production of sucker shoots may play an important role, by ensuring a position in the forest for any tree whose major trunk is destroyed by windfall, lightning, or old age. A tree with well-developed sucker shoots attached to a well-developed root system can more quickly fill the void left by its principal trunk than can one that is in the seedling stage at the time the void is created—I have observed sucker shoots that produced a new trunk even where the fall of the main trunk had uprooted much of the root system.

Most of the small trees and shrubs are plants of the forest, though a few occur only in clearings. These include:

Adenaria floribunda
Cordia spinescens
Solanum asperum
S. jamaicense
S. ochraceo-ferruginum
S. rugosum
S. subinerme
S. umbellatum
Triumfetta lappula
Vernonia patens

As a habit class, small trees and shrubs merge imperceptibly with larger trees, on the one hand, and with suffruticose herbs, on the other. What would normally be an herb in an annually cleared area can become a stout woody shrub in the forest. A good example is *Witheringia solanacea.*

Climbing plants. Climbing plants, including both lianas and herbaceous vines and to some extent much smaller numbers of climbing shrubs and trees, are unique among habit classes in being able to move considerable distances in a relatively short time to reach a source of light. They are thus not so seriously hampered by the low light conditions in the forest as are the herbs.

Lianas are restricted to the forest and are best developed in the oldest forest. Of all growth forms they perhaps best characterize a tropical forest, simply because

they are so infrequent in temperate forests. There are 171 species (13% of the native flora) of lianas, climbing shrubs, and climbing trees on BCI. They are found principally in the following families, which contain 82% of all species of BCI lianas:

Bignoniaceae (24 species)
Leguminosae (22 species)
Sapindaceae (19 species)
Malpighiaceae (13 species)
Apocynaceae (11 species)
Dilleniaceae (8 species)
Vitaceae (6 species)
Smilacaceae (5 species)
Hippocrateaceae (5 species)
Combretaceae (5 species)
Connaraceae (4 species)
Rubiaceae (4 species)
Aristolochiaceae (3 species)
Menispermaceae (3 species)
Loganiaceae (3 species)
Convolvulaceae (3 species)
Verbenaceae (3 species)

Herbaceous vines are fewer in number in the forest than are the lianas. There are 94 herbaceous vines, 11 of which are epiphytic or hemiepiphytic. Vines generally do not grow over the surface of the canopy, as do lianas, but are most often growing *within* the canopy. Among the species of vines that regularly occur in the forest are the following:

Cayaponia granatensis
Cissus erosa
C. microcarpa
C. pseudosicyoides
C. rhombifolia
C. sicyoides
Cynanchum recurvum
Dalechampia cissifolia
D. dioscoreifolia
D. tiliifolia
Dioscorea haenkeana
D. macrostachya
D. polygonoides
D. sapindoides
D. urophylla
Fevillea cordifolia
Gurania coccinea
G. makoyana
Ipomoea phillomega
Lygodium venustum
Mendoncia gracilis
M. littoralis
Mucuna mutissiana
Passiflora nitida
P. williamsii
Piper aristolochiifolium
Psiguria bignoniacea
P. warscewiczii
Sabicea villosa var. *adpressa*
Sicydium coriaceum
Smilax lanceolata
S. mollis
S. panamensis
S. spinosa
S. spissa
Wulffia baccata

Though the distinction between lianas (woody climbers) and vines (herbaceous climbers) is usually readily apparent, it is sometimes difficult to tell if a climbing species is herbaceous or woody. This is especially true of climbers in some of the dicotyledonous families, including the Cucurbitaceae, Aristolochiaceae, Vitaceae, Leguminosae, Passifloraceae, Sapindaceae, Convolvulaceae, Apocynaceae, and Asclepiadaceae. In addition, climbers in two of the monocotyledonous families, the Dioscoreaceae and Smilacaceae, are sometimes woody.

Characteristic of the behavior of lianas is their relatively slow development in girth until they reach the light near the top of the canopy. They then develop larger stems and spread through and especially over the canopy. Also characteristic of both lianas and vines growing on or near the forest floor is their development of long branches that bear reduced leaves or no leaves at all. In either case, the internodes are very much more elongated than comparable parts that have begun to spread through the canopy. Leafless portions are often very long, and in some species they may extend across the forest floor for 100 m or more. Peñalosa (1975) has shown that at least in some cases a very small percentage of all branches reach the top of the canopy. Since most branches specialized for searching are probably operating at a photosynthetic loss, it can be assumed that the canopy portions of the plant are providing food for the searching portions. Since lianas may be very long-lived, a single individual may eventually occupy several spots in the canopy. Relatively few, however, are found to cross from one canopy tree to another. Lianas often survive, after the tree in which they were growing falls, by climbing another tree and becoming reestablished. A history of their success and failure can often be followed by tracing the largest trunk of the plant through the forest. In some cases a fallen liana produces adventitious roots, so that additional parts of the plant are less dependent on the original trunk for water and nutrients.

Lianas and vines have evolved a variety of adaptations that facilitate their climb to the canopy from the forest floor. These adaptations are often specific to a family. Tendrils are used for climbing in the Bignoniaceae, Vitaceae, Sapindaceae, Leguminosae (*Bauhinia*), Rhamnaceae (*Gouania*), and Passifloraceae. Sharp, recurved woody stipules are used in the genus *Machaerium* (Leguminosae). Stout, recurved axillary spines are employed in *Uncaria* (Rubiaceae), *Celtis* (Ulmaceae), *Pisonia* (Nyctaginaceae), and sometimes *Combretum* (Combretaceae) (see the figure on the next page). In *Combretum,* the spines are accompanied by persistent petioles that become woody and help the plant hold its position in the same way the spines do. *Byttneria aculeata* (Sterculiaceae) and *Solanum lanciifolium* (Solanaceae) and some species of *Smilax* (Smilacaceae) bear recurved prickles all along the stem; prickles are also present on the lower blade surface of *Byttneria* and *Solanum lanciifolium.* Such adaptations have the effect of causing a plant to climb by allowing it to work its way upward (but not down again) during movements caused by the wind or by animals.

Lianas of the Hippocrateaceae utilize an unusual method for holding themselves in position. In most members of the family, and perhaps in *Securidaca diversifolia* (Polygalaceae), twining branches grasp branches of other plants with which they come in contact. In some groups, such as *Cissus* (Vitaceae) and *Aristolochia* (Aristolochiaceae), the plants develop a corky periderm, or outer bark, which is less subject to slippage than is a smooth periderm and may thus be helpful to the plant in maintaining its position in the canopy.

The conspicuous swelling of the nodes in *Gnetum*

Understory vegetation along Donato Trail

Two armed forest species: juvenile tree of *Zanthoxylum setulosum* at left, stems of *Combretum decandrum* at right

Liana in the old forest

(Gnetaceae) and in many of the Bignoniaceae probably assists plants in holding their position by preventing them from slipping back. Many lianas and high-climbing herbaceous vines (indeed, about 50% of all scandent plants) have opposite branching, which often prevents the plant from falling by providing a wider area of support.

Vines, as well as plants that are late in becoming woody, such as the Convolvulaceae, Apocynaceae, Piperaceae (*Piper aristolochiifolium*), Rubiaceae (*Manettia* and *Sabicea*), Schizaeaceae, Compositae (*Wulffia*), and Asclepiadaceae, usually climb by twining around the trunks or branches of trees. Vines of the genus *Desmoncus* (Palmae) climb by means of modified leaflets that form stout, recurved spines. *Scleria bracteata* (Cyperaceae), a vine of weedier forest edges, climbs over and into trees by means of retrorse pubescence on its stems and leaves. Juvenile stems of the liana *Prionostemma aspera* bear similar trichomes, as do the young herbaceous stems of many other vines and lianas, such as the Dilleniaceae. Such adaptations are most advantageous higher in the canopy or in open areas where movement by the wind is more effective.

Juvenile stages of a number of species climb the sides of trunks or trees by producing roots that grow into the bark (Araceae; *Hydrangea,* Saxifragaceae) or by using tendrils that are claw-shaped (*Macfadyena unguis-cati,* Bignoniaceae).

A number of species are intermediate in habit in the sense that they may be either arborescent or scandent, depending on the conditions under which they grow. Ten species are scandent or climbing trees or shrubs, rather than lianas. In the canopy or along the lake or at the margins of clearings they may be difficult to separate from lianas, but they generally have a stout, more or less erect, and often unsupported trunk. These include:

Cassia undulata	*S. tenuifolia*
Dalbergia monetaria	*Strychnos brachistantha*
Heterocondylus vitalbis	*Tournefortia angustiflora*
Justicia graciliflora	*T. cuspidata*
Securidaca diversifolia	*Wulffia baccata*

Two other climbing shrubs are hemiepiphytic:

Hydrangea peruviana	*Souroubea sympetala*

Twelve of the lianas may sometimes be climbing shrubs:

Acacia riparia	*C. turczaninowii*
Allamanda cathartica	*Heteropteris laurifolia*
Byttneria aculeata	*Machaerium arboreum*
Chamissoa altissima	*Pisonia aculeata*
Chomelia psilocarpa	*Pouzolzia obliqua*
Connarus panamensis	*Strychnos panamensis*

Herbaceous plants. The herbaceous element of BCI's flora is even more diverse in habit type than is the woody element. Even excluding the many palms that are arborescent in habit and woody in the stems, the herbaceous flora remains more diverse than the woody element. The herbs may be annual, perennial, or suffruticose; they may be erect, sprawling, vinelike, epiphytic, hemiepiphytic, saprophytic, parasitic, or aquatic; and they include the small palms and other, often giant, monocotyledonous herbs (such as many members of the Musaceae, Zingiberaceae, and Marantaceae) that may compete with the shrubs for light.

Most of the herbaceous ground plants in the flora occur principally in man-made clearings and at the margin of the lake. Of the 560 phanerogamic herbs on BCI (including 94 vines), only 79 (including 4 saprophytes) are restricted to the forest floor. In contrast, 197 herb species (including suffruticose herbs) occur in clearings, and 54 species are aquatic. The smaller number of herbaceous species that inhabit the forest floor is no doubt due to the small amount of light that reaches the ground. Many of these species have broad leaves adapted to absorbing a maximum of light in these relatively dark parts of the forest.

Saprophytic plants, relatively uncommon on BCI, are restricted to the genera *Voyria* (Gentianaceae) and *Thismia* (Burmanniaceae). The orchid genus *Triphora* is also, apparently, to some extent saprophytic.

One herbaceous species, *Apodanthes casearіae* (Rafflesiaceae), survives the relative absence of light near the forest floor by parasitizing the trunks of *Casearia* (Flacourtiaceae). The visible part of the plant consists of a single small flower.

The ecological conditions of the aquatics are unique in the sense that the plants suffer no deficiency of water and rarely a serious deficiency of light. This habit type is discussed in detail in the section on shorelines and marshes (p. 9).

Suffruticose herbs are often difficult to place in a habit class, since, depending on their age, they may either be herbaceous throughout or have a stout woody stem. This pattern of development is especially common in the Malvaceae and Acanthaceae. Suffruticose herbs are common in areas of repeated disturbance, such as clearings and trailsides, since cutting them back seldom causes permanent damage.

Epiphytic and hemiepiphytic plants. Most true epiphytes in BCI's flora are herbaceous (defined as including vines). They are found in the following families: Orchidaceae (82 species), Polypodiaceae (31), Araceae (24), Bromeliaceae (18), Piperaceae (10), Hymenophyllaceae (9), Cactaceae (3), and Begoniaceae, Cyclanthaceae, Gesneriaceae, Lycopodiaceae, and Rubiaceae (1 each). The only woody epiphytes in the flora are *Codonanthe* and *Columnea* (Gesneriaceae).

For the true epiphytes, light does not need to be a limiting factor, since they may be found at any level in the forest, from near the ground to the top of the canopy. Apparently, the advantage of moving higher to receive more light is offset by the increasingly arid conditions at the higher levels and the fewer nutrients available in fallen debris, for the majority of epiphytes are in fact found at lower to intermediate levels. It is interesting to note that the only species known to live at the very top of the canopy in full sunlight is *Aechmea tillandsioides* (Bromeliaceae), which is a tank epiphyte with a built-in

water reservoir, and is usually found growing on ant nests. The nutrients derived from the microfauna in the tank reservoir and from the ant nest apparently compensate for its otherwise nutrient-poor position.

Epiphytes have developed several methods of obtaining an adequate water supply in the relatively acute dry season. In the case of *Trichomanes* (Hymenophyllaceae) and some species of *Polypodium* (Polypodiaceae), plants may be rejuvenated even after serious dessication. Orchids and most *Anthurium* (Araceae) have roots that absorb moisture from the air. The Bromeliaceae bear specialized peltate scales that absorb and hold moisture. Most epiphytes have a thick epidermis that prevents the escape of water, and their thick tissues also act as storage organs for water. In some epiphytes (especially Bromeliaceae and *Anthurium*), the leaves are arranged in rosettes that may catch and hold debris from which the roots may withdraw nutrients and water.

Epiphytes may be found attached on nearly any part of a tree. The larger ones, however, are usually found in the crotches of trunks or branches, owing to the greater support and collection of detritis afforded there. Small epiphytic plants, such as *Codonanthe* and *Columnea,* may attach themselves even to the vertical surfaces of trunks, by means of small roots.

Hemiepiphytes are those that rely on another plant for support but whose roots are in the ground. Most hemiepiphytes are shrubs or small trees, but a few are herbaceous, especially *Monstera, Philodendron,* and *Rhodospatha* (Araceae), as well as *Diodia sarmentosa* (Rubiaceae) and *Polybotrya* and *Maxonia* (Polypodiaceae). Woody hemiepiphytic plants include *Marcgravia* and *Souroubea* (Marcgraviaceae), *Havetiopsis* and *Clusia* (Guttiferae), *Ficus* and *Coussapoa* (Moraceae), *Topobaea* (Melastomataceae), *Oreopanax* (Araliaceae), *Markea* and *Lycianthes* (Solanaceae), *Columnea purpurata* (Gesneriaceae), *Cosmibuena* (Rubiaceae), and *Hydrangea* (Saxifragaceae).

It is not always easy to distinguish true epiphytes from hemiepiphytes. Some groups of herbaceous plants, such as *Philodendron, Rhodospatha,* and *Monstera* in the Araceae, begin life as hemiepiphytes but later may become true epiphytes. Others, such as *Ficus, Clusia,* and *Cosmibuena,* begin as true epiphytes and ultimately send roots to the ground. *Philodendron radiatum* also follows this pattern, though for most *Philodendron* the reverse is true.

The woody hemiepiphytes range in size from the small *Diodia sarmentosa* (Rubiaceae) to *Ficus* and *Coussapoa panamensis* (Moraceae). Most hemiepiphytic shrubs and trees grow high in the canopy and are supported either by a stout branch or by the crotch of a large tree. From this point a stout, usually solitary, stem extends down the side of the supporting trunk to the ground. These species usually have no other obvious adventitious roots that could absorb water. Some species, such as *Clusia* and *Havetiopsis* (Guttiferae) and *Cosmibuena* (Rubiaceae), compensate for this lack by retaining moisture in their very thick, leathery leaves. Still others, such as *Topobaea praecox* (Melastomataceae), are leafless during part of the dry season, and the plant may be somewhat dormant at this time. Other genera, such as *Coussapoa* (Moraceae) and *Souroubea* (Marcgraviaceae), may produce numerous roots, at least some of which do not reach the ground; these species probably acquire part of their nutrients from the accumulation of falling debris before it reaches the ground.

Ficus is unusual in sending a number of stems to the ground, the stems ultimately coalescing to form a united structure that strangles the host tree.

The hemiepiphytic Araceae attach themselves to tree trunks by means of small rootlets that become fastened to cracks in the tree's bark. Plants such as *Clusia* and some species of *Ficus,* such as *F. obtusifolia,* have more elaborate methods of attachment: in general, seedlings of these species are found on the side of a tree trunk, often growing from a small crack; as the seedling grows and its trunk elongates (usually at a sharp angle to the host trunk), it develops roots that encircle the trunk of the supporting tree as well as its own trunk to bind the two firmly together.

Since hemiepiphytes are usually rooted into the soil, they clearly have an advantage in obtaining water and nutrients that true epiphytes do not share. Nevertheless, the usually small diameter of the stems or trunks must put them at some disadvantage in this respect. The stem of *Markea ulei* (Solanaceae) is particularly small, but this species often compensates by developing a swollen enlargement of the stem that presumably acts as a storage organ during times of stress.

Perhaps the most unusual habit of woody plants, as opposed to herbs, is the parasitic habit. Although there is one parasitic herb in the flora, all other parasitic plants on BCI (seven species) are shrubs or somewhat woody vines of the family Loranthaceae. All seven of these are photosynthetic, but they obtain their water and presumably part of their nutrients from their host. All grow in the canopy and especially along the shore in exposed areas.

Floristic Composition

In his *Flora of Barro Colorado Island* (1933), Standley included a list of the nonvascular plants known from the island. This list, totaling 204 species, included algae in the families Desmidiaceae (34 species), Characeae (1), and Rhodophyceae (1), as well as myxomycete fungi (11), ascomycete fungi (54), basidiomycete fungi (55), imperfect fungi (9), lichens (9), hepatics (11), and mosses (15). Although no thorough modern survey of any of the above groups has been published for BCI, it can be assumed that Standley's list represents only a small portion of the nonvascular plants occurring on the island.

The present work deals only with the vascular flora of BCI, which includes 1,369 taxa. Of these, 104 (8%) are cryptogams, 2 are gymnosperms, 353 (25.8%) are monocotyledons, and 910 (66.5%) are dicotyledons. The average number of native species per genus is 1.9. The largest genera are *Piper* (Piperaceae), 21 species; *Psychotria* (Rubiaceae), 20; *Inga* (Leguminosae), 18; *Ficus* (Mora-

Polypodium phyllitidis and *Nephrolepis pendula,* growing as tree-crotch epiphytes at 20 m (65 ft)

A strangling *Ficus* climbing its host. . .

. . . and the void once filled by the host

ceae), 17; *Miconia* (Melastomataceae), 14; *Polypodium* (Polypodiaceae), 13; *Philodendron* (Araceae), 13; *Epidendrum* (Orchidaceae), 13; *Anthurium* (Araceae), 12; *Cyperus* (Cyperaceae), 11; *Solanum* (Solanaceae), 11; *Panicum* (Gramineae), 10; *Peperomia* (Piperaceae), 10; and *Trichomanes* (Hymenophyllaceae), 10. A detailed listing of numbers of genera and species per family, the families arranged by order and division, can be found in the section on classification and family sequence (p. 61). A few species of recently introduced cultivated plants are not treated in this work, both because they are considered unimportant and because they cannot be identified with certainty.

A few species that are cultivated elsewhere are treated here as native because they are seemingly naturalized on the island. These include *Chrysophyllum cainito, Mangifera indica, Phoebe mexicana, Syzygium jambos, Theobroma cacao,* and *Vanilla fragrans.* The 53 species that are cultivated on the island are described in this flora, but they have been excluded for the most part from the discussion of seasonal behavior and geographical affinities. The cultivated species, excluding the six that are evidently naturalized, are the following:

Acalypha wilkesiana
Amaryllis belladonna
Anacardium occidentale
Ananas conosus
Annona muricata
Araucaria excelsa
Artocarpus altilis
Averrhoa carambola
Bactris gasipaes
Bambusa arundinacea
B. glaucescens
Caesalpinea pulcherrima
Cajanus bicolor
Caladium bicolor
Calathea villosa
Capsicum annuum
Carica papaya
Citrus (6 species)
Clerodendrum paniculatum
Cocos nucifera
Codiaeum variegatum
Coleus blumei
Cordyline fruticosa
Dioscorea alata
D. trifida
Ervatamia coronaria
Eugenia uniflora
Ficus retusa
Garcinia mangostana
Heliconia metallica
H. pogonantha
Hibiscus rosa-sinensis
Ipomoea batatas
Ixora coccinea
Jacquinia macrocarpa
Jatropha curcas
Mammea americana
Manihot esculenta
Musa sapientum
Persea americana
Polyscias guilfoylei
Psidium guajava
Saccharum officinarum
Spathodea campanulata
Syngonium sp.
Thunbergia erecta
Xanthosoma nigrum
Zingiber officinale

Sexual Characteristics

Of the 1,265 phanerogamic plants (including cultivated plants) known for the flora, 304 (24%) have unisexual flowers. Of these, 115 (9%) are dioecious:

Abuta (2 species)
Acalypha macrostachya (also monoecious)
Adelia triloba
Alchornea costaricensis
A. latifolia
Alibertia edulis
Amaioua corymbosa
Apodanthes caseariae
Araucaria excelsa (also monoecious; cultivated)
Astronium graveolens
Baccharis trinervis
Bursera simaruba (polygamodioecious)
Carica cauliflora
C. papaya (cultivated)
Catopsis sessiliflora (also monoecious)
Castilla elastica (also monoecious)
Cayaponia granatensis
Cecropia (4 species)
Chamaedorea wendlandiana
Cissampelos (2 species)
Chondrodendron tomentosum
Clusia odorata
Coccoloba coronata
Cordia panamensis
Coussapoa (2 species)
Dioscorea (7 species, 2 cultivated)
Diospyros artanthifolia
Dorstenia contrajerva
Drypetes standleyi
Fevillea cordifolia
Gnetum leyboldii var. *woodsonianum*
Guapira standleyanum
Guarea glabra
G. multiflora
Gurania (3 species)
Gynerium sagittatum
Hampea appendiculata var. *longicalyx*
Havetiopsis flexilis
Hydrilla verticillata
Hyeronima laxiflora
Iresine celosia
Jacaratia spinosa
Limnobium stoloniferum
Maquira costaricana
Margaritaria nobilis
Momordes powellii
Myriocarpa yzabalensis
Neea amplifolia
Ocotea (4 species)
Odontocarya (2 species)
Olmedia aspera
Perebea xanthochyma
Picramnia latifolia
Pisonia aculeata
Pourouma guianensis
Pouteria stipitata
Protium costaricense
P. panamense
P. tenuifolium
Pseudolmedia spuria
Psiguria (2 species)
Randia (2 species)

Rheedia acuminata (polygamodioecious)
R. edulis
Scheelea zonensis (also monoecious)
Sicydium coriaceum
Simarouba amara
Siparuna pauciflora
Smilax (5 species)
Sorocea affinis
Struthanthus orbicularis
Stylogyne standleyi
Tetragastris panamense
Tovomita longifolia
T. stylosa
Trattinnickia aspera
Trichilia (4 species)
Triplaris cumingiana
Trophis racemosa
Urera eggersii
Virola (2 species)
Xylosma (2 species)
Zanthoxylum (4 species)

There are 139 monoecious species in the flora:

Acalypha (4 species, 1 cultivated)
Amaranthus viridis
Araucaria excelsa (cultivated)
Artocarpus altilis (cultivated)
Asplundia alata
Astrocaryum standleyanum
Bactris (5 species, 1 cultivated)
Begonia (3 species)
Boehmeria cylindrica
Brosimum alicastrum
Caladium bicolor (cultivated)
Calyptrocarya glomerulata
Carludovica (2 species)
Castilla elastica (also dioecious)
Catasetum (2 species)
Catopsis sessiliflora (also dioecious)
Cayaponia (2 species)
Cedrela odorata
Celtis iguaneus
Ceratophyllum demersum
Chamaesyce (4 species)
Clibadium surinamense
Coccoloba (4 species)
Cocos nucifera (cultivated)
Codiaeum virgatum (cultivated)
Croton (3 species)
Cyclanthus bipartitus
Dalechampia (3 species)
Desmoncus isthmius
Dieffenbachia (3 species)
Elaeis oleifera
Ficus (17 species, 1 cultivated)
Garcia nutans
Geonoma (3 species)
Homalomena wendlandii
Hura crepitans
Jatropha curcas (cultivated)
Lithachne pauciflora
Ludovia integrifolia
Mabea occidentalis
Mammea americana (cultivated)
Manihot esculenta (cultivated)
Melothria (2 species)
Momordica charantia
Montrichardia arborescens
Musa sapientum (cultivated)
Oenocarpus panamanus
Olyra latifolia
Omphalea diandra
Pharus (2 species)
Philodendron (13 species)
Phoradendron (2 species)
Phyllanthus (3 species)
Pilea microphylla
Pistia stratiotes
Poinsettia heterophylla
Posadaea sphaerocarpa
Poulsenia armata
Pouzolzia obliqua
Sagittaria lancifolia
Sapium (2 species)
Scheelea zonensis (also dioecious)
Scleria (5 species)
Siparuna guianensis
Socratea durissima
Sterculia apetala
Synechanthus warscewiczianus
Syngonium (2 species)
Trema micrantha
Trichospermum mexicanum
Typha domingensis
Xanthosoma (3 species)

The following species, included on both of the preceding lists, may be either monoecious or dioecious:

Acalypha macrostachya
Araucaria excelsa (cultivated)
Castilla elastica
Catopsis sessiliflora
Scheelea zonensis

Finally, there are 54 polygamous species on the island:

Allophylus psilospermus (polygamodioecious)
Baltimora recta
Chaptalia nutans
Cladium jamaicense
Conyza (2 species)
Cupania (4 species)
Eclipta alba
Erechtites hieracifolia
Garcinia mangostana (cultivated)
Heliocarpus popayanensis (gynomonoecious)
Mammea americana (also monoecious, cultivated)
Maytenus schippii
Melampodium divaricatum

Oreopanax capitatus
Paullinia (9 species)
Pluchea odorata
Rhynchospora (3 species)
Schistocarpha oppositifolia
Serjania (9 species)
Synedrella nodiflora
Talisia (2 species)
Tetracera (3 species, androdioecious)
Thinouia myriantha
Tovomitopsis nicaraguensis
Tridax procumbens
Verbesina gigantea
Vismia billbergiana
Vitis tiliifolia
Wedelia trilobata

Geographical Affinities

The BCI flora has substantial geographic affinities with the Central and South American floras. A study of these affinities by Croat and Busey (1975) reviews the geological history of the isthmus and treats the epiphytes, the lianas, and the common tree species. The data presented here embrace all of the species in the flora, except the cultivated species.

Each species in the flora (with the few exceptions mentioned later) is assignable to one of five range categories:

Type I	Endemic: restricted to Panama
Type II	Wide endemic: mainly in Panama but extending to Costa Rica and/or northern Colombia
Type III	Central American: mostly from Mexico to Panama
Type IV	South American: mostly from Panama to South America, but also sometimes to Costa Rica if widespread in South America
Type V	Pan-American: mostly from Mexico to South America

Table 4 lists the numbers of BCI species in each of these categories, by major habit-and-habitat classes. Each percentage shown is the percentage of the total habit-and-habitat class assignable to the indicated range category. Since most BCI species that are found also in the West Indies are wide-ranging (Type V) species, it is unnecessary to treat the West Indian distributions as a separate category. Rather, the number of BCI species occurring also in the West Indies is listed beneath the total for each category (and is *already included* in the upper number). West Indian species are restricted to categories III, IV, and V. For the purpose of this study Trinidad was considered a part of South America and not the West Indies.

A few species —*not reflected in any of the categories*— are known only from the West Indies and Panama, or only from the West Indies plus Costa Rica, Panama, and northern Colombia. Those species known only from Panama and the West Indies are *Habenaria bicornis* (Orchidaceae) and *Polypodium costatum* (Polypodiaceae). In addition, there are two species—*Tillandsia subulifera* (Bromeliaceae) and *Securidaca tenuifolia* (Polygalaceae) —that occur only in Panama and Trinidad. Three species —*Vriesia ringens* and *V. sanguinolenta* (Bromeliaceae) and *Beilschmiedia pendula* (Lauraceae)—are known from Costa Rica to Colombia as well as from the West Indies. *Hydrilla verticillata* (Hydrocharitaceae) is excluded from consideration; it is known from the Old World, but the range in the New World is poorly known. A number of other Old World species are included if their range in the New World is known. *Sacciolepis striata* (Gramineae), known from the United States, the West Indies, and Panama, is excluded because its range does not fit any of the categories. *Vatairea erythrocarpa* (Leguminosae) is excluded because its determination is doubtful. All of the species considered cultivated are also excluded.

Each of the five range categories is discussed briefly in what follows. In the discussions, climbing shrubs and trees are included with lianas. Because of the limited numbers of species in some of the other groups—the parasitic shrubs, hemiepiphytes, tree ferns, suffruticose herbs, parasitic herbs, and saprophytic herbs—their distribution by category will not be discussed.

Type I: Endemic to Panama. A total of 92 BCI species (7%) are endemic to Panama. There are no endemic aquatic or suffruticose herbs or cryptogams and only three endemic clearing herbs. In each of the remaining habit-and-habitat classes, 6–13% of the species are endemic to Panama. Thus no class is significantly more endemic than any other.

Type II: Wide endemic. Wide endemics account for 122 BCI species (9%). No aquatic herbs and only two clearing herbs and one suffruticose herb are found in this category. Vascular cryptogams are represented in about the same proportion as seed plants. The remaining classes each constitute from 6 to 15% of this range category. Most significant is the fact that 15% of all shrubs are wide endemics.

Type III: Central American. A total of 180 BCI species (14%) are distributed only in Central America. Of these, 36 (20%) are also found in the West Indies. Very small percentages of aquatic and clearing herbs are found in this category. In each of the remaining habit-and-habitat classes, 7–22% of the species are in this category.

Although there is an insignificant difference between the total numbers of Central American and South American species on the island (180 vs. 135), there are significantly more large trees (those more than 10 m tall) with a Central American distribution than with a South American distribution. The same is true of shrubs. Also significant is the fact that ten large trees of Type III distribution occur also in the West Indies, whereas there are only two Type IV species in the West Indies. There are about twice as many Type III arborescent species in the West Indies as Type IV arborescent species, but considering the sample size the numbers are probably not significant.

Terrestrial cryptogams also show a significantly larger number of species with Central American distribution than with South American distribution.

TABLE 4
Geographical affinities of the BCI flora
(lower number is number occurring also in West Indies)

Habit-and-habitat class	Total species	Range category (see text) I	II	III	IV	V	Other
VASCULAR CRYPTOGAMS							
Aquatic cryptogams	6				2	4	
Epiphytic cryptogams	42		2(5%)	5(13%) 2	7(18%) 3	27(64%) 23	1
Terrestrial cryptogams	51		5(10%)	11(22%) 1	2(4%)	33(65%) 26	
Tree ferns	5		1		1	3 2	
TOTAL VASCULAR CRYPTOGAMS	104		8(8%)	16(15%) 3	12(12%) 3	67(64%) 49	1
PHANEROGAMS							
Trees more than 10 m tall	211	16(8%)	28(12%)	45(21%) 10	20(10%) 2	99(47%) 44	3 1
Small trees and shrubs (not including those that are only shrubs)	154	20(13%)	19(12%)	25(17%) 5	21(13%) 3	69(45%) 30	
Shrubs (always less than 3 m tall)	93	9(10%)	14(15%)	17(18%) 2	4(4%) 1	49(53%) 28	
Hemiepiphytic shrubs or trees	16	1	1	4	3	7 2	
Parasitic shrubs	7				3 3	4 1	
TOTAL ARBORESCENT PHANEROGAMS	481	46(9%)	62(13%)	91(19%) 22	51(11%) 9	228(47%) 105	3 1
Lianas (including climbing trees and shrubs)	171	13(8%)	13(8%)	26(15%) 4	26(15%) 1	91(53%) 37	2
Vines	83	5(6%)	8(10%)	6(7%)	17(21%) 5	46(55%) 25	1
Hemiepiphytic or epiphytic vines	11	1	2	2	1	5 2	
TOTAL SCANDENT PHANEROGAMS	265	19(7%)	23(9%)	34(13%) 5	44(17%) 8	142(54%) 60	3
Forest herbs	75	7(9%)	7(9%)	8(11%) 1	3(4%) 1	49(65%) 20	1 1
Aquatic herbs	54			2(4%) 1	1(2%) 1	49(91%) 32	2
Clearing herbs	179	3(2%)	2(1%)	7(4%) 3	5(3%) 2	162(90%) 127	
Epiphytic herbs	135	16(12%)	18(13%)	20(15%) 1	16(12%) 2	62(46%) 33	3
Parasitic and saprophytic herbs	5	1	1	1	1	1	
Suffruticose herbs	18		1	1	2 1	14 10	
TOTAL HERBACEOUS PHANEROGAMS	466	27(6%)	29(6%)	39(9%) 6	28(6%) 7	337(72%) 222	6 1
TOTAL PHANEROGAMS	1,212	92(8%)	114(9%)	164(14%) 33	123(10%) 24	707(58%) 387	12 2
TOTAL SPECIES	1,316	92(7%)	122(9%)	180(14%) 36	135(10%) 27	774(59%) 436	13 2

In contrast to the trees, shrubs, and terrestrial cryptogams, there are more herbaceous vines with South American distribution than with Central American distribution (17 (21%) Type IV vs. 6 (7%) Type III).

Type IV: South American. A total of 135 BCI species (10%) have a chiefly South American distribution. Of these, 27 (20%) also occur in the West Indies. There are an insignificant number of aquatic herbs and very small numbers of clearing and forest herbs, terrestrial cryptogams, and shrubs in this category. In the remaining classes, 10 to 21% of the species have Type IV distributions.

Comparisons between Central and South American distributions are made above, in the discussion of the Type III category. Although the total numbers of Type III and Type IV species in each habit-and-habitat class differ insignificantly, the greater number of species from Central America is somewhat surprising, since the South

American continent must have had a larger number of species to contribute to the isthmian flora. This is perhaps explained by the fact that the same uplift which created the isthmian land bridge in the late Tertiary also elevated the Andes mountains and blocked direct overland migration from a substantial part of the South American continent (Croat & Busey, 1975).

Type V: Pan-American. The largest distribution category for nearly every habit-and-habitat class is Type V, species extending throughout much or all of the tropical regions of North and South America and occasionally the West Indies, as well. Of all BCI species, 774 (59%) are in this category. Of the total Type V species, 436 (56%) are also found in the West Indies.

The habit-and-habitat class with the largest Type V distribution is aquatic herbs, 91% of which are wide-ranging, including 32 species also found in the West Indies. Close behind are the clearing herbs, 90% of which are Type V, including 127 species in the West Indies. In the remaining habit-and-habitat classes, 46 to 65% of the species are of Type V distribution. Some of these differences may be significant. I would not have expected epiphytic herbs to have one of the lowest percentages of Type V species, since a large proportion of epiphyte seeds are wind-dispersed. But as might be expected, many of the animal-dispersed epiphytic species, such as members of the Araceae, are less widely distributed. It is not surprising that a large proportion of vascular cryptogams are in the Type V category, since these spore-bearing plants are known to be widespread, no doubt owing to the ease with which their minute spores are borne on the wind.

There is little doubt that the species common to Central and South America and the West Indies have reached the West Indies (or migrated from the West Indies) by long-distance dispersal, since there is no evidence that the West Indies were ever connected to the mainland (Darlington, 1957; Graham, 1972). Presumably, long-distance dispersal could explain the migration of these species between Central and South America, as well, though other mechanisms might have been involved.

Of the 1,316 species considered here, only 501 (38%) are found in the West Indies, whereas 954 (72%) are found in Central America (not including endemics in Types I and II), 909 (69%) in South America. This closer relationship to contiguous land masses would seem to be evidence that modern distributions resulted chiefly from overland migrations rather than from long-distance dispersal; for if long-distance dispersal had been more generally important, one would expect a higher percentage of BCI species in the West Indies.

Historical and Recent Changes in the Flora

The flora of BCI has undergone significant modification since the creation of the island in 1914. At that time the island was only a series of hills with rapidly flowing streams. Though these hills included no permanent standing body of water that could support the rich aquatic community which flourishes in the area today, the Río Chagres flowed past on the north and east only a short distance away. And indeed, the channel of the Panama Canal follows roughly the old valley of the Chagres as it passes Barro Colorado Island. By the time Kenoyer made his ecological studies 15 years later (Kenoyer, 1928, 1929), the aquatic vegetation of the shore was much as it is today. His descriptions of the aquatic associations found there differ from mine only in two respects: he listed far fewer species for the associations; and the shoreline now has many fewer emergent tree stumps. Though the advancement of hydrarch succession over half a century has very likely fostered the addition of species to the aquatic associations, Kenoyer's lower species count was probably due primarily to inadequate sampling of the associations.

The presence of large, chiefly water-dispersed trees, such as *Erythrina fusca, Cynometra bauhiniifolia,* and *Pachira aquatica,* which are restricted to the shore, is evidence that such trees were also able, rather early, to invade the newly formed shore. These species are found along the shore in the areas of hydrarch succession but not on the eroded banks on the north and east sides of the island. At the same time, it seems likely that along some parts of the shore there are a number of species persisting that would not normally occur so near water.

Other changes in the flora have been brought on by the silting of the numerous coves and by the resulting formation of sandbars, which have added niches (as discussed on p. 13).

Although less dramatic than the floristic changes along the shore, the changes in the forest have been significant. About half of BCI was used intermittently for agriculture until shortly before its establishment as a preserve (Chapman, 1938). Successional changes were thus very great in the flora, especially in the first few years of the island's existence, and a number of species may have been eliminated through succession. The reduction in the number and size of clearings eliminated a number of plant species and some bird species as well (Willis, 1974). Species of plants that may no longer be present, either as a result of succession or because their weedy habitats were eliminated, include:

Aciotis levyana
Alternanthera sessilis
Amaranthus viridis
Anthurium flexile
Bidens pilosa
Casearia corymbosa
Cayaponia glandulosa
C. racemosa
Centropogon cornutus
Columnea purpurata
Corchorus siliquosus
Crotalaria retusa
Cyphomandra allophylla
Desmodium cajanifolium
D. distortum
D. tortuosum
Erechtites hieracifolia var. *cacalioides*
Gomphrena decumbens
Hebeclinium macrophyllum
Heliotropium indicum
Indigofera mucronata
Iresine celosia
Mandevilla subsagittata
Melothria trilobata
Merremia umbellata
Microtea debilis
Pavonia paniculata
Piper peracuminatum
Posadaea sphaerocarpa
Rivina humilis

Schistocarpha oppositifolia
Siparuna guianensis
Solanum ochraceo-ferrugineum
S. rugosum
Spananthe paniculata
Stachytarpheta jamaicense

Many of the above are cultivated plants or weeds of cultivated fields that probably disappeared after the large garden area north of the present Laboratory Clearing was allowed to revert to forest. Very likely, many species of crop weeds once present on the island were either missed by Standley (1933) in his listing of species or had already disappeared by 1930. Many weedy plants commonly associated with crops do not persist long once cultivation ceases.

Other very rare or restricted species may also be on the verge of disappearing from the island. These include:

Acalypha arvensis
Banara guianensis
Cleome parviflora
Cochlospermum vitifolium
Dioclea guianensis
Elytraria imbricata
Lycopodium cernuum
Pavonia dasypetala
Phytolacca rivinoides
Pluchea odorata

A number of species whose seedlings do not survive well in the forest are considered by Knight (1975a) to be infrequent reproducers, as discussed and listed on p. 8. Some of these species might be eliminated as succession progresses.

Other species were not seen during the course of my work on the island. They are all believed to be rare, and some may by now have dropped out of the flora. These are:

Abuta panamensis
Adiantum lunulatum
A. seemannii
Anthephora hermaphrodita
Asplenium pteropus
Bacopa salzmannii
Begonia patula
Bellucia grossularioides
Blechum serrulatum
Ceratopteris pteridoides
Combretum cacoucia
Ctenitis sloanei
Diastema raciferum
Dicranopteris flexuosa
Digitaria ciliaris
Dryopteris sordida
Elaphoglossum hayesii
Fischeria funebris
Gonolobus allenii
Hemidictyum marginatum
Hyptis brevipes
Ichnanthus tenuis
Leptochloa virgata
Limnobium stoloniferum
Marsdenia crassipes
Matalea pinquifolia
Mecardonia procumbens
Mikania guaco
M. hookeriana
Mucuna rostrata
Ophioglossum reticulatum
Oryza latifolia
Paspalum repens
Passiflora menispermifolia
P. seemannii
P. williamsii
Pitcairnia heterophylla
Pithecellobium barbourianum
Polygonum acuminatum
P. hydropiperoides
Portulaca oleracea
Prestonia acutifolia
Psychotria uliginosa
Pteris grandifolia
P. pungens
Rhynchospora micrantha
Saurauia laevigata
Scirpus cubensis
Securidaca tenuifolia
Spermacoce tenuior
Stemodia verticillata
Tetrapteris seemannii
Thelypteris balbisii
Tillandsia fasciculata var. *convexispica*
T. subulifera
Tournefortia maculata
Trichopteris microdonta
Vriesia gladioliflora
V. ringens

Other changes in the flora have been brought about by introduced weeds or pasture grasses. Some, such as *Saccharum spontaneum,* are believed to have been introduced into Panama recently. Certain other species are believed to be transient clearing weeds that do not persist long but are later reintroduced. The Rear #8 Lighthouse Clearing has been particularly rich in species that at least *appear* to be transient members of the flora. Each year some additional species are collected there, but some species seen in previous years are often not in evidence—and perhaps the new ones will not be next year. These species, however, are relatively few in number.

Phenological Characteristics

Leaf fall and leaf flushing. Phenological observations of the three classical sorts—flowering, fruiting, and leaf fall—have been made for most species. Observations of leaf fall were based on field notes made on BCI and in adjacent areas of the Canal Zone during the years 1967–74. Observations of flowering and fruiting were made at the same time, and were supplemented by studies of herbarium specimens (Croat, 1975d).

Many plants, particularly the trees and lianas, lose their leaves in the dry season. In many species, the leaves fall at or near the onset of the dry season, but in some, leaf shedding is continuous throughout the dry season. Studies conducted by the U.S. Army Tropic Test Center (1966) at the Albrook Air Force Base test site on the Pacific slope in Panama show that litter fall declines sharply in February and March. Litter accumulation increases until May, then drops sharply. Similar studies by the Smithsonian Environmental Monitoring Program (Rubinoff, 1974) show maximum leaf-litter accumulations in December and January, followed by a rapid decrease in February and further diminishment in April and May. By February, the forest canopy begins to look bare, at least relative to its appearance in the rainy season, and the atmospheric humidity is much lower. Winds, which increase markedly during the dry season, may be felt even at ground level in the depths of the forest.

Leaf litter, which includes falling flowers and fruits and other debris, accumulates to a depth of several inches in some places by the end of the dry season (personal observation). Measurements by Woods and Gallegos on BCI (1970) show that more than 10 metric tons per hectare of litter accumulate during the months June through August.

The beginning of the rainy season brings a rapid increase in the decay of the leaf litter, for the increased soil moisture and atmospheric humidity greatly increase the number of decomposing organisms. The largest part of the leaf litter decomposes within a few weeks of the first rains (I. Healey, pers. comm.). At least in the early stages of the rainy season, some leaf litter may be washed away, for the water currents in the streams can become quite strong—during heavy rainstorms, debris is carried

by water currents along trails even in the flat areas of the forest. The rains, however, serve mostly to compact the litter.

Williams (1941) reported that there is a renewal of litter organisms in May, with the beginning of the rains, and that by the early part of July there is a marked increase in the number of forms present. Fungal organisms as well, which are not common during the dry season, are abundant during the rainy season.

Since many nutrients become available shortly after the onset of the rainy season, it can be assumed that plants are absorbing them at a greater rate during the early weeks of the rainy season, though it is not known how long it takes the plants to assimilate these nutrients. If the assimilation were sufficiently rapid, this influx of nutrients might have some effect on seed germination, leaf maturation, or flower and fruit production. Indeed, emerging seedlings appear to be the most abundant at the end of May and the beginning of June (N. Garwood, pers. comm.), but this may reflect only the increase in soil moisture—that is, it may be unrelated to nutrient availability. Frankie, Baker, and Opler (1974) have shown that for lowland wet forest in Costa Rica, the peak of leaf flushing occurs during the major dry season, especially in February, and a second peak occurs in September, just after the minor dry season. On BCI my general impression is that most flushing of new leaves occurs early in the rainy season. However, random observations on 103 shrubs and trees show that there is no marked difference between the number of species that put on new leaves early in the rainy season and those that put them on in the dry season. Six species show leaf flushing both early in the rainy season and in the dry season, whereas 45 show leaf flushing in the dry season and 42 early in the rainy season. An additional 10 species show leaf flushing both late in the dry season and early in the rainy season, and should be considered as rainy-season leaf flushers. But even if these are included with the rainy-season species, the difference between 45 in the dry and 52 in the rainy is not significant.

Although some species lose and replace their leaves more or less regularly throughout the year, and are never completely leafless, those species that probably contribute most to the accumulation of leaf litter in the dry season are the deciduous species that lose all or nearly all of their leaves for all or part of the dry season; they are the following:

Annona spraguei
Bauhinia guianensis
Bombacopsis quinata
B. sessilis
Bursera simaruba
Cavanillesia platanifolia
Cedrela odorata
Ceiba pentandra
Cochlospermum vitifolium
Dalbergia retusa
Enterolobium cyclocarpum
Erythrina fusca
Jacaranda copaia
Pseudobombax septenatum
Pterocarpus officinalis
Sapium caudatum
Tabebuia guayacan
Topobaea praecox
Trichilia hirta
Xylophragma seemannianum
Xylosma chloranthum
Zanthoxylum belizense
Z. panamense
Z. setulosum
Zuelania guidonia

A few species are leafless during the rainy season. Among these are:

Cordia alliodora
Erythrina costaricensis
Ochroma pyramidale
Triplaris cumingiana

Many species are leafless for only a short time, usually just prior to flowering; often, the leaves are replaced while the plant is in flower. Among the species in this group are the following:

Anacardium excelsum
Antirrhoea trichantha
Apeiba membranacea
A. tibourbou
Casearia corymbosa
C. guianensis
Cassia fruticosa
Castilla elastica
Coccoloba acapulcensis
C. manzanillensis
Combretum decandrum
Dendropanax arboreus
Dipteryx panamensis
Eugenia nesiotica
E. oerstedeana
Genipa americana
Hura crepitans
Inga fagifolia
Lindackeria laurina
Lonchocarpus velutinus
Luehea seemannii
L. speciosa
Machaerium arboreum
Malouetia guatemalensis
Margaritaria nobilis
Omphalea diandra
Ormosia coccinea var. *subsimplex*
Peltogyne purpurea
Pisonia aculeata
Pithecellobium macradenium
Platymiscium pinnatum
Platypodium elegans
Poulsenia armata
Psidium anglohondurense
Randia armata
Schizolobium parahybum
Sloanea terniflora
Spachea membranacea
Spondias mombin
S. radlkoferi
Sterculia apetala
Strychnos panamensis
Tachigalia versicolor
Terminalia amazonica
Tetrathylacium johansenii
Trattinnickia aspera
Trichospermum mexicanum
Trophis racemosa
Virola surinamensis

Some species lose their leaves more than once per year. These include *Tabebuia rosea* and *Quararibea asterolepis,* which lose their leaves twice a year, and *Ficus* spp., which lose all leaves several times a year. Other species, such as *Beilschmiedia pendula, Byrsonima crassifolia, Jatropha curcas,* and *Guazuma ulmifolia,* replace their leaves gradually, but may at times be almost completely leafless, as well.

Frankie, Baker, and Opler (1974) studied leaf production in a number of species from lowland wet forest in Costa Rica. Many of these same species occur on BCI and may react similarly on BCI, though the seasons are not exactly comparable.

Flowering and fruiting. The data presented in this section are the result of field observations and herbarium studies made between 1967 and 1974, and include observations made during more than three years in Panama and a survey of more than 50,000 herbarium specimens from BCI and adjacent areas.

In these data no attempt has been made to outline the phenology of *individual plants,* though numerous individuals were repeatedly observed. Instead, the data represent what is thought to be the normal phenological variation for *each species*—its historical pattern of flower-

ing. No attempt has been made to include the "broad outlier," especially when the phenology of the species involved is well known. In the better-known species, 95% or more of the flowering or fruiting probably falls within the timespan indicated.

The flowering or fruiting period given for most species is broader than that for any single year; because plants have probably evolved a phenology that is compatible with a particular climatic *condition* (as opposed, say, to calendar month), I have chosen to look at overall phenological patterns rather than what might happen in any one year. The year-to-year variation in phenological pattern for any given species is considerable, and variation can also be great between individuals in a given year, in terms of both timing and duration.

Although other phenological studies have been made (Rovirosa, 1892; Fournier & Salas, 1966; Janzen, 1967b; Smythe, 1970; Foster, 1974; Frankie, Baker & Opler, 1974), this is the only known attempt to define an entire flora in a phenological manner.

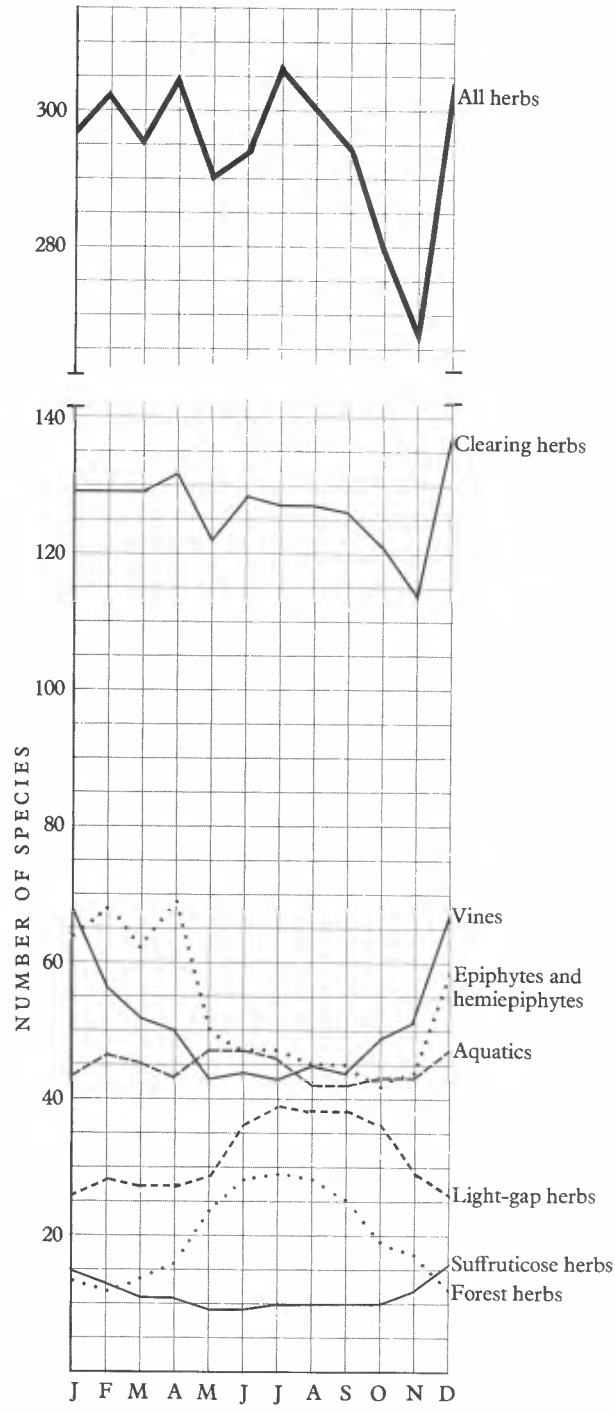
Excluded from most aspects of this study were the 53 cultivated species; excluded altogether were the 104 species of vascular cryptogams. Earlier studies (Croat, 1969a) have shown that different habit types exhibit different phenological behavior. In this section and in an earlier version of it (Croat, 1975d), different habitats are also shown to produce different phenological behavior. Graphs of flowering and fruiting activity have been prepared for all major habit-and-habitat classes for the flora:

- Herbaceous plants
  - All herbaceous species
  - Epiphytes and hemiepiphytes
  - Vines
  - Suffruticose herbs
  - Clearing herbs
  - Forest herbs (not in light-gaps)
  - Herbs of light-gaps and forest edges
  - Aquatics
- Woody plants
  - Trees and shrubs of the forest
    - Tall and medium-sized trees (more than 10 m tall)
    - Small trees (less than 10 m tall)
    - Shrubs (1–2 (3) m tall)
  - Trees and shrubs of open areas, clearings, etc.
  - Lianas
- Climbing species vs. arborescent species

In the graphs, the number of species in flower or fruit in any month is recorded, though months for evident deviates were not tallied in cases where the phenology of a species is well known.

Herbaceous plants, as a single class of organisms, are quite diverse in terms of both habit and habitat, and as a result are more finely subdivided here than the woody plants are. In all, there are 560 herbaceous plants in the BCI flora, accounting for 42.6% of the native flora. Of these, there are 94 vines, 135 epiphytes, 330 terrestrial herbs (including 18 suffruticose herbs and four saprophytic herbs), and one herb parasitic on trees. Because they are inconsequential, saprophytes and parasites are included in the class "forest herbs."

Graphs 2 and 3 show flowering and fruiting curves for all types of herbs studied. I believe that phenological patterns are at least in part determined by fluctuations in climatic conditions. Aquatic herbs and suffruticose herbs are aseasonal, perhaps because they are less subject to the effects of a severe dry season. Aquatics would not be expected to be seasonally cued by availability of pre-



Graph 2. Numbers of herb species in flower, by month and habit-and-habitat class.

cipitate water, but suffruticose herbs, with their well-developed woody root system and underground stems, apparently are also little affected by seasonal changes.

The remaining subclasses of herbs are seasonal. The onset of the dry season, with its reduction of soil moisture and atmospheric humidity, as well as its high insolation, appears to act as a cue to flowering. Flowering times for the different habit-and-habitat classes seem to correlate well with their capacity for withstanding conditions of drought.

Clearing herbs, for example, being the class most exposed to changes in the environment, reach their peak of flowering activity early in the dry season, in December. Flowering then drops off to a relatively steady rate throughout the remainder of the year, except for a slight dip in May and a deeper decline at the end of the rainy season, in November. Because the fruits of most species are small and develop quickly, the fruiting curve closely resembles the flowering curve. Flowering activity in the clearing herbs wanes most at the beginning and end of the rainy season.

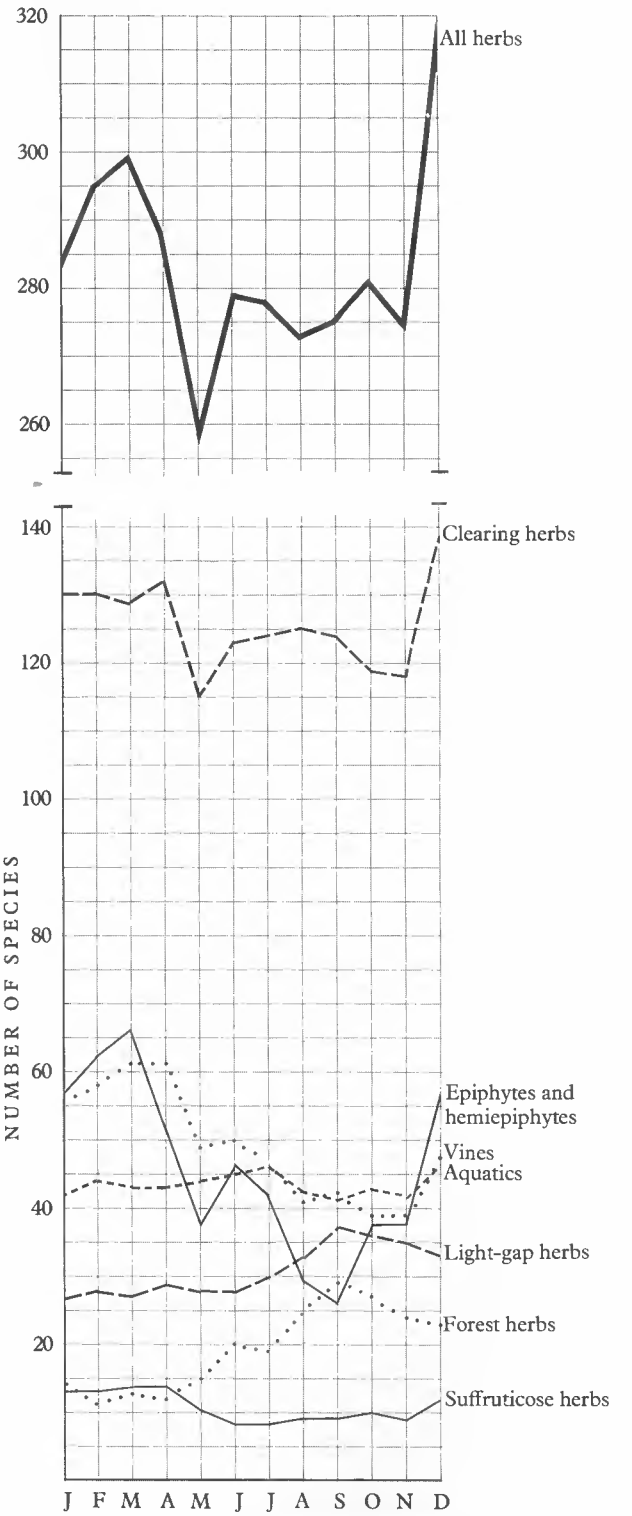
Forest herbs, by contrast, reach the peak of their flowering activity early in the rainy season, and their peak of fruiting midway to late in the rainy season. As suggested by Foster (1974), these groups are probably triggered to flower by intense rains following a period of drought. He has shown that typically rainy-season trees will flower in the dry season if a dry period is followed by heavy rains.

For the herbs of forest light-gaps and forest edges, the amount of light received is relatively more stable, and they are protected from excessive insolation. Their flowering and fruiting activity therefore peaks during the rainy season.

Epiphytic herbs do most of their flowering midway to late in the dry season, with small peaks in February and April, which are perhaps a response to the advancing aridity caused by the increasingly leafless canopy of the forest. Most epiphyte fruiting also occurs in the dry season, and the small airborne fruits are dispersed during the same dry season. A smaller peak of fruiting, early in the rainy season in July, consists principally of the animal-dispersed fruits. Of all epiphyte species whose fruiting is restricted to the dry season, 97% produce principally wind-dispersed seeds, the remainder principally animal-dispersed seeds. Rainy-season epiphytes, by contrast, produce wind-dispersed seeds in only 23% of their species, animal-dispersed fruits in 77%. These figures correlate well with the markedly stronger winds of the dry season—to which wind-dispersed seeds or fruits are particularly well adapted. According to Foster (1974), the leaflessness of the canopy may be more important than winds in the dispersal of airborne diaspores, since many are dispersed after the rains are renewed but before the trees have put on new leaves.

Perhaps because herbaceous vines in the forest usually occur in well-lighted areas and are often restricted to exposed surfaces of the canopy, they do not react appreciably differently from those that occur in clearings. I have therefore treated all herbaceous vines as a group. The flowering peak for herbaceous vines is in December and January, with a second much smaller peak in June. The curve for fruiting in vines, though lacking strong peaks, shows major activity in the dry season. The June peak represents species that appear to be triggered by wet rather than dry conditions.

Of all habit types, the herbs are the least phenologically



Graph 3. Numbers of herb species in fruit, by month and habit-and-habitat class.

variable. As many as 224 species (40%) flower and fruit most or all of the year.

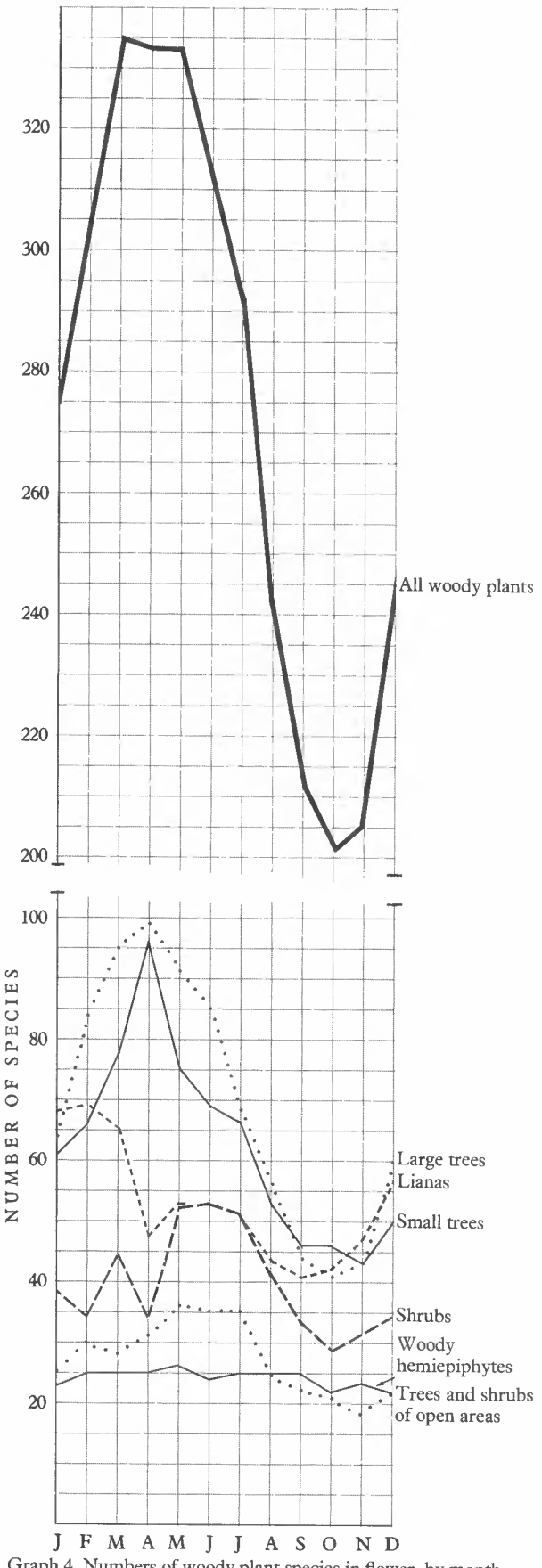
The graph for all species of herbs (Graph 2) shows a decrease in flowering activity late in the rainy season, but from the low of 267 species flowering in November to the peak of 307 flowering in July is only a 15% increase. Certain categories of herbs do, however, show significant increases in flowering activity. For example, there is an increase of 58% for vines, 65% for epiphytes, and 79% for all forest herbs (excluding vines).

When not restricted to open areas, such as in clearings or along the lakeshore, woody plants tend to be more seasonal than herbaceous plants (Graphs 4 and 5). As a class, the trees and shrubs of open areas are not very seasonal. Three of the forest habit classes—lianas, large and medium-sized trees, and small trees—reach their principal peak of activity in the dry season. Flowering in the lianas is most active from January to March, especially in February, substantially ahead of the flowering peak for large and medium-sized trees. This disparity probably reflects the fact that the bulk of the leaf biomass of lianas is restricted to the surface of the canopy and is thus quickly affected by conditions of drought. The fruiting peak for lianas occurs late in the dry season, in March and April, and is stronger than the flowering peak —a circumstance perhaps due to the fact that many species of lianas produce wind-dispersed fruits, even though they may flower in the rainy season. For example, there are six species of bignoniaceous lianas that flower in the rainy season and fruit in the dry season. Of liana species that fruit only in the dry season, as many as 80% have wind-dispersed seeds, whereas just 22% of the liana species that fruit only in the rainy season have wind-dispersed seeds.

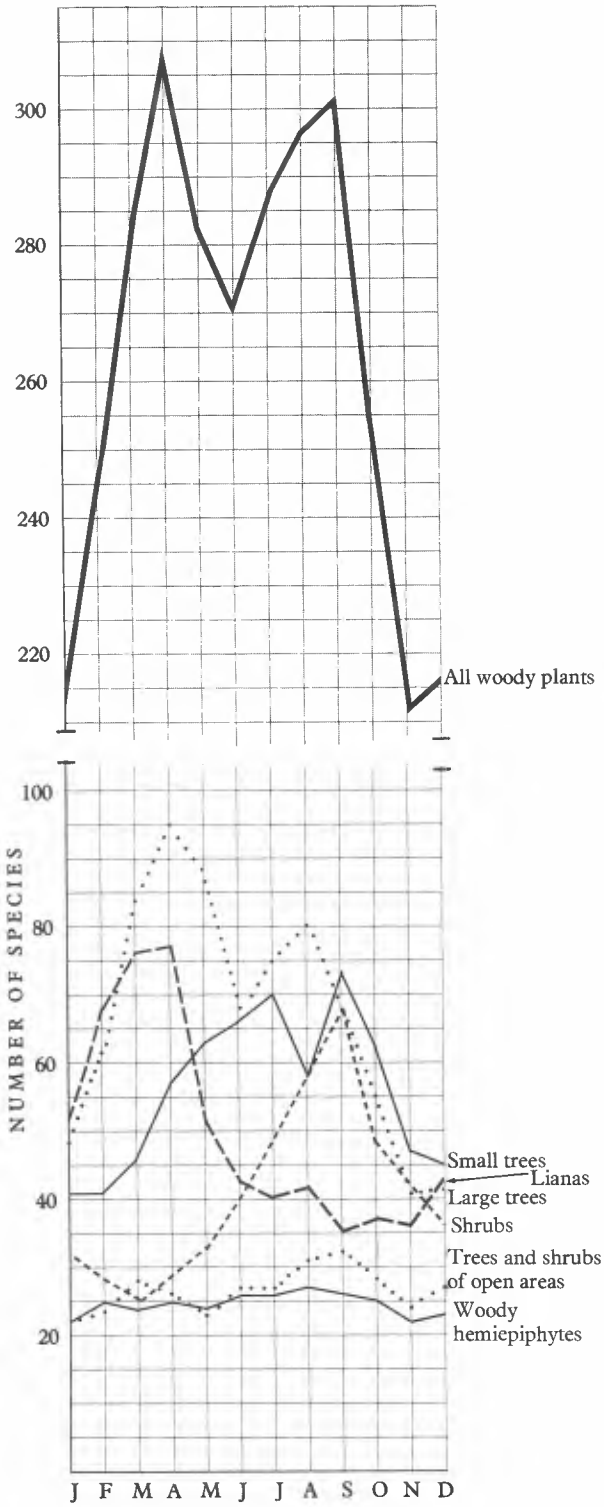
Large and medium-sized trees reach their peak of flowering activity from February to June, especially in March and April, at the end of the dry season. Though triggered by conditions of drought, they do not react so quickly to changes in the environment as the herbs, vines, and lianas do, perhaps owing to the fact that they are much less exposed to the environment than these other classes are. It may be that a great many of the trees flowering in the dry-wet transition period are triggered to flower by the first heavy rains, as suggested by Foster (1974). Fruiting activity in the large and medium-sized trees shows two peaks, one in April and a second, smaller, one in August. The earlier peak is made up for the most part by wind-dispersed species, whereas the second, rainy-season, peak is made up of species that are mostly animal-dispersed.

The flowering peak of March and April for large and medium-sized trees on BCI contrasts rather sharply with the May and July peaks in the wet forest of Costa Rica (Frankie, Baker & Opler, 1974). However, the April and August fruiting peaks on BCI compare well with the May and September peaks in Costa Rica. The flowering and fruiting curves for small trees and shrubs would be somewhat flatter if they also included the class "arborescent in open areas."

Lianas and herbaceous vines are very similar phenologically. If all climbing plants are compared with all



Graph 4. Numbers of woody plant species in flower, by month and habit-and-habitat class.



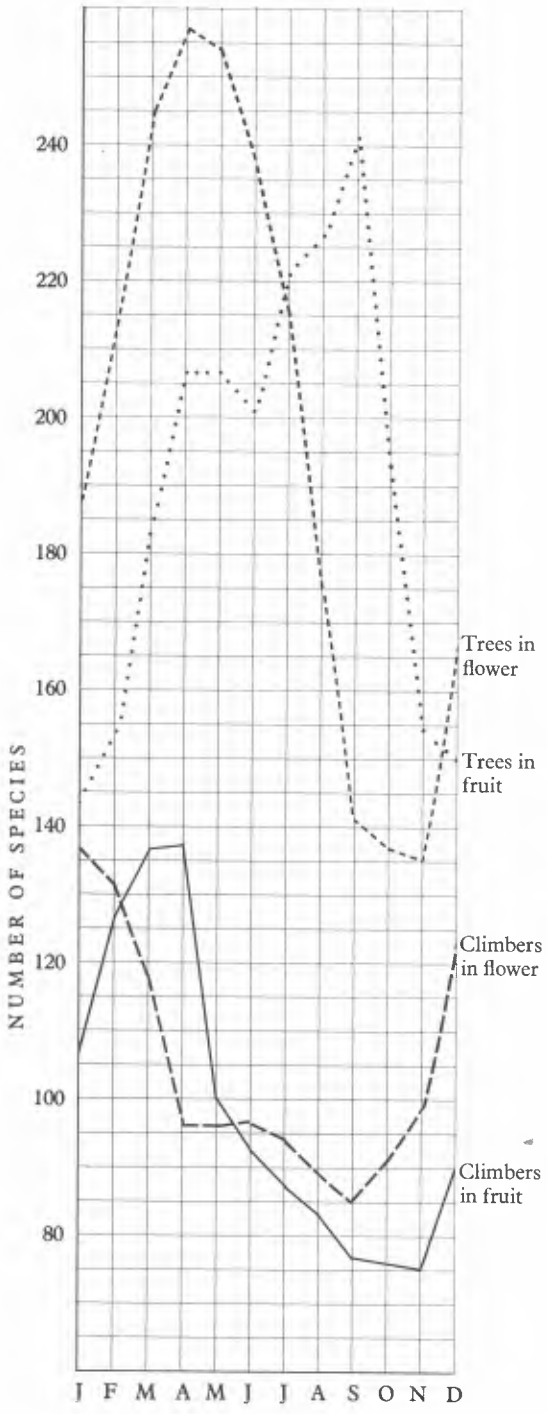
Graph 5. Numbers of woody plant species in fruit, by month and habit-and-habitat class.

arborescent plants (Graph 6), some interesting differences become apparent. As a group, the climbing-plant species reach their peaks of flowering and fruiting earlier than the arboreal plants do. Climbers share the ability to position themselves where they are exposed to light. By the same token, of course, they are subjected to a high degree of exposure when climatic conditions become harsh, as at the beginning of the dry season. It is, I believe, the onset of the dry season that precipitates flowering in many species, including a great many of the lianas, herbaceous vines, and epiphytes, as well as many trees—though most of the trees flower in the dry-wet transitional period and may be induced to flower prematurely by unseasonally wet conditions. Whether this dry-season phenomenon is in general the result of the drying conditions, photoperiodicity, or otherwise is unknown, but the fact that the flowering period of many species coincides with the dry season is no mere coincidence. The flowering curve for all BCI species considered jointly shows a pronounced peak of activity in the dry season (Graph 7). Fruiting shows two peaks, one in the dry-wet transition period and one in the middle of the rainy season. There is a dearth of activity in both flowering and fruiting during October and November, but acute reactivation in December, with the onset of the dry season.

These conclusions differ significantly from those of Foster (1974), who held that the peak month for overall flowering occurs from one to two months after the start of the rains, i.e., in May or June. My studies for overall flowering show significantly fewer species in flower during May and June than in March and April. Foster's conclusion may derive in part from the fact that he was dealing not with the entire flora but with an area of mostly mature forest containing few of the species that are common in open areas or forest edges. Moreover, his detailed sampling procedures deal principally with fruiting, rather less with flowering.

Notwithstanding the overall flowering peak in the dry season, a number of habit-and-habitat classes and a substantial proportion of the species as a whole are apparently cued to flower sometime after the rainy season begins. Foster (1974) has documented this finding for the BCI *Psychotria* species. Shrubs, forest herbs, and herbs of light-gaps and forest edges all show increased activity in the rainy season. The same can be said for many individual families, especially monocotyledonous herbs such as Marantaceae, Musaceae, Zingiberaceae, and Amaryllidaceae.

It is enlightening to compare the seasonal behavior of these habit-and-habitat classes by examining the number of species in flower in a given month as a percentage of the total number of species in the class (Graphs 8 and 9). Thus, although 96 species of trees more than 10 m tall flower in April, this figure represents only 43% of all such trees, whereas the 43 aquatic herbs that flower in April constitute 75% of all aquatic-herb species. The percent-flowering curves follow the same contours as the absolute flowering curves, but the heights of the curves are substantially different. Even at their peak of flowering activity, the percentage of trees and lianas in flower is smaller than the flowering percentage of any other category. A significantly larger percentage of small trees are flowering or fruiting in every season, peak or low. Several habitat classifications have been combined here for simplification: all small trees and shrubs, including those restricted to open areas, are combined; the curve for all species includes both woody and herbaceous plants, the herbs showing a greater percentage of activity than the woody

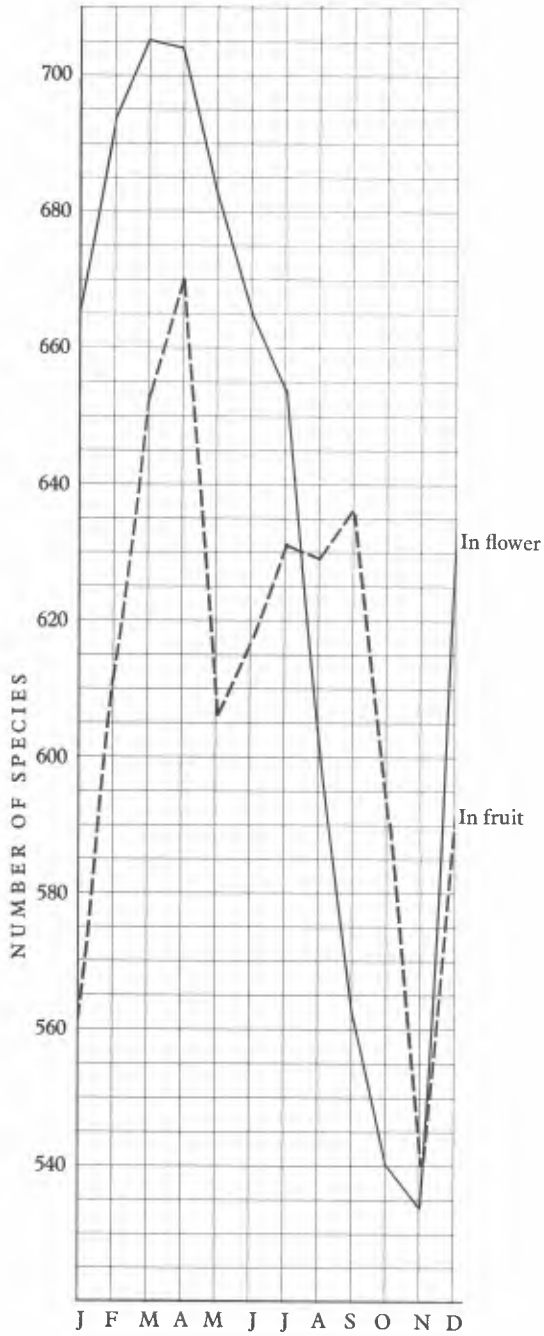


Graph 6. Numbers of species of trees and climbers in flower and fruit, by month.

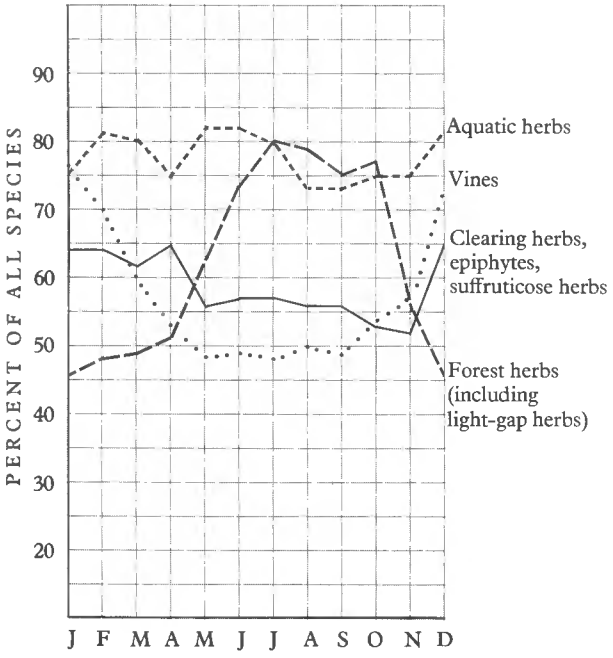
plants do; and the forest herbs and herbs of forest light-gaps and edges are combined, as well as clearing, epiphytic, and suffruticose herbs.

Comparing the fruiting percentages yields a similar pattern, i.e., the same contour as the absolute fruiting curves and at levels corresponding to the percentages for flowering. Of all large and medium-sized trees (excluding bimodal species) whose fruiting occurs strictly in the rainy season, 85% are animal-dispersed and only 12% are wind-dispersed. Of the comparable species that fruit strictly in the dry season, only 36% are animal-dispersed and 57% are wind-dispersed. Comparable figures for small trees and shrubs are 35% animal-dispersed fruits and 21% wind-dispersed fruits in the dry season (the others are mechanically dispersed or are not clearly adapted for either animal or wind dispersal) and nearly 100% animal-dispersed fruits in the wet season.

Small trees are those less than 10 m tall, excluding plants that are always shrubs (i.e., plants usually 1–2(3) m tall) and excluding, as well, all small trees and shrubs that are restricted to clearings. Small trees as a class have a strong peak of activity late in the dry season, in April; being understory trees they produce, as one would expect,



Graph 7. Numbers of vascular plant species in flower and fruit, by month.



Graph 8. Percentage of species flowering, by month, four groups.

mostly animal-dispersed seeds, for winds are usually not strong enough in the lower levels of the forest, even during the dry season, to disperse successfully most wind-borne seeds or fruits. The fruiting of the small trees, although not as conspicuously peaked as their flowering, occurs mostly in the rainy season, with a small peak in July and another in September.

The flowering activity of shrubs is not very seasonal, but more flowering occurs early in the wet season than at any other time. Shrub fruiting, by contrast, shows a fairly definite peak in September. Finally, trees and shrubs restricted to open areas show no marked seasonal variation as a class.

In contrast to the 15% difference between high and low points for flowering activity in herbs, there is a difference of 67% for all arborescent plants. This finding includes a difference of 134% for large and medium-sized trees, 123% for small trees, 83% for shrubs, and 68% for lianas.

Another useful means of comparing plants of different habits and habitats is to compare the average lengths of the flowering or fruiting seasons. Since these are taken from what I have termed the usual pattern of flowering, they do not represent the length of flowering or fruiting for any individual or even for any species in a given year, but rather the length of time over which a species has been known to be in flower or fruit. Table 5 shows these figures for most of the classes already discussed. The aquatic herbs, which are markedly aseasonal, are shown to flower and fruit more than 9 months per year on the average, whereas such classes as epiphytic herbs, lianas, and trees, which are all seasonal in their flowering behavior, flower and fruit on the average for substantially shorter periods of time.

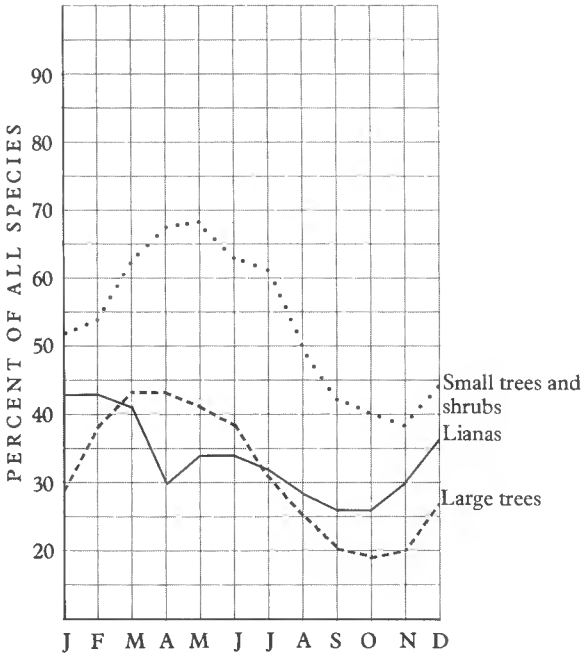
Despite the fact that many species are distinctly "dry-season species" or "wet-season species," by no means all of the species that are seasonal are restricted to one of these two periods. Table 6 shows a categorization of seasonality types. It can be seen that at least 346 species are transitional between the two seasons, in either flowering or fruiting behavior. Some of these conclusions can clearly be disregarded, because of year-to-year fluctuations in the onset of the rainy season, but field observations have confirmed that many typically dry-season species, such as *Cochlospermum vitifolium,* may begin flowering in November, the wettest month of the year, or extend into a period that is definitely rainy season. The same is of course true of wet-season species that begin before or end after the rainy season.

A total of 126 species were excluded from consideration here because too little is known about their phenological patterns; a number of these are cultivated species. But all cultivated species for which the phenology is known are included here. Because the bimodal species are so difficult to classify into seasonality types, no attempt has been made to do so, for many of these are also transitional in their flowering or fruiting behavior.

There are 294 species that flower and fruit all year, 164 of which exhibit no discernible peak. For others, there is a peak of activity in the dry or wet season, and in a few cases flowering is bimodal (e.g., with a peak of activity at the beginning of the dry season and another at the beginning of the wet season). In still other cases, the peak of activity is transitional, straddling both the dry and wet seasons.

The most heavily represented seasonality types flower and fruit either in the wet season (176 species) or in the dry season (133 species).

Some species that flower for more than 9 months, and thus overlap the established seasonal-type categories,



Graph 9. Percentage of species flowering, by month, three more groups.

TABLE 5
Flowering and fruiting extension, by habit-and-habitat class
(in months)

Habit-and-habitat class	Average flower extension	Average fruit extension
Large trees (to 30 m or more)	4.3	4.4
Medium-sized trees (10–30 m)	3.5	3.3
Small trees or shrubs (less than 10 m)	6.3	6.1
Lianas	4.0	3.8
Vines	6.9	6.5
Epiphytic herbs	4.8	4.0
Clearing herbs	8.6	8.5
Aquatic herbs	9.4	9.1
Forest herbs	7.4	7.2
ALL CLASSES	6.4	6.1

TABLE 6
Flowering and fruiting seasonality types

Seasonality types	Number of species: In flower less than 9 months	In flower more than 9 months (peak-period type)	Total
1. Flowers and fruits dry season	133		133
2. Flowers and fruits dry-wet	46		46
3. Flowers and fruits wet season	177		177
4. Flowers and fruits wet-dry	24		24
5. Flowers dry; fruits dry-wet	41	1	42
6. Flowers dry; fruits wet	57	7	64
7. Flowers dry; fruits wet-dry	4		4
8. Flowers dry-wet; fruits wet	90	4	94
9. Flowers dry-wet; fruits wet-dry	12		12
10. Flowers dry-wet; fruits dry	14	1	15
11. Flowers dry; fruits dry 1 year later	7		7
12. Flowers dry-wet; fruits dry-wet 1 year later	7		7
13. Flowers wet; fruits wet-dry	29	1	30
14. Flowers wet; fruits wet 1 year later	3		3
15. Flowers wet; fruits dry	71	7	78
16. Flowers wet; fruits dry-wet	10	2	12
17. Flowers wet-dry; fruits dry	27	4	31
18. Flowers wet-dry; fruits dry-wet	17	2	19
19. Flowers wet-dry; fruits wet	9		9
20. Flowers and fruits bimodally			36
21. Flowers and fruits all year, no peak		164	164
22. Flowers and fruits all year, especially wet		81	81
23. Flowers and fruits all year, especially dry		24	24
24. Flowers and fruits all year, wet-dry peak		9	9
25. Flowers and fruits all year, dry-wet peak		11	11
26. Flowers and fruits all year, bimodal peaks		5	5
27. Seasonality incompletely known			126
28. Flowers dry; fruits all year		1	1
29. Flowers dry-wet; fruits all year		1	1
TOTAL	778	325	1,265

nevertheless exhibit a peak of activity corresponding to a particular seasonal type; these appear in a separate column in Table 6.

From all of these data we can determine whether more species take advantage of the dry season, for flowering or fruiting, than prefer the rainy season. A total of 509 seasonal species (excluding bimodal species) do all or part of their flowering during the dry season; of these, 242 (47%) restrict their flowering to the dry season. A total of 559 seasonal species (excluding bimodal species) do all or part of their flowering in the rainy season; of these, 290 (52%) restrict their flowering to the rainy season.

Comparable figures for the seasonally fruiting species are 462 that set all or part of their fruits in the dry season, 253 (55%) that restrict their fruiting to the dry season, and 542 that set all or part of their fruits in the rainy season (341 (63%) restrict their fruiting to the rainy season).

On the strength of general observations in the field, one might conclude that more species take advantage of the dry season to flower, since it is during this period when many of the more conspicuous species come into bloom. Even the flowering curves indicate that there is a decided preference for flowering in the dry season, since most habit-and-habitat classes reach their peak of activity at that time. However, many trees that attain their peak of flowering late in the dry season and into the dry-wet transitional period may in fact be triggered to flower by the onset of the rainy season. Two other groups, the understory shrubs and forest herbs, definitely reach their peak of flowering activity in the rainy season (Foster, 1974); and both groups are relatively inconspicuous by contrast with the showier dry-season species.

Since the rainy season is substantially longer than the dry season, *more species of plants flower and fruit during the rainy season than during the dry season,* notwithstanding the fact that there is an overall peak of flowering and fruiting activity in the dry season.

The following lists, by family, all of the species assignable to each of the seasonality types* given in Table 6:

1. Flowers and fruits in the dry season

Typhaceae	*Typha domingensis*
Gramineae	*Bothriochloa pertusa*
	Chloris virgata
	Ischaemum indicum
	I. rugosum[1]
	Oplismenus burmanni
	Orthoclada laxa
	Streptogyne americana
Cyperaceae	*Scleria macrophylla*
Bromeliaceae	*Pitcairnia heterophylla*
Dioscoreaceae	*Dioscorea trifida*

*The superscript numbers following some of the species names indicate the following: [1]rarely flowers late wet; [2]rarely fruits early dry; [3]rarely fruits early wet; [4]rarely flowers and fruits early wet; [5]rarely flowers late dry; [6]rarely flowers and fruits early dry; [7]rarely fruits late dry; [8]rarely flowers early wet.

1. Flowers and fruits in the dry season (cont.)

Orchidaceae	*Aspasia principissa*
	Bulbophyllum pachyrrhachis
	Caularthron bilamellatum
	Chysis aurea
	Cochleanthes lipscombiae[1]
	Dichaea panamensis
	Epidendrum imatophyllum[4]
	E. lockhartioides
	E. schlechterianum
	Gongora quinquenervis
	G. tricolor
	Leochilus scriptus[1]
	Lockhartia pittieri
	Maxillaria variabilis
	Mormodes powellii
	Notylia barkeri
	N. pentachne
	Oncidium ampliatum
	O. stipitatum[4]
	Ornithocephalus bicornis[4]
	Polystachya masayensis[1]
	Scaphyglottis graminifolia
	Sobralia panamensis
	Trigonidium egertonianum[4]
Urticaceae	*Myriocarpa yzabalensis*
Polygonaceae	*Coccoloba acapulcensis*
	Triplaris cumingiana
Amaranthaceae	*Iresine angustifolia*
	I. celosia
Phytolaccaceae	*Microtea debilis*
Leguminosae	*Aeschynomene americana* var. *glandulosa*
	Albizia guachapele[3]
	Cajanus bicolor
	Calopogonium caeruleum
	C. mucunioides
	Cassia obtusifolia[1]
	C. reticulata
	Desmodium scorpiurus
	D. triflorum
	Machaerium floribundum
	Mimosa casta
	M. pudica[1]
	Mucuna rostrata
	Rhynchosia pyramidalis
	Teramnus uncinatus
	T. volubilis
Oxalidaceae	*Averrhoa carambola*
Malpighiaceae	*Stigmaphyllon hypargyreum*
	Tetrapteris discolor
Polygalaceae	*Securidaca diversifolia*
Euphorbiaceae	*Adelia triloba*
	Phyllanthus amarus
Anacardiaceae	*Astronium graveolens*
Sapindaceae	*Paullinia fuscescens* var. *glabrata*
	Serjania atrolineata[3]
	S. circumvallata
	S. cornigera
	S. decapleuria
	S. mexicana[3]
	S. trachygona
	Thinouia myriantha
Rhamnaceae	*Colubrina glandulosa*
Vitaceae	*Cissus pseudosicyoides*
Elaeocarpaceae	*Sloanea terniflora*
Tiliaceae	*Heliocarpus popayanensis*[3]
	Luehea seemannii[3,1]
	L. speciosa
	Triumfetta lappula
Malvaceae	*Pavonia dasypetala*
	P. paniculata[3]
Bombacaceae	*Bombacopsis quinata*[3]
	B. sessilis[3]
	Cavanillesia platanifolia[3]
	Ceiba pentandra
	Pseudobombax septenatum
Sterculiaceae	*Melochia lupulina*
	M. melissifolia
	Waltheria glomerata
Marcgraviaceae	*Marcgravia nepenthoides*[1]
	Souroubea sympetala[3]
Cochlospermaceae	*Cochlospermum vitifolium*[3]
Violaceae	*Hybanthus prunifolius*[3]
Combretaceae	*Terminalia chiriquensis*[3]
Myrtaceae	*Eugenia galalonensis*
	E. oerstedeana
Gentianaceae	*Schultesia lisianthoides*
Convolvulaceae	*Ipomoea batatas*
	I. squamosa
Labiatae	*Hyptis capitata*
	H. mutabilis
	Salvia occidentalis
Bignoniaceae	*Tabebuia guayacan*[4]
	T. ochracea
Acanthaceae	*Aphelandra sinclairiana*
	Blechum brownei
	B. costaricense
	Elytraria imbricata
	Hygrophila guianensis[1]
	Justicia pectoralis
	Mendoncia gracilis
	Nelsonia brunellodes[4]
	Ruellia metallica
	Teliostachya alopecuroidea
	Trichanthera gigantea
Rubiaceae	*Manettia reclinata*
Compositae	*Ayapana elata*
	Baltimora recta
	Chromolaena odorata[1]
	Elephantopus mollis
	Fleischmannia sinclairii[4]
	Heterocondylus vitalbis[4]
	Koanophyllon wetmorei[1]
	Melanthera aspera
	Mikania guaco
	M. leiostachya

	Neurolaena lobata
	Rolandra fruticosa
	Spiracantha cornifolia
	Synedrella nodiflora
	Verbesina gigantea
	Vernonia canescens
	V. patens

2. Flowers and fruits dry-wet

Alismataceae	*Sagittaria lancifolia*
Gramineae	*Panicum polygonatum*
	Paspalum saccharoides
Cyperaceae	*Calyptrocarya glomerulata*
	Rhynchospora corymbosa
	Scleria mitis
Piperaceae	*Peperomia macrostachya*
	P. obscurifolia
	Piper culebranum
Lacistemaceae	*Lacistema aggregatum*
Moraceae	*Pseudolmedia spuria*
Loranthaceae	*Phoradendron piperoides*
	Struthanthus orbicularis
Amaranthaceae	*Chamissoa altissima*
Chrysobalanaceae	*Hirtella racemosa* (may flower more than once per year)
Leguminosae	*Dalbergia brownei*
Rutaceae	*Citrus reticulata*
Malpighiaceae	*Heteropteris laurifolia*
	Hiraea reclinata
	Mascagnia nervosa
Euphorbiaceae	*Alchornea latifolia*
Sapindaceae	*Paullinia bracteosa*
Malvaceae	*Pavonia rosea*
Guttiferae	*Havetiopsis flexilis*
	Marila laxiflora
Violaceae	*Rinorea sylvatica*
Flacourtiaceae	*Casearia guianensis* var. *guianensis*
	Hasseltia floribunda
	Xylosma oligandrum
Lythraceae	*Cuphea carthagenensis*
Combretaceae	*Combretum cacoucia*
	C. decandrum
	Terminalia amazonica
Myrtaceae	*Eugenia venezuelensis*
Melastomataceae	*Miconia argentea*
	M. elata
Onagraceae	*Ludwigia leptocarpa*
Boraginaceae	*Heliotropium indicum*
	Tournefortia bicolor
	T. cuspidata
Scrophulariaceae	*Bacopa salzmannii*
Rubiaceae	*Bertiera guianensis*
	Diodia denudata
Cucurbitaceae	*Gurania makoyana*
Compositae	*Conyza apurensis*

3. Flowers and fruits wet season

Gramineae	*Andropogon virginicus*
	Lasiacis procerrima
	Panicum mertensii
	P. milleflorum
	Paspalum notatum
	P. plicatulum
	Rhipidocladum racemiflorum
	Saccharum spontaneum
	Setaria paniculifera
	S. vulpiseta
Cyperaceae	*Cyperus giganteus*[2]
	C. rotundus
	C. simplex
	Rhynchospora micrantha
Palmae	*Cryosophila warscewiczii*
Cyclanthaceae	*Carludovica drudei*
	Ludovia integrifolia
Araceae	*Caladium bicolor*
	Dieffenbachia longispatha
	Dracontium dressleri
	Philodendron fragrantissimum
	P. grandipes
	P. inconcinnum
	P. pterotum
	P. radiatum
	P. tripartitum
	Rhodospatha moritziana
	R. wendlandii
	Xanthosoma helleborifolium
	X. nigrum
	X. pilosum
Bromeliaceae	*Aechmea magdalenae*
Commelinaceae	*Campelia zanonia*
	Dichorisandra hexandra
Pontederiaceae	*Eichhornia azurea*
Amaryllidaceae	*Zephyranthes tubispatha*
Musaceae	*Heliconia catheta*
	H. irrasa
	H. latispatha
	H. pogonantha
Zingiberaceae	*Costus allenii*
	C. guianensis var. *macrostrobilus*
	C. laevis
	Renealmia alpinia
	R. cernua[5]
	Zingiber officinale
Marantaceae	*Calathea inocephala*[5]
	C. insignis
	C. latifolia
	C. marantifolia
	C. micans
	C. panamensis
	C. villosa
	Ischnosiphon leucophaeus
	Stromanthe jacquinii
Burmanniaceae	*Thismia panamensis*
Orchidaceae	*Brassia caudata*
	Dichaea trulla
	Encyclia triptera
	Palmorchis powellii

3. Flowers and fruits wet season (cont.)

Piperaceae	*Peperomia mameiana*
Lacistemaceae	*Lozania pittieri*
Ulmaceae	*Celtis iguanaeus*
	Trema micrantha
Moraceae	*Dorstenia contrajerva*
	Trophis racemosa[5]
Urticaceae	*Boehmeria cylindrica*
	Pouzolzia obliqua
	Urera eggersii
Olacaceae	*Heisteria costaricensis*[5]
	H. longipes
Rafflesiaceae	*Apodanthes caseariae*
Polygonaceae	*Coccoloba coronata*
	C. parimensis
Caryophyllaceae	*Drymaria cordata*[6]
Nymphaeaceae	*Nymphaea blanda*
Menispermaceae	*Abuta racemosa*
	Chondrodendron tomentosum
	Odontocarya tamoides var. *canescens*
Lauraceae	*Phoebe mexicana*
Saxifragaceae	*Hydrangea peruviana*
Leguminosae	*Crotalaria vitellina*[6]
	Inga hayesii
	Leucaena multicapitula
	Ormosia coccinea var. *subsimplex*
	Pithecellobium barbourianum
	Pterocarpus officinalis[5]
	P. rohrii
Rutaceae	*Zanthoxylum panamense*
Malpighiaceae	*Byrsonima spicata*
	Hiraea quapara
	Mascagnia hippocrateoides
	Spachea membranacea[5]
	Stigmaphyllon puberum
Polygalaceae	*Polygala paniculata*
Euphorbiaceae	*Acalypha arvensis*
	Croton billbergianus[5]
	Drypetes standleyi
	Margaritaria nobilis
	Poinsettia heterophylla
	Sapium caudatum
Anacardiaceae	*Mosquitoxylum jamaicense*
Sapindaceae	*Cupania cinerea*
	C. latifolia
	Paullinia rugosa
	Serjania pluvialiflorens
Rhamnaceae	*Gouania adenophora*
Vitaceae	*Cissus microcarpa*
	C. rhombifolia
Elaeocarpaceae	*Sloanea zuliinsis*
Bombacaceae	*Quararibea asterolepis*
	Q. pterocalyx
Dilleniaceae	*Doliocarpus major*
	D. olivaceus
	Saurauia laevigata
Flacourtiaceae	*Banara guianensis*
	Casearia arborea
	C. commersoniana
Cactaceae	*Rhipsalis cassytha*
Lecythidaceae	*Gustavia fosteri*
Myrtaceae	*Eugenia coloradensis*
	Myrcia fosteri
	M. gatunensis
	Psidium anglohondurense
Melastomataceae	*Arthrostema alatum*
	Bellucia grossularioides
	Henriettea succosa
	Miconia lateriflora
	M. shattuckii
Onagraceae	*Ludwigia octovalvis*
Araliaceae	*Dendropanax arboreus*
	D. stenodontus[5]
Myrsinaceae	*Ardisia bartlettii*
	Parathesis microcalyx[5]
Sapotaceae	*Pouteria unilocularis*
	P. stipitata
Gentianaceae	*Voyria alba*
	V. tenella
Asclepiadaceae	*Marsdenia crassipes*
Boraginaceae	*Cordia panamensis*
	Tournefortia hirsutissima
Verbenaceae	*Aegiphila cephalophora*
	A. elata
	Vitex cooperi
Solanaceae	*Cestrum latifolium*
	Lycianthes synanthera
	Solanum asperum
	S. jamaicense
Scrophulariaceae	*Lindernia crustacea*
	L. diffusa
Gesneriaceae	*Chrysothemis friedrichsthaliana*
	Diastema raciferum
	Nautilocalyx panamensis
Acanthaceae	*Herpetacanthus panamensis*
Rubiaceae	*Alibertia edulis*
	Amaioua corymbosa
	Cephaelis discolor
	Geophila croatii
	G. repens
	Hamelia axillaris
	Palicourea guianensis[5]
	Psychotria acuminata
	P. brachybotrya
	P. deflexa
	P. micrantha
	P. pubescens
	P. racemosa
	Randia formosa
Cucurbitaceae	*Cayaponia glandulosa*
	Fevillea cordifolia
Compositae	*Clibadium surinamense*
	Conyza bonariensis
	Eleutheranthera ruderalis
	Erechtites hieracifolia var. *cacalioides*
	Fleischmannia microstemon

	Wedelia trilobata[5]
	Wulffia baccata

4. Flowers and fruits wet-dry

Gramineae	*Andropogon glomeratus*
	Brachiaria mutica
	Cenchrus brownii
	Ichnanthus pallens
	Lasiacis oaxacensis
	Olyra latifolia
	Panicum grande
	Paspalum microstachyum
	Phragmites australis
	Polytrias amaura
	Schizachyrium microstachyum
Commelinaceae	*Callisia ciliata*
Piperaceae	*Peperomia killipi*
	P. obtusifolia
Leguminosae	*Aeschynomene ciliata*
	Clitoria rubiginosa
Simaroubaceae	*Quassia amara*
Melastomataceae	*Miconia borealis*
	Schwackaea cupheoides
Convolvulaceae	*Ipomoea tiliacea*
Gesneriaceae	*Drymonia serrulata*[6]
Rubiaceae	*Borreria densiflora*
Compositae	*Calea prunifolia*
	Pseudoelephantopus spicatus

5. Flowers dry; fruits dry-wet

Cyclanthaceae	*Carludovica palmata*
Araceae	*Anthurium littorale*
Bromeliaceae	*Billbergia macrolepis*
Commelinaceae	*Phaeosphaerion persicariifolium*
Orchidaceae	*Cattleya patinii*
	Epidendrum radicans
	Ionopsis satyrioides
Piperaceae	*Peperomia cordulata*
Moraceae	*Pourouma guianensis*
Chrysobalanaceae	*Licania hypoleuca*
Leguminosae	*Cassia undulata*[1]
	Clitoria javitensis[1]
	Dioclea guianensis[3]
	Enterolobium schomburgkii[3]
	Lonchocarpus velutinus
	Machaerium kegelii
	M. milleflorum
	Schizolobium parahybum
Simaroubaceae	*Picramnia latifolia*
	Simarouba amara var. *typica*
Anacardiaceae	*Anacardium excelsum*
Sapindaceae	*Cupania rufescens*
	C. sylvatica[1]
	Serjania paucidentata
Malvaceae	*Hibiscus bifurcatus*
Dilleniaceae	*Davilla nitida*
	Doliocarpus dentatus
	D. multiflorus
Flacourtiaceae	*Casearia aculeata*
	C. arguta[1]
Cactaceae	*Epiphyllum phyllanthus* var. *columbiense*
Melastomataceae	*Miconia hondurensis*
	M. impetiolaris
Myrsinaceae	*Stylogyne standleyi*
Convolvulaceae	*Merremia umbellata*
Boraginaceae	*Cordia alliodora*
	C. lasiocalyx
Rubiaceae	*Macrocnemum glabrescens*
	Uncaria tomentosa
Cucurbitaceae	*Cayaponia granatensis*
	Melothria trilobata

5a. Flowers dry; fruits dry-wet (flowers more than 9 months)

Bombacaceae	*Pachira aquatica*

6. Flowers dry; fruits wet

Palmae	*Bactris coloniata*
Araceae	*Anthurium clavigerum*
	A. friedrichsthalii
	A. tetragonum
	Monstera dilacerata
Bromeliaceae	*Aechmea pubescens*
Orchidaceae	*Lockhartia acuta*
Piperaceae	*Piper arieianum*
Moraceae	*Artocarpus altilis*
	Brosimum alicastrum
	Cecropia insignis[7]
Nyctaginaceae	*Pisonia aculeata*[7]
Menispermaceae	*Odontocarya truncata*[7]
Monimiaceae	*Siparuna pauciflora*
Lauraceae	*Beilschmiedia pendula*
	Ocotea skutchii
	Persea americana
Chrysobalanaceae	*Hirtella americana*[8]
Leguminosae	*Acacia melanoceras*
	Bauhinia guianensis
	Hymenaea courbaril
	Inga cocleensis
	I. fagifolia[8]
	I. thibaudiana
	Pithecellobium dinizii
	P. macradenium[7,8]
Rutaceae	*Citrus aurantifolia*
	C. aurantium
	C. sinensis
	Zanthoxylum procerum[8]
	Z. setulosum[7]
Meliaceae	*Trichilia verrucosa*[8]
Anacardiaceae	*Mangifera indica*
Sapindaceae	*Allophylus psilospermus*
	Talisia nervosa
Sterculiaceae	*Herrania purpurea*[7]
Theaceae	*Ternstroemia tepezapote*
Guttiferae	*Garcinia mangostana*
	Rheedia acuminata[7]
	R. edulis

6. Flowers dry; fruits wet (cont.)

Flacourtiaceae	*Laetia procera*
	Zuelania guidonia[7,8]
Passifloraceae	*Passiflora ambigua*
	P. nitida[7,8]
Caricaceae	*Carica cauliflora*
Combretaceae	*Conbretum laxum* var. *epiphyticum*
Melastomataceae	*Miconia prasina*
Theophrastaceae	*Jacquinia macrocarpa*
Loganiaceae	*Strychnos toxifera*
Apocynaceae	*Malouetia guatemalensis*[7]
	Odontadenia puncticulosa
Convolvulaceae	*Maripa panamensis*[7,8]
Solanaceae	*Cestrum megalophyllum*
Bignoniaceae	*Jacaranda copaia*[8]
	Tabebuia rosea
Rubiaceae	*Faramea luteovirens*[8]
Cucurbitaceae	*Gurania coccinea*

6a. Flowers dry; fruits wet (flowers more than 9 months)

Araceae	*Anthurium scandens*
	Syngonium podophyllum
Piperaceae	*Piper grande*
Moraceae	*Cecropia peltata*
Passifloraceae	*Passiflora coriacea*
Solanaceae	*Solanum lanciifolium*
Rubiaceae	*Psychotria limonensis*

7. Flowers dry; fruits wet-dry

Annonaceae	*Desmopsis panamensis*
Leguminosae	*Entada monostachya*
Sapindaceae	*Paullinia baileyi*
Myrtaceae	*Psidium guajava*

8. Flowers dry-wet; fruits wet

Cyperaceae	*Cladium jamaicense*
Palmae	*Bactris barronis*
	B. gasipaes
	Geonoma interrupta
	G. procumbens
Cyclanthaceae	*Asplundia alata*
	Cyclanthus bipartitus
Araceae	*Anthurium ochranthum*
	Homalomena wendlandii
	Philodendron guttiferum
	P. inaequilaterum
	P. nervosum
	P. panamense
	Spathiphyllum phryniifolium
	Syngonium erythrophyllum
Bromeliaceae	*Aechmea setigera*
	A. tillandsioides
Zingiberaceae	*Costus villosissimus*
Orchidaceae	*Ionopsis utricularioides*
	Stellis crescentiicola
Piperaceae	*Peperomia ebingeri*
	P. glabella
	Piper aequale
	P. arboreum
	P. darienense
	P. hispidum
	P. perlasense
	P. pubistipulum
	P. reticulatum
Moraceae	*Castilla elastica*
	Cecropia longipes
	Coussapoa panamensis
	Maquira costaricana
Nyctaginaceae	*Guapira standleyanum*
Annonaceae	*Annona hayesii*
	A. spraguei
Monimiaceae	*Siparuna guianensis*
Lauraceae	*Ocotea cernua*
Leguminosae	*Brownea macrophylla*
	Cynometra bauhiniifolia
	Inga pauciflora
	I. pezizifera
	I. vera subsp. *spuria*
	Lonchocarpus pentaphyllus
	Ormosia panamensis
	Pithecellobium rufescens
Burseraceae	*Protium tenuifolium* var. *sessiliflorum*
Meliaceae	*Guarea glabra*
	Trichilia montana
Malpighiaceae	*Byrsonima crassifolia*
Euphorbiaceae	*Acalypha diversifolia*
	Alchornea costaricensis
	Jatropha curcas (rarely also bimodal)
	Omphalea diandra
Anacardiaceae	*Spondias mombin*
	S. radlkoferi
Celastraceae	*Maytenus schippii*
Staphyleaceae	*Turpinia occidentalis* subsp. *breviflora*
Guttiferae	*Tovomita longifolia*
Flacourtiaceae	*Laetia thamnia*
	Tetrathylacium johansenii
	Xylosma chloranthum
Passifloraceae	*Passiflora williamsii*
Lecythidaceae	*Gustavia superba*
Myrtaceae	*Eugenia nesiotica*
Melastomataceae	*Clidemia collina*
	C. purpureo-violacea
	Conostegia bracteata
	Miconia affinis
	M. lacera
	M. lonchophylla
	M. serrulata
	Topobaea praecox
Myrsinaceae	*Ardisia pellucida*
Apocynaceae	*Forsteronia peninsularis*
	F. viridescens
Boraginaceae	*Cordia bicolor*
	Tournefortia maculata
Solanaceae	*Lycianthes maxonii*
Bignoniaceae	*Cydista heterophylla*

Rubiaceae	*Alseis blackiana*
	Antirrhoea trichantha
	Chimarrhis parviflora
	Faramea occidentalis
	Hoffmania woodsonii
	Psychotria carthagenensis
	P. emetica
	P. horizontalis
	P. pittieri
	Randia armata

8a. Flowers dry-wet; fruits wet (flowers more than 9 months)

Amaryllidaceae	*Crinum erubescens*
Leguminosae	*Andira inermis*
	Inga quaternata
Euphorbiaceae	*Phyllanthus acuminatus*

9. Flowers dry-wet; fruits wet-dry

Palmae	*Bactris major*
Iridaceae	*Neomarica gracilis*
Orchidaceae	*Campylocentrum micranthum*
Leguminosae	*Myroxylon balsamum* var. *pereirae*
	Platymiscium pinnatum
Burseraceae	*Bursera simaruba*
Malpighiaceae	*Bunchosia cornifolia*
Euphorbiaceae	*Hura crepitans*
Flacourtiaceae	*Casearia corymbosa*
Lythraceae	*Adenaria floribunda*
Apocynaceae	*Prestonia obovata*
Rubiaceae	*Psychotria furcata*

10. Flowers dry-wet; fruits dry

Bromeliaceae	*Guzmania monostachya*
	Tillandsia monadelpha
Orchidaceae	*Epidendrum difforme*
Annonaceae	*Xylopia frutescens*
Leguminosae	*Dalbergia retusa*
	Platypodium elegans
	Swartzia panamensis
	Tachigalia versicolor
Euphorbiaceae	*Garcia nutans*
Apocynaceae	*Odontadenia macrantha*
Bignoniaceae	*Arrabidaea chica*
	Ceratophytum tetragonolobum
	Macfadyena unguis-cati
	Xylophragma seemannianum

10a. Flowers dry-wet; fruits dry (flowers more than 9 months)

Apocynaceae	*Prestonia portobellensis*

11. Flowers dry; fruits dry 1 year later

Bromeliaceae	*Vriesia gladioliflora*
Annonaceae	*Annona glabra*
Leguminosae	*Enterolobium cyclocarpum*
Hippocrateaceae	*Hylenaea praecelsa*
	Prionostemma aspera
Sterculiaceae	*Sterculia apetala*
Bignoniaceae	*Pleonotoma variabilis*

12. Flowers dry-wet; fruits dry-wet 1 year later

Palmae	*Scheelea zonensis*
Annonaceae	*Annona muricata*
Leguminosae	*Inga spectabilis*
Hippocrateaceae	*Tontelea richardii*
Apocynaceae	*Lacmellea panamensis*
	Tabernaemontana arborea
Rubiaceae	*Tocoyena pittieri*

13. Flowers wet; fruits wet-dry

Palmae	*Geonoma cuneata*
Araceae	*Dieffenbachia pittieri*
Bromeliaceae	*Guzmania lingulata* var. *minor*
Haemodoraceae	*Xiphidium caeruleum*
Zingiberaceae	*Costus pulverulentus*
	C. scaber
Marantaceae	*Ischnosiphon pruinosus*
Orchidaceae	*Catasetum bicolor*
	Habenaria alata
Piperaceae	*Peperomia ciliolibractea*
Moraceae	*Sorocea affinis*
Annonaceae	*Annona acuminata*
Leguminosae	*Erythrina costaricensis* var. *panamensis*
	Swartzia simplex var. *grandiflora*
Malpighiaceae	*Tetrapteris macrocarpa*
Trigoniaceae	*Trigonia floribunda*
Guttiferae	*Tovomita stylosa*
	Vismia macrophylla
Flacourtiaceae	*Casearia sylvestris*
Loganiaceae	*Strychnos panamensis*[5]
Convolvulaceae	*Ipomoea phillomega*
Verbenaceae	*Aegiphila panamensis*
Acanthaceae	*Mendoncia littoralis*
Rubiaceae	*Coussarea curvigemmia*
	Isertia haenkeana
	Pentagonia macrophylla[5]
	Psychotria granadensis
	P. uliginosa
	Warscewiczia coccinea[5]

13a. Flowers wet; fruits wet-dry (flowers more than 9 months)

Piperaceae	*Piper marginatum*

14. Flowers wet; fruits wet 1 year later

Araceae	*Philodendron hederaceum*
Leguminosae	*Dioclea wilsonii*
Sapotaceae	*Pouteria sapota*

15. Flowers wet; fruits dry

Palmae	*Socratea durissima*
Araceae	*Dieffenbachia oerstedii*
	Philodendron sagittifolium
Bromeliaceae	*Catopsis sessiliflora*

15. Flowers wet; fruits dry (cont.)

	Tillandsia anceps
	Vriesia heliconioides
	V. ringens
	V. sanguinolenta
Dioscoreaceae	*Dioscorea sapindoides*
	D. urophylla
Orchidaceae	*Catasetum viridiflavum*
	Dimerandra emarginata
	Epidendrum rigidum
	E. sculptum
	E. strobiliferum
	Liparis elata
	Maxillaria neglecta
	Peristeria elata
	Polystachya foliosa
	Sobralia fragrans
	S. suaveolens
	Trichopilia maculata
	T. subulata
Aristolochiaceae	*Aristolochia gigantea*
Connaraceae	*Cnestidium rufescens*
Leguminosae	*Acacia glomerosa*
	A. hayesii
	A. riparia
	Adenopodia polystachya
	Bauhinia reflexa
	Dipteryx panamensis
	Inga punctata
	Machaerium arboreum[2]
	M. seemannii
	Peltogyne purpurea
Rutaceae	*Zanthoxylum belizense*
Burseraceae	*Trattinnickia aspera*
Meliaceae	*Cedrela odorata*
	Trichilia hirta
Malpighiaceae	*Tetrapteris seemannii*
Sapindaceae	*Paullinia glomerulosa*
	P. pinnata
Tiliaceae	*Apeiba membranacea*
	Corchorus siliquosus
Malvaceae	*Hampea appendiculata* var. *longicalyx*
Sterculiaceae	*Byttneria aculeata*
Dilleniaceae	*Tetracera volubilis*
Guttiferae	*Mammea americana*
Flacourtiaceae	*Lindackeria laurina*
Lythraceae	*Lafoensia punicifolia*
Lecythidaceae	*Couratari panamensis*
Combretaceae	*Combretum laxum* var. *laxum*
Araliaceae	*Didymopanax morototoni*
Sapotaceae	*Chrysophyllum cainito*
Gentianaceae	*Chelonanthus alatus*
Apocynaceae	*Aspidosperma cruenta*
	A. megalocarpon
	Prestonia ipomiifolia
Asclepiadaceae	*Blepharodon mucronatum*
	Matalea pinquifolia
	M. trianae
	M. viridiflora
Bignoniaceae	*Adenocalymma arthropetiolatum*
	Arrabidaea florida
	A. patellifera
	A. verrucosa
	Pithecoctenium crucigerum
	Tynnanthus croatianus
Gesneriaceae	*Kohleria tubiflora*
Rubiaceae	*Cosmibuena skinneri*
	Coutarea hexandra

15a. Flowers wet; fruits dry (flowers more than 9 months)

Orchidaceae	*Maxillaria crassifolia*
Leguminosae	*Swartzia simplex* var. *ochnacea*
Tiliaceae	*Apeiba tibourbou*
Malvaceae	*Sida acuta*
Begoniaceae	*Begonia filipes*
Bignoniaceae	*Anemopaegma chrysoleucum*
	Callichlamys latifolia

16. Flowers wet; fruits dry-wet

Palmae	*Astrocaryum standleyanum*
	Desmoncus isthmius
	Elaeis oleifera
Liliaceae	*Cordyline fruticosa*
Annonaceae	*Xylopia macrantha*
Burseraceae	*Tetragastris panamensis*
Meliaceae	*Guarea multiflora*
Euphorbiaceae	*Dalechampia dioscoreifolia*
Guttiferae	*Calophyllum longifolium*
	Tovomitopsis nicaraguensis

16a. Flowers wet; fruits dry-wet (flowers more than 9 months)

Piperaceae	*Piper villiramulum*
Bignoniaceae	*Martinella obovata*

17. Flowers wet-dry; fruits dry

Gramineae	*Lasiacis sorghoidea*
Orchidaceae	*Eulophia alta*
	Maxillaria powellii
	M. uncata
Leguminosae	*Desmodium cajanifolium*
	Inga mucuna
	Machaerium microphyllum
	Mucuna mutisiana
Malpighiaceae	*Banisteriopsis cornifolia*
	Hiraea grandifolia
Euphorbiaceae	*Dalechampia tiliifolia*[3]
Sapindaceae	*Paullinia fibrigera*
	P. turbacensis
	Serjania rhombea[3]
Rhamnaceae	*Gouania lupuloides*[3]
Tiliaceae	*Trichospermum mexicanum*
Ochnaceae	*Cespedezia macrophylla*
	Ouratea lucens
Passifloraceae	*Passiflora seemannii*
Begoniaceae	*Begonia guaduensis*
Combretaceae	*Combretum fruticosum*

Apocynaceae	*Prestonia acutifolia*
Bignoniaceae	*Amphilophium paniculatum*
	Arrabidaea candicans
Acanthaceae	*Justicia graciliflora*
Rubiaceae	*Calycophyllum candidissimum*
	Pogonopus speciosus

17a. Flowers wet-dry; fruits dry (flowers more than 9 months)

Commelinaceae	*Gibasis geniculata*
Euphorbiaceae	*Mabea occidentalis*
Apocynaceae	*Mesechites trifida*
Boraginaceae	*Cordia spinescens*

18. Flowers wet-dry; fruits dry-wet

Cyperaceae	*Hypolytrum schraderianum*
	Rhynchospora cephalotes
Dioscoreaceae	*Dioscorea macrostachya* (possibly bimodal)
Piperaceae	*Piper carrilloanum*
	P. imperiale
Moraceae	*Perebea xanthochyma*
Aristolochiaceae	*Aristolochia chapmaniana*
Myristicaceae	*Virola surinamensis*
Lauraceae	*Nectandra globosa*
Leguminosae	*Canavalia dictyota*
	Dalbergia monetaria
	Erythrina fusca
Anacardiaceae	*Anacardium occidentale*
Bixaceae	*Bixa orellana*
Passifloraceae	*Passiflora auriculata*
Boraginaceae	*Tournefortia angustiflora*
Cucurbitaceae	*Cayaponia racemosa*

18a. Flowers wet-dry; fruits dry-wet (flowers more than 9 months)

Bombacaceae	*Ochroma pyramidale*
Bignoniaceae	*Pachyptera kerere*

19. Flowers wet-dry; fruits wet

Palmae	*Chamaedorea wendlandiana*
Piperaceae	*Piper cordulatum*
Polygonaceae	*Coccoloba manzanillensis*
Leguminosae	*Dioclea reflexa*
	Inga goldmanii
	I. multijuga
	I. sapindoides
	I. umbellifera
Rubiaceae	*Psychotria marginata*

20. Flowers and fruits bimodally

Gnetaceae	*Gnetum leyboldii* var. *woodsonianum*
Palmae	*Oenocarpus panamanus*
	Synechanthus warscewiczianus
Araceae	*Monstera dubia*
Olacaceae	*Heisteria concinna*
Myristicaceae	*Virola sebifera*
Lauraceae	*Nectandra purpurascens*
Capparidaceae	*Capparis frondosa*
Connaraceae	*Connarus panamensis*
	C. turczaninowii
	Rourea glabra
Leguminosae	*Inga marginata*
	Prioria copaifera
Erythroxylaceae	*Erythroxylum multiflorum*
	E. panamense
Burseraceae	*Protium costaricense*
	P. panamense
Meliaceae	*Trichilia cipo*
Vochysiaceae	*Vochysia ferruginea*
Polygalaceae	*Securidaca tenuifolia*
Euphorbiaceae	*Acalypha macrostachya*
	Hyeronima laxiflora
Hippocrateaceae	*Anthodon panamense*
Sterculiaceae	*Guazuma ulmifolia*
Dilleniaceae	*Tetracera hydrophila*
Guttiferae	*Vismia baccifera*
	V. billbergiana
Araliaceae	*Oreopanax capitatus*
Sapotaceae	*Cynodendron panamense*
Solanaceae	*Cestrum nocturnum*
	Solanum arboreum
	S. argenteum
	S. umbellatum
Rubiaceae	*Cephaelis ipecacuanha*
	Guettarda foliacea
	Psychotria psychotriifolia

21. Flowers and fruits all year, no peak

Gramineae	*Acroceras oryzoides*
	Andropogon leucostachyus
	Bothriochloa intermedia
	Chloris radiata
	Cynodon dactylon
	Hyparrhenia rufa
	Isachne polygonoides
	Oryza latifolia
	Panicum trichoides
	Paspalidium geminatum
	Pharus latifolius
	P. parvifolius
	Schizachyrium brevifolium
	Streptochaeta spicata
Cyperaceae	*Cyperus brevifolius*
	C. diffusus
	C. luzulae
	C. odoratus
	C. sesquiflorus
	C. tenuis
	Eleocharis caribaea
	E. plicarhachis
	Fuirena umbellata
	Rhynchospora nervosa
	Scleria pterota
	S. secans
Araceae	*Anthurium brownii*
	A. gracile

21. Flowers and fruits all year, no peak (cont.)

	Montrichardia arborescens
	Philodendron scandens
Commelinaceae	*Commelina erecta*
Pontederiaceae	*Pontederia rotundifolia*
Smilacaceae	*Smilax mollis*
	S. panamensis
	S. spinosa
	S. spissa
Musaceae	*Heliconia mariae*
Orchidaceae	*Ornithocephalus powellii*
	Pleurothallis brighamii
	P. grobyi
	Scaphyglottis longicaulis
	Triphora gentianoides
Piperaceae	*Pothomorphe peltata*
Moraceae	*Cecropia obtusifolia*
	Ficus (all species)
	Olmedia aspera
Urticaceae	*Pilea microphylla*
Loranthaceae	*Oryctanthus alveolatus*
	O. cordifolius
	O. occidentalis
	Phoradendron quadrangule
	Phthirusa pyrifolia
Polygonaceae	*Coccoloba acuminata*
	Polygonum acuminatum
	P. hydropiperoides
	P. punctatum
Amaranthaceae	*Gomphrena decumbens*
Phytolaccaceae	*Phytolacca rivinoides*
Portulacaceae	*Portulaca oleracea*
Menispermaceae	*Cissampelos pareira*
	C. tropaeolifolia
Annonaceae	*Guatteria amplifolia*
	G. dumetorum
Capparidaceae	*Cleome parviflora*
Leguminosae	*Aeschynomene sensitiva*
	Crotalaria retusa
	Desmodium axillare var. *acutifolium*
	D. canum
	D. distortum
	D. tortuosum
Malpighiaceae	*Stigmaphyllon ellipticum*
	S. lindenianum
Euphorbiaceae	*Chamaesyce hirta*
	C. hypericifolia
	C. hyssopifolia
	Dalechampia cissifolia subsp. *panamensis*
	Phyllanthus urinaria
Hippocrateaceae	*Hippocratea volubilis*
Vitaceae	*Cissus sicyoides*
Elaeocarpaceae	*Muntingia calabura*
Malvaceae	*Hibiscus rosa-sinensis*
	H. sororius
	Sida rhombifolia
Guttiferae	*Clusia odorata*
Turneraceae	*Turnera panamensis*
Passifloraceae	*Passiflora biflora*
	P. foetida var. *isthmia*
	P. menispermifolia
	P. punctata
Caricaceae	*Carica papaya*
Begoniaceae	*Begonia patula*
Rhizophoraceae	*Cassipourea elliptica*
Myrtaceae	*Psidium friedrichsthalianum*
Melastomataceae	*Aciotis levyana*
	Adelobotrys adscendens
	Clidemia capitellata
	C. dentata
	C. ocotona
	C. septuplinervia
	Conostegia speciosa
	C. xalapensis
	Leandra dichotoma
	Miconia nervosa
	Ossaea quinquenervia
	Tibouchina longifolia
Onagraceae	*Ludwigia decurrens*
	L. helminthorrhiza
Umbelliferae	*Hydrocotyle umbellata*
Myrsinaceae	*Ardisia fendleri*
Gentianaceae	*Voyria truncata*
Menyanthaceae	*Nymphoides indica*
Apocynaceae	*Allamanda cathartica*
	Catharanthus roseus
	Ervatamia coronaria
	Mandevilla subsagittata
	Rhabdadenia biflora
	Stemmadenia grandiflora
	Thevetia ahouai
Asclepiadaceae	*Asclepias curassavica*
	Sarcostemma clausum
Convolvulaceae	*Aniseia martinicensis*
Verbenaceae	*Lantana camara*
	Petrea aspera
	Stachytarpheta jamaicensis
Solanaceae	*Capsicum annuum*
	Cyphomandra hartwegii
	Physalis angulata
	P. pubescens
	Solanum hayesii
	S. subinerme
Bignoniaceae	*Cydista aequinoctalis*
	Spathodea campanulata
Gesneriaceae	*Columnea purpurata*
Rubiaceae	*Cephaelis tomentosa*
	Diodia ocimifolia
	D. sarmentosa
	Ixora coccinea
Cucurbitaceae	*Gurania megistantha*
	Momordica charantia
	Psiguria bignoniacea
Compositae	*Baccharis trinervis*
	Chaptalia nutans
	Eclipta alba
	Emilia sonchifolia
	Hebeclinium macrophyllum

	Melampodium divaricatum
	Tridax procumbens
	Vernonia cinerea

22. Flowers and fruits all year, especially wet season

Gramineae	*Andropogon bicornis*
	Anthephora hermaphrodita
	Axonopus compressus
	Digitaria ciliaris
	D. horizontalis
	Eleusine indica
	Gynerium sagittatum
	Homolepis aturensis
	Leersia hexandra
	Leptochloa virgata
	Lithachne pauciflora
	Panicum fasciculatum
	P. pilosum
	Paspalum decumbens
	P. paniculatum
	P. repens
	P. virgatum
	Rottboellia exaltata
	Setaria geniculata
Cyperaceae	*Cyperus haspan*
	Fimbristylis dichotoma
	Scleria eggersiana
Araceae	*Anthurium acutangulum*
	A. bakeri
	Spathiphyllum friedrichsthalii
Commelinaceae	*Tripogandra serrulata*
Amaryllidaceae	*Hymenocallis pedalis*
Musaceae	*Heliconia vaginalis*
Marantaceae	*Calathea lutea*
Orchidaceae	*Epidendrum anceps*
	Maxillaria alba
Piperaceae	*Piper auritum*
Amaranthaceae	*Alternanthera sessilis*
	Amaranthus viridis
Nyctaginaceae	*Neea amplifolia*
Phytolaccaceae	*Petiveria alliacea*
Chrysobalanaceae	*Hirtella triandra* (flowering 2 or 3 times per year)
Leguminosae	*Desmodium adscendens*
	D. axillare var. *stoloniferum*
	Mimosa pigra
	Phaseolus peduncularis
	P. trichocarpus
	Pithecellobium hymeneaefolium
	Vigna vexillata
Euphorbiaceae	*Chamaesyce thymifolia*
	Croton hirtus
	C. panamensis
Vitaceae	*Cissus erosa*
Malvaceae	*Abelmoschus moschatus*
Guttiferae	*Symphonia globulifera*
Myrtaceae	*Calycolpus warscewiczianus*
Melastomataceae	*Conostegia cinnamomea*
Umbelliferae	*Spananthe paniculata*
Loganiaceae	*Spigelia anthelmia*
	S. humboldtiana
Apocynaceae	*Mandevilla villosa*
Convolvulaceae	*Ipomoea quamoclit*
Solanaceae	*Cyphomandra allophylla*
	Solanum ochraceo-ferrugineum
	S. rugosum
	Witheringia solanacea
Scrophulariaceae	*Scoparia dulcis*
Bignoniaceae	*Phryganocydia corymbosa*
Gesneriaceae	*Besleria laxiflora*
	Codonanthe crassifolia
	C. uleana
	Columnea billbergiana
Lentibulariaceae	*Utricularia foliosa*
Acanthaceae	*Thunbergia erecta*
Rubiaceae	*Borreria latifolia*
	Chiococca alba
	Genipa americana
	Posoqueria latifolia
	Psychotria brachiata
	P. capitata
	P. chagrensis
	P. grandis
	Spermacoce tenuior
Cucurbitaceae	*Melothria pendula*
	Psiguria warscewiczii
Compositae	*Schistocarpha oppositifolia*

23. Flowers and fruits all year, especially dry season

Gramineae	*Oplismenus hirtellus*
	Panicum pulchellum
Cyperaceae	*Cyperus densicaespitosus*
	Scirpus cubensis
Araceae	*Anthurium bombacifolium*
	Stenospermation angustifolium
Musaceae	*Heliconia wagneriana*
Marantaceae	*Thalia geniculata*
Orchidaceae	*Maxillaria friedrichsthalii*
	Psygmorchis pusilla
Piperaceae	*Piper dilatatum*
Amaranthaceae	*Alternanthera ficoidea*
	Cyathula prostrata
Phytolaccaceae	*Rivina humilis*
Leguminosae	*Centrosema pubescens*
	Indigofera mucronata
Dilleniaceae	*Tetracera portobellensis*
Umbelliferae	*Eryngium foetidum*
Solanaceae	*Browallia americana*
	Markea ulei
Scrophulariaceae	*Stemodia verticillata*
Bignoniaceae	*Paragonia pyramidata*
Rubiaceae	*Borreria ocimoides*
	Oldenlandia corymbosa

24. Flowers and fruits all year, especially wet-dry

Gramineae	*Hymenachne amplexicaulis*
	Panicum maximum
	P. trichanthum
	Sacciolepis striata
Orchidaceae	*Epidendrum nocturnum*

24. Flowers and fruits all year, especially wet-dry (cont.)

	Habenaria repens
Labiatae	*Hyptis brevipes*
Compositae	*Mikania micrantha*
	Spilanthes alba

25. Flowers and fruits all year, especially dry-wet

Gramineae	*Paspalum conjugatum*
	Sporobolus indicus
Araceae	*Anthurium flexile*
Musaceae	*Heliconia metallica*
Zingiberaceae	*Dimerocostus strobilaceus*
Piperaceae	*Peperomia rotundifolia*
Moraceae	*Poulsenia armata*
Leguminosae	*Caesalpinia pulcherrima*
Vitaceae	*Vitis tiliifolia*
Solanaceae	*Solanum antillarum*
Rubiaceae	*Hamelia patens* var. *glabra*

26. Flowers and fruits all year, bimodal peaks

Gramineae	*Ichnanthus tenuis*
Leguminosae	*Cassia fruticosa*
Melastomataceae	*Mouriri myrtilloides* subsp. *parvifolia*
Rubiaceae	*Borreria laevis*
	Sabicea villosa var. *adpressa*

27. Seasonality incompletely known

Araucariaceae	*Araucaria excelsa*
Hydrocharitaceae	*Hydrilla verticillata*
	Limnobium stoloniferum
Gramineae	*Bambusa amplexifolia*
	B. arundinacea
	B. glaucescens
	Chusquea simpliciflora
	Digitaria violascens
	Ichnanthus brevivaginatus
	Saccharum officinarum
Palmae	*Cocos nucifera*
Araceae	*Pistia stratiotes*
	Syngonium sp.
Bromeliaceae	*Ananas comosus*
	Tillandsia bulbosa
	T. fasciculata var. *convexispica*
	T. fasciculata var. *fasciculata*
	T. subulifera
Smilacaceae	*Smilax lanceolata*
Amaryllidaceae	*Amaryllis belladonna*
Dioscoreaceae	*Dioscorea alata*
Musaceae	*Musa sapientum*
Orchidaceae	*Campylocentrum pachyrrhizum*
	Elleanthus longibracteatus
	Encyclia chacaoensis
	E. chimborazoensis
	Epidendrum coronatum
	E. rousseauae
	Notylia albida
	Scaphyglottis prolifera
	Trichocentrum capistratum
Piperaceae	*Piper aristolochiifolium*
	P. peracuminatum
	P. pseudo-garagaranum
	P. viridicaule
Moraceae	*Coussapoa magnifolia*
Ceratophyllaceae	*Ceratophyllum demersum*
Menispermaceae	*Abuta panamensis*
Annonaceae	*Anaxagorea panamensis*
	Crematosperma sp.
	Unonopsis pittieri
Lauraceae	*Nectandra cissiflora*
	N. savannarum
Leguminosae	*Acacia acanthophylla*
	Cymbosema roseum
	Machaerium riparium
	Vatairea erythrocarpa
Humiriaceae	*Vantanea occidentalis*
Rutaceae	*Citrus grandis*
	C. limon
Malpighiaceae	*Hiraea faginea*
Euphorbiaceae	*Codiaeum variegatum*
	Manihot esculenta
	Sapium aucuparium
Sterculiaceae	*Theobroma cacao*
Violaceae	*Rinorea squamata*
Caricaceae	*Jacaratia spinosa*
Myrtaceae	*Eugenia principium*
	E. uniflora
Melastomataceae	*Miconia rufostellulata*
Onagraceae	*Ludwigia torulosa*
Araliaceae	*Polyscias guilfoylei*
Sapotaceae	*Pouteria fossicola*
Loganiaceae	*Strychnos darienensis*
Apocynaceae	*Forsteronia myriantha*
Convolvulaceae	*Operculina codonantha*
Labiatae	*Coleus blumei*
Scrophulariaceae	*Mecardonia procumbens*
Lentibulariaceae	*Utricularia obtusa*
Cucurbitaceae	*Cayaponia denticulata*
	Posadaea sphaerocarpa
	Sicydium coriaceum
Campanulaceae	*Centropogon cornutus*
Compositae	*Clibadium asperum*
	Mikania hookeriana
	M. tonduzii
	Pluchea odorata

27a. Flowers known; fruits unknown

Pontederiaceae	*Eichhornia crassipes*
Dioscoreaceae	*Dioscorea haenkeana*
	D. polygonoides
Orchidaceae	*Coryanthes maculata*
	Epidendrum stangeanum
	Habenaria bicornis
	Lycaste powellii
	Masdevallia livingstoneana
	Maxillaria camaridii
	Pleurothallis trachychlamys
	P. verecunda
	Sievekingia suavis

	Sobralia rolfeana
	Spiranthes lanceolata
	Triphora mexicana
	Vanilla fragrans
	V. pompona
	Xylobium foveatum
Proteaceae	*Roupala montana*
Aristolochiaceae	*Aristolochia pilosa*
Nymphaeaceae	*Nymphaea ampla*
Lauraceae	*Ocotea oblonga*
	O. pyramidata
Chrysobalanaceae	*Licania platypus*
Leguminosae	*Desmodium wydlerianum*
	Inga minutula
	I. ruiziana
	Ormosia macrocalyx
Malpighiaceae	*Malpighia romeroana*
Euphorbiaceae	*Acalypha wilkesiana*
Sapindaceae	*Talisia princeps*
Passifloraceae	*Passiflora vitifolia*
Cactaceae	*Epiphyllum phyllanthus* var. *rubrocoronatum*
Lecythidaceae	*Grias fendleri*
Myrtaceae	*Syzygium jambos*
Ebenaceae	*Diospyros artanthifolia*
Loganiaceae	*Strychnos brachistantha*
Asclepiadaceae	*Cynanchum cubense*
	C. recurvum
	Fischeria funebris
	Gonolobus allenii
Convolvulaceae	*Iseia luxurians*
Verbenaceae	*Clerodendrum paniculatum*
Solanaceae	*Cestrum racemosum*
Bignoniaceae	*Adenocalymma apurense*
	Clytostoma binatum

27b. Flowers unknown; fruits known

Palmae	*Bactris coloradonis*
Ulmaceae	*Celtis schippii*
Sapindaceae	*Paullinia pterocarpa*
Rubiaceae	*Chomelia psilocarpa*

28. Flowers dry; fruits all year

Gramineae	*Streptochaeta sodiroana*

29. Flowers dry-wet; fruits all year

Bignoniaceae	*Stizophyllum riparium*

History of Panama and the Canal Zone

The Spanish first came to Panama in 1501, and the first settlements were established in 1508, at Santa Maria la Antigua de Darién and at Nombre de Dios. During the succeeding decades, the Spanish completed their conquest of the region. In 1718 Panama became part of the viceroyalty of New Granada (Colombia), and the isthmus soon became the principal route for all traffic to and from Peru and environs. Nonetheless, little development took place outside a narrow belt along both coasts in the region of the isthmus.

In 1821 Panama declared independence from Spain and began an unstable alliance with Colombia. Following numerous revolutionary outbreaks, Panama finally split with Colombia in 1903 when the Colombian legislature failed to ratify a treaty with the United States to build a canal across the isthmus. In the same year the United States obtained the Canal Zone through a treaty with Panama and commenced construction of the Panama Canal in 1907. The Canal was finished and in operation by 1914. The opening of the Canal greatly affected the region of the isthmus, and the city of Panamá soon became a major trading and banking center. Much of the region has at times been almost completely deforested, and for a time the Canal Zone administration leased its land and encouraged settlement and farming. Later policy dictated that no new land be leased, and that all existing leases be terminated upon the death of the original lessee. Since then much of the Canal Zone has become reforested, but a number of the original lessees are still living on the land—or their descendents, in any case, have not been evicted. Still other, obviously clandestine, agricultural operations are under way in remote parts of the Canal Zone, especially in the area around Frijoles. The best forest in the Canal Zone besides that on BCI is in Madden Forest (now a reserve) and along the northeast side of the Canal bordering the naval oil pipeline that crosses the isthmus.

Although BCI was created in 1914 by the rising waters of Gatun Lake, no attempt to preserve its forest was made until it was set aside as a permanent reservation by the governor of the Canal Zone on April 17, 1923. Establishment of the preserve was brought about largely through the efforts of Thomas Barbour and James Zetek. The preserve was first operated by the Institute for Tropical Research, and later came under the direction of the Smithsonian Tropical Research Institute, which still manages it.

History of Botanical Studies

Panama and the Canal Zone. The earliest botanical collections in Panama were made about 1700 by James Wallace, who was associated with the old Scottish settlement of New Caledonia, and though they are still extant in London they have not been carefully studied to this day. Serious botanical activity began in Panama about 1825, when J. E. Billberg collected near Portobelo in Colón Province. Other nineteenth-century collectors include B. C. Seemann (1846–49), P. D. Duchassaing (1849–51), A. Fendler (1850), K. Halsted (1850), and Sutton Hayes (1860–63). Early twentieth-century collectors of note in Panama were R. S. Williams (1908), C. W. Powell (1907–27), H. F. Pittier (1911, 1914–15), W. R. Maxon (1911, 1923), E. P. Killip (1917–18, 1922), C. V. Piper (1923), P. C. Standley (1923–25), G. P. Cooper (1927–28), A. M. Chickering (1928), Brother Paul (1934), M. E. Spence Davidson (later Mrs. R. A. Terry; 1938, mainly from Chiriquí), and M. E. Terry and R. A. Terry from Darién (late 1930's).

Until 1930 the collectors who came to Panama visited only a relatively small portion of the country and, with the notable exception of Henri Pittier, most collected in

a relatively restricted area, many of them never leaving the region of the isthmus.

Botanical activity leading to a *Flora of Panama* began in 1934 with the efforts of R. E. Woodson, Jr., and his associates from the Missouri Botanical Garden. Among those who participated in these efforts in the 1930's were R. W. Schery, R. J. Seibert, J. A. Steyermark, P. C. Allen, A. A. Hunter, and Carol Dodge. Particularly notable was Paul C. Allen, who collected more widely in Panama than anyone up to that time. About 10,000 numbers were collected during this prewar era; as a result of this activity, Woodson and Schery initiated the *Flora of Panama* project in 1943. Subsequent collecting in Panama by staff and students of the Missouri Botanical Garden has yielded an estimated 73,000 collections.

During World War II, San José Island in the Bay of Panama was intensively collected by I. M. Johnston, C. O. Erlanson, and others, resulting in publication of a flora, and in 1940–41 H. von Wedel collected extensively in Bocas del Toro. Little other collecting was done in Panama during or after World War II.

Financial support for the *Flora of Panama* project was obtained from the National Science Foundation beginning in 1957 and continues through to the completion of the project, which is expected in 1978. Field work in Panama by the Missouri Botanical Garden was renewed in 1959 by John D. Dwyer, working with Kenton Chambers, William Stern, and John Ebinger (all associated with Yale University). Working independently, Dwyer made three additional expeditions to Panama between 1961 and 1964.

Full-scale reactivation of the field program in Panama began in 1966, under the direction of Walter H. Lewis, with increased financial assistance from the National Science Foundation. Four expeditions were made to Panama under Lewis's direction between 1966 and 1969, accumulating 5,581 collections. Participating in these expeditions were staff and students including John Dwyer, André Robyns, Derek Burch, Tom Croat (principal investigator 1972–77), Marshall Crosby, Duncan Porter (principal investigator 1971–72), Tom Elias, D. F. Austin, Royce L. Oliver, Kenneth R. Robertson, Will H. Blackwell, Jr., Joan W. Nowicke, Bruce MacBryde, John E. Ridgeway, L. H. Durkee, John L. Hawker, Susan E. Verhoek-Williams, Jerry R. Castillon, and Richard K. Baker.

A field station and herbarium were established in Panama in 1969 by the Missouri Botanical Garden and the Panama Canal Company, through the efforts of Walter Lewis, then director of the herbarium at Missouri, and A. 1. Baumann, then supervisor of the Community Services Division of the Panama Canal Company. The facility was named Summit Herbarium (SCZ), and it has received support from the National Science Foundation. Others important in the initial organization of the station were Edwin L. Tyson, then with Florida State University in the Canal Zone, and Roy Sharp, then supervisor of Grounds and Maintenance for the Panama Canal Company. The initial collection of approximately 6,000 mounted sheets was made by Tyson and others under the auspices of the Army Tropic Test Center in the Canal Zone. The field station, with a residence for the curator and a field vehicle, has enabled Missouri to maintain successive collectors in Panama since that time: Tom Croat (1971), Al Gentry (1972), Helen Kennedy (1973), Michael Nee (1974), Scott Mori (1975), and James Folsom (1977), with a repeat by Tom Croat during 1976. Since the establishment of Summit Herbarium, Missouri has made 50,000 collections in Panama.

The herbarium and drying facilities of Summit Herbarium, now located at Ancon in the Canal Zone, are sponsored jointly by the Smithsonian Tropical Research Institute (STRI) and the Missouri Botanical Garden. The drying facilities, now housed in the STRI Tivoli Building, feature about 8,500 watts of electric dryers in a fireproof room and are adequate for a sustained collecting program.

In addition to resident collectors employed by the *Flora of Panama* project, Missouri Botanical Garden has sponsored other expeditions to Panama. In 1972, the National Geographic Society helped sponsor a phytogeographic survey of the Burica Peninsula by Tom Croat. With the assistance of Ron Liesner and Philip Busey, 3,600 collections were made. In 1975, Al Gentry, with support from the National Geographic Society and assistance from Scott Mori, made an expedition to Cerro Tacarcuna on the Colombian border, netting 1,100 collections.

John Dwyer, both independently and with his students, has made about 6,000 collections in Panama on several expeditions since 1964. Among Dwyer's students who have collected in Panama are Joseph Kirkbride, Victoria Hayden, T. S. Elias, B. R. Lallathin, David Spellman, and Richard Wunderlin. Joseph Kirkbride, with James A. Duke, collected about 1,000 numbers in Panama. The most important of these are from an overland expedition from Bocas del Toro on the Caribbean to Chiriquí.

Numerous expeditions to Panama have been made by Tom Croat since 1967 on the Flora of Barro Colorado Island project (also partially NSF funded). Since 1969 the *Flora of Panama* project has funded collecting trips by Walter Lewis, John Dwyer, Duncan Porter, W. G. D'Arcy, and Tom Croat. With support from the *Flora of Panama* project, and with separate NSF funding, W. G. D'Arcy made about 4,000 collections during five visits to Panama.

Other institutions that have been active in Panama include the University of Panama, Duke University, and Florida State University. The University of Panama, principally through the efforts of Mireya D. Correa A. and N. Escobar and their students, has made a significant number of collections in Panama. Robert L. Wilbur, of Duke University, has made eight expeditions to Panama. Students of Wilbur's who have participated in these expeditions include F. Almeda, J. Terri, P. Armond, J. Luteyn, J. Utley, and R. Weaver. Robin Foster, an ecologist trained at Duke, has made numerous collections on Barro Colorado Island and elsewhere in Panama.

Florida State University, through the efforts of R. K. Godfrey, E. L. Tyson, H. Loftin, Sidney McDaniel,

K. Blum, and R. L. Lazor, has also made numerous collections in Panama. Particularly noteworthy are the collections of E. L. Tyson between the years 1962 and 1972. During part of this time he was employed by the Army Tropic Test Center, where he established the collection of approximately 6,000 specimens now incorporated with Summit Herbarium. Noteworthy also are L. R. Holdridge and E. A. Lao, who made collections associated with forestry investigations in Panama during the 1960's, and A. Weston, who made recent collections at high elevations in western Panama.

Most noteworthy among botanists not associated with the above-mentioned institutions are Robert L. Dressler of STRI and Jim Duke. Dressler's wide-ranging and selective collecting has yielded numerous interesting and new species. Duke is best known for his collections from Darién, which were made while he was employed by Battelle Memorial Institute as part of a program investigating a new sea-level canal route.

Barro Colorado Island. Probably the first significant plant collecting on the island was that done by Paul Carpenter Standley, who in the course of 8 days (January 17, 1924, and a week in November 1925) made 800 collections. It was principally on the basis of these collections that Standley (1927) published his first checklist for the island. During the summer of 1927, Leslie A. Kenoyer, of Western State Teachers College in Kalamazoo, Michigan, conducted extensive ecological studies on the island. In the course of his work he made 690 collections, and on the basis of these collections, Kenoyer and Standley published in 1929 the first supplement to the *Flora of Barro Colorado Island.* A second supplement was published by Standley in 1930.

Because of the increase in botanical work on the island during 1931 and 1932, so many collections were accumulated that Standley decided to completely revise the flora. The revision was published in 1933. Collections made during 1931 and 1932 were principally by C. L. Wilson, L. H. and E. Z. Bailey, D. E. Starry, Silvestre Aviles (a local assistant to Bailey), Otis Shattuck, R. H. Wetmore and E. C. Abbe, and R. H. Woodworth and P. A. Vestal. A few collections were also made by C. Ray Carpenter during his studies of monkeys. James Zetek, who together with Thomas Barbour was principally responsible for the establishment of Barro Colorado Island as a preserve, was also the first resident manager. He collected fewer plants than most collectors of his time but his collections are among the most selective. Though Zetek was not a botanist by profession, his correspondence with Standley indicates that he had a keen botanical awareness.

The following list gives the names of all collectors known to have worked on Barro Colorado Island, and when known the number and date of collections:

Abbe, E. C. (see Wetmore and Abbe)
Aviles, S. (few, 1931; see note following list)
Bailey, L. H., and E. Z. Bailey (700, 1931)
Bangham, W. N. (many, late 1920's)
Bartlett, H. H., and T. Lasser (few, 1940)
Brown, W. L. (few)
Busey, P. (few, 1973)
Carleton, M. A. (few)
Carpenter, C. R. (few, 1931–33)
Chardon, C. E. (few)
Chickering, A. M. (few, 1928)
Cook, O. F. (few, early 1920's)
Croat, T. B. (6,614, 1967–75)
D'Arcy, W. G. (few, 1970)
Dare, R. (few, 1972)
Dodge, C. W. (few, 1925)
Dressler, R. L. (few, early 1960's)
Duke, J. A. (few, early 1960's)
Dwyer, J. D. (few, 1961)
Dwyer, Correa, and Pasco (81, 1968)
Ebinger, J. (few, 1960)
Fairchild, G. B. (few, early 1940's)
Faull, J. H. (few)
Folsom, J. (few, 1977)
Foster, R. (1,000, 1969–77)
Garwood, N. (few, 1976–77)
Gentry, A. (few, 1969 and 1971)
Graham, S. (few)
Hayden, M. V. (few, 1965)
Hladik, A. (544, 1967)
Hood, J. D. (few, early 1930's)
Hunnewell, F. W. (few)
Kennedy, H. (few, 1970–72)
Kenoyer, L. A. (680, 1927)
Killip, E. P. (few, 1948)
Knight, D. H. (numerous sterile collections, 1967–68)
Luteyn, J. (few, 1968)
Maxon, W. R. (few, 1923)
McDaniel, S. (few, 1964 and 1972)
Montgomery, G. (300, 1973)
Munch, S. (few, 1973)
Netting, M. G. (few, early 1920's)
Nolla, J. (few)
Oppenheimer, J. (few, 1967–68)
Robyns, A. (few, 1965)
Salvoza, F. M. (few, late 1920's)
Shattuck, O. E. (870, 1930–34)
Standley, P. C. (800, 1924–25)
Starry, D. E. (328, 1931)
Steiner, K. (few, 1976)
Stevens, F. L. (few, 1924)
Stimpson, W. (few, 1967)
Stoutamire, W. P. (few, 1956)
Svenson, H. K. (few)
Terry, M. E., and R. A. Terry (few, late 1930's)
Tyson, E. (few, 1966)
Van Tyne, J. (few, late 1920's)
Weaver, R., and R. Foster (few, 1968)
Wetmore, R. H., and E. C. Abbe (225, 1931–32)
Wetmore, R. H., and R. H. Woodworth (many, late 1920's and early 1930's)
White, P. (few, late 1930)
Wilbur, R. L. (few, 1967)
Wilson, C. L. (158, 1931)
Woodworth, R. H., and P. A. Vestal (450, 1932)
Zetek, J. (few, 1930–43)

Aviles used Shattuck's labels on many of his collections. This has resulted in considerable confusion; the plants collected by Aviles are often cited as Shattuck's collections.

More recent botanical work on the island has been ecologically oriented. Among the projects carried out in the past 10 years are work on bee pollination of orchid flowers, by Robert L. Dressler; on phytosociology, by Dennis H. Knight; on nutrient recycling, by I. N. Healey; and on reproductive potential, by Robin Foster. (Foster was also important as a plant collector, making approximately 1,000 collections on the island.) Zoological work in recent years has dealt principally with studies of animal behavior.

Background of work on the present flora. Standley's final *Flora of Barro Colorado Island,* published in 1933, gives names and brief descriptions of 1,058 species of vascular plants (as well as 201 nonvascular plants). Relatively little collecting was done on the island between the appearance of Standley's *Flora* and the beginning of this work. BCI was even at that time the best-collected and presumably the best-known botanically of any tropical area in the New World. No fewer than 5,000 collections had already been made from an area of about 15.6 km^2 (6 square miles). Being somewhat of a tropical novice when I began the work, I envisioned a two- or three-year project. I was even told that the flora was so well known that the idea of revising the *Flora* was ill conceived. Knowing what I now know about the richness of lowland tropical rain forests and the very low frequency of many widespread species, I might have argued that such a flora could never be completed.

The project has taken 10 years to complete. My work began at the Missouri Botanical Garden in August 1967, with a two-week trip to the island in December of that year and successive collecting trips in April and May 1968, in September and October 1968, and from January to March 1969. In March 1970, I moved to the Canal Zone to serve as the first curator of Summit Herbarium, and continued my study of the flora of BCI for 18 months. This long, uninterrupted period of study during 1970 and 1971 provided the opportunity to make many of the phenological observations I feel are so important to this work. Many of the descriptions were also written while I was in the field. This is especially important for palms, certain Araceae, and some other plants that cannot, whether because of their ephemeral nature or their size, be easily described from herbarium material or even from fresh specimens carried back to the laboratory on the island or to Summit Garden. In some cases, BCI species that occur elsewhere in the Canal Zone (especially near Summit Garden, where I was living) were collected and used for descriptions. When I left the Canal Zone in 1971, approximately 60% of the species were described, nearly all of them from living material. Some of the species that are the least detrimentally affected by pressing and drying, e.g., grasses and ferns, were left to be described from herbarium material.

The value of describing plants from living material is that many aspects of the flower or fruit that may be lacking in a dried specimen can be recorded—such features as the disposition of the parts before, during, and after anthesis, and the size and shape of the parts before drying. This approach is especially valuable for mature fruits, since collections of them are rarely found in herbaria.

Methods of field work. Barro Colorado Island has been described by many botanists as a difficult place to collect plants. Insects and other pests, such as ticks, are abundant on the island—perhaps because of the abundance of larger animals, which help to sustain the blood-sucking creatures. Other animals, including snakes, are usually no problem, although I was viciously attacked by a collared peccary one morning on the way to the dining hall from my cabin.

The trails, though generally laid out along ridges and thus offering the easiest ascent to the center of the island, are nonetheless often steep and can be hazardous, especially in the rainy season. Since the island is a preserve and no felling of trees is permitted, collecting within the forest is very difficult. Along the trails the forest is more open, but the light is relatively poor. Even with the aid of binoculars it is difficult to determine which plant, of the several overhead, is the one dropping its flowers or fruits. Sometimes, all that can be done is to find the densest area of fallen parts and then, on the basis of the characteristics of the species, choose the tree that appears most suspect. Often, of course, the plant is a liana or hemiepiphyte, generally not visible from subcanopy levels.

To get into the canopy to collect plants I generally used climbing irons (Croat, 1969). In addition, I carried a sheath knife, a machete, a 50-foot cotton rope with a lead weight, binoculars, and often camera equipment. The technique of climbing with climbing irons, once mastered, is not dangerous. I suffered only one serious fall during the BCI work, and that when I too zealously avoided a swarm of wasps. Ants, especially the large stinging *Paraponera,* are sometimes hazardous to climbing, but the smaller biting ants that may cover your arms until they are black are always more of a nuisance. Ants are encountered in nearly every tree, especially the flowering trees.

Climbing the wrong tree is a common problem, but switching to another tree from the canopy is usually relatively easy. The most difficult trees to climb are those that have very slender trunks, and thus offer little lateral stability, and those whose girth is so great that the safety rope will not encircle them. Even these can generally be climbed, however, since the stout lianas or hemiepiphytes that press along the trunk of most large trees can be used for support. Trees with very hard bark or wood are also dangerous, since they cannot be penetrated deeply enough to ensure that the gaffs will not slip out. Trunks covered with lianas or epiphytes can be difficult to climb, as well. It is often necessary in these cases to remove the safety rope to get through the tangle—a safe enough proposition, since it would be difficult to fall out of these tangles even if you wanted to. At times I became so entangled I regretted that I could *not* fall out!

By contrast, collecting along the shore is relatively

easy. Because BCI has so recently come to be an island, the shoreline does not support the exclusively riparian vegetation found in a natural situation. Consequently, some species not normally found along water's edge can still be collected along the shore of the island. Perhaps more important, many shoreline trees represent regrowth of trees that have fallen into the lake, and branching may occur near the ground and over the lake, allowing for easy collecting of many of the same species that in the forest would demand an energetic climb. Lianas are exceedingly difficult to collect in the forest, even from the canopy, because they tend to grow only across the surface of the canopy, and are difficult to reach without venturing far out on a limb. However, along the shore, many liana species come down almost to the water and can be collected easily.

Collecting from a boat can be troublesome, because anything accidentally dropped over the edge may disappear into as much as 20 feet of murky water, even very near the shore. Two cameras, a pair of eyeglasses, binoculars, and a host of other miscellaneous things met their end in this manner during my work on this project. The advantages of the shore—easy access and a multiplicity of species—are somewhat offset by other inconveniences. A boat seldom offers a very stable platform on which to work, especially if the water is choppy, and the larger waves created by passing ships can be even more vexing. On one collecting trip, my boat was struck from the stern by a large wave and immediately sank. Fortunately, I was near the shore. Running onto barely submerged tree stumps is another hazard of shoreline collecting. Still another is the many wasps' nests that hang low over the water; often, I did not spot these until I was hopelessly mired in *Hydrilla* and unable to beat a quick retreat.

The most poorly collected part of the shore lies between the end of Armour Trail and the western tip of Peña Blanca Point. The waters here are choked with tree trunks, and navigation is difficult. The forest that adjoins this area on the western side of the island—the farthest point from the Laboratory Clearing and the boat dock—is also poorly collected, and the area can be counted upon for more species new to the flora.

Key Structure

Since identification is expected to be a major use of this work, keys have been given careful attention. *All statements in the keys apply to BCI specimens,* not necessarily to specimens of the same species collected elsewhere. Where possible, characters for both flowers and fruits, as well as vegetative parts, have been incorporated. The most dependable separating characters are the first in each couplet; no other attempt is made to be consistent about the order of the characters. For the most part, the opposing statements in each couplet are parallel; in some cases, additional characters are added at the end of one half of the couplet, usually on a final dichotomy, to assure the reader that he has the correct plant. In keys extending more than a page, pairs of symbols have been added at the beginning of one or more couplets to facilitate progress through the key.

The keys to families within divisions are not based on traditional characters. I have tried to make these keys easier to use by avoiding technical characters wherever possible. For a key to families based on natural characters, see Hutchinson (1967).

The keys to taxa within families terminate with genera, species, or both. A genus with two or more species on BCI is usually provided with its own key to species, unless the family is small.

The key to major plant groups in the flora is given below (p. 63).

Key to sterile woody plants. Although other sterile keys have been constructed for BCI (Knight, 1970), the one on p. 861 is the first to include all the woody plants. It will thus enable scientists to make surveys of the forest at any time of year. Because the species in the flora are generally quite seasonal, only a small percentage can be collected in fertile condition at a given time. Someone with an interest in studying the vegetation might not be able to manage the many visits to the island that would be required to find all of the species in the sample in flower or fruit. Moreover, a substantial part of the flora will be juvenile in any event. Thus the key to sterile plants will be useful. For several reasons, herbaceous plants are not included: in general, they are much better known and thus relatively easy to identify; they tend to flower and fruit for longer periods; and the incorporation of all the herbaceous plants would have made the key a great deal longer and thus more difficult to construct and more unwieldy to use.

Approximately 700 species are included in the key to sterile woody plants. Excluded from the key are species that are both cultivated and known only from the Laboratory Clearing; species that are usually mostly herbaceous, e.g., *Aristolochia*; and some species that are probably no longer on the island, e.g., *Columnea purpurata.* At the same time, some of the more common coarse herbaceous vines that occur in the forest are included because they will be more frequently encountered in surveys of the forest and would otherwise be difficult to identify.

Needless to say, there are substantial problems attending the construction of a key to sterile plants for so many taxa. The greatest difficulty arises in trying to separate the numerous species having simple alternate leaves. Every attempt has been made to account for intraspecific variation—species that are quite variable appear in the key several times—but in some cases the variation is excessive and the plant may not key out. Moreover, it was impossible to include all juvenile forms in the key, and many of these will not key out. Using the sterile key, approximately 60% of the woody plants on BCI can be identified with little difficulty, the remainder with varying degrees of difficulty. The characters that are generally the most variable are pubescence, leaf shape and size, and the condition of the blade margin (i.e., toothed or entire).

Some plants that will not key out in the sterile key are juvenile forms that do not resemble the adult plants. Others may be species that are new to the flora and have not been found in fertile condition. Any systematic attempt to identify large quantities of sterile material from

the island will probably produce other species new to the flora. Already, many sterile, unidentifiable plants have accumulated that probably represent species new to the flora.

The nature of the key suggests that identifications made with it be thoroughly checked against the text descriptions and compared with herbarium specimens where possible. Where the choices become difficult to make, the troublesome couplets should be marked and the plant keyed out two or more ways, for even if the process yields several possibilities, it is faster and easier to check these in an herbarium than to attempt identification in most other ways. Those who have field-tested the sterile key report that it is difficult to use successfully at first, but that it becomes quite useful after some experience has been gained.

Family Descriptions

Family descriptions apply to genera and species on BCI, except where other data are added parenthetically. Flowers are presumed to have one pistil unless otherwise stated. Information concerning the number of ovules in the ovary and the number of seeds in the fruit is not necessarily repeated; for example, if a fruit is described as being 5-locular with many seeds per locule, it is assumed that the ovary is many-ovulate.

The number of genera and species in a family, as well as the range of the family, have been extracted from standard works such as Willis (1966) and Lawrence (1964) or from recent monographs.

Ecological information of a general nature or pertinent to more than one species is included with the family description. Ecological information of a more detailed nature and pertinent to a particular species—or general information on the only BCI species in a family—follows the species description. The information given is applicable only to those species or genera on BCI, and statements are not necessarily relevant to other species or genera occurring elsewhere. The ecological information given for a genus refers to at least some members of the genus, but not necessarily to all of the species on BCI. Unless otherwise worded, statements concerning possible pollinators or possible dispersal vectors are based on the morphology of the species and what is already known about the pollination and fruit dispersal of related taxa, rather than on actual observation.

When specific information is available concerning the interaction between the plants and animals of BCI, I have included it here. I have frequently mentioned, for example, that white-faced or howler monkeys are known to eat certain fruits (the information is based on the studies of Oppenheimer, Hladik & Hladik, and C. Smith, and citations are given with the text discussions). It can probably be assumed that most of the fruits eaten by these monkeys are also eaten by other fruit-eating animals in the forest, for most fallen fruit that is taken by one of the animals which frequent the forest floor is likely to be taken by many other animals (N. Smythe, pers. comm.). Although little reference is made to them because of the lack of necessary studies, a number of animals that are seldom referred to, such as lizards (especially iguanas), may be important in the dispersal of many fruits. Most of the references I have made to the fauna have used common names. The following list gives the zoological names of the most commonly mentioned mammals:

Opossum	*Didelphis marsupialis ctensis*
Coati	*Nasua narica panamensis*
Kinkajou	*Potos flavus isthmicus*
Squirrel monkey or marmoset	*Oedipomidas geoffroyi*
Howler monkey	*Alouatta paliata inconsonans*
Night monkey	*Aotus zonalis*
White-faced monkey	*Cebus capucinus imitator*
Tamarin	*Sanguinnus geoffroyi*
Squirrel	*Sciurus gerrardi morulus, Microsciurus alfari venustulus*
Spiny rat	*Proechimys semispinosus panamensis*
Agouti	*Dasyprocta punctata isthmica*
Paca	*Cuniculus paca virgatus*
Collared peccary	*Peccari angulatus bangsi*
White-lipped peccary	*Tayassu peccari spiradens*
Three-toed sloth	*Bradypus griseus*
Two-toed sloth	*Choloepus hoffmanni*

A complete discussion of the mammals of the island is given in Enders (1935). Many publications reporting recent work on the fauna are referred to in the ecological discussions of plant-animal interactions.

Genus Descriptions

To conserve space, formal generic descriptions are not presented, and pertinent information has been incorporated into the family descriptions. For example, "Epiphytic or terrestrial (*Ananas* and *Aechmea*)" says that all the genera are epiphytic except *Ananas* and *Aechmea*. In other cases, morphological or ecological information is given following the genus heading; this is usually done only for large genera, in order to avoid repetition in species descriptions.

Species Descriptions

Synonymy. Synonyms listed herein are restricted to the following: names used by Standley in his revised *Flora of Barro Colorado Island* (1933); names, since changed, that were used by Woodson and Schery in the *Flora of Panama*; and synonyms commonly used for Panamanian species in families that at the time of this writing have not been completed in the *Flora of Panama*.

Common names. The common names reported are those used in Panama or reportedly used in Panama. They have been extracted from herbarium labels and also from the following works: *Flora of Panama* (Woodson & Schery, 1944–), *Flora of the Canal Zone* (Standley, 1928), *Flora of Barro Colorado Island* (Standley, 1933), *The Rain Forests of Golfo Dulce* (Allen, 1956), and *Darién Ethnobotanical Dictionary* (Duke, 1968).

Morphology. Species descriptions apply to material

as it occurs on BCI. In some cases, local populations elsewhere may differ in some substantial manner, but such cases are usually rare, and a description will in general be consistent with normal variation throughout the range of a species. Species are usually described in detail; exceptions are sometimes made where (1) too few specimens are available to make a complete description, (2) the species is believed to be no longer present on the island, or (3) the taxon differs only slightly from another and is merely compared with it. Those species described from fresh plants are described in greater detail than those described from herbarium specimens, especially where flowers or mature fruits were collected in the field. Because many descriptions have been made from living material, they differ frequently from those prepared from parts that are dried or secondarily softened before study.

Measurements in parentheses, for example in the span (5)10–15(20), account for extremes in variability, probably less than 5% of the observed individuals of a species, or they are unconfirmed reports for the species from other sources, principally the *Flora of Panama.* In the case of tree height, however, the measurements in parentheses reflect reported heights of the species elsewhere in Panama. The upper height *not* in parentheses is the maximum observed height on BCI. And for purposes of size classification—that is, whether a tree should be designated small, medium-sized, or tall—I considered only those heights recorded on BCI.

Many characters should be presumed unless otherwise stated: stipules absent unless described; blades simple and entire; parts glabrous, unarmed, and smooth. If pubescence is of a generally consistent character throughout the plant, it is usually mentioned only once, near the beginning of the description. Flowers should be assumed to be regular unless described as zygomorphic. Fruits are presumed to be fresh and ripe.

Where practical, terms that are likely to be unfamiliar to the average biologist have been avoided, though a certain amount of technical terminology is unavoidable. No glossary is provided; the reader is referred to Lawrence (1955) and Jackson (1928) for definitions of most botanical terms used here.

The term *domatia* has in general been used rather broadly; often it identifies structures that are sunken or pitlike; but in other contexts it implies mere tufts of pubescence in leaf axils that appear to be forming shelter for insects (though in most cases it has not been confirmed that insects actually inhabit these areas).

Colors used in descriptions are those in common usage. However, for reference purposes, the following list gives the equivalent names and numbers for the most commonly used colors, as given in the *Color Chart of the Royal Horticultural Society* (1966 edition): blue, 100; violet-purple, 77; violet, 82; blue-violet, 93; mulberry (cyclamen-purple), 74; orchid, 84; lavender, 76; thistle (imperial purple), 78; pink, 49; magenta, 66; orange-red, 34; maroon, 60; red-violet, 63; Indian red, 75; brick-red, 180; red, 45; red-orange, 30; salmon, 48; orange, 24; melon, 35; bittersweet (burnt orange), 31.

Specimens cited. The morphological description of a species generally terminates with a citation (in italic type) of the herbarium specimen(s) on which the description is based in part. Usually, only one or two collections are cited, and they are my own collections, unless a better specimen is available or I have never collected the species fertile. The citing of specimens is intended only to help future workers in the event that there is confusion about the taxon in question. Unless otherwise indicated, all collections cited are deposited at the Missouri Botanical Garden (MO). Many are well duplicated, and duplicates are in most cases deposited at Summit Herbarium in the Canal Zone (SCZ), the University of Panama (PMA), the Field Museum (F), the New York Botanical Garden (NY), and Duke University (DUKE). In a few cases no specimens are cited, e.g., those orchids reported by Dressler for which he made no collection, or the species reported by Standley (1933), and likely to be on the island, but for which I could find no specimen.

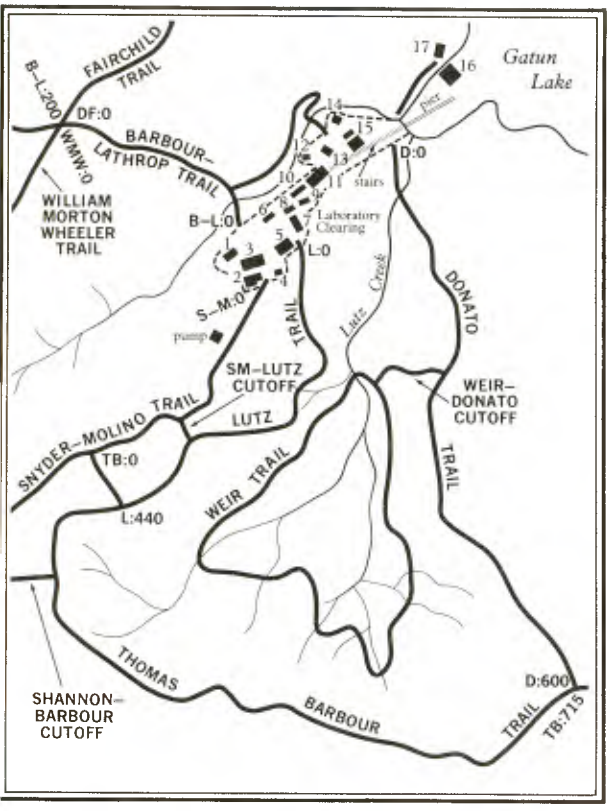
Abundance on the island. Statements of abundance are based principally on estimates pegged to a scale of 1 to 5, made both by myself and by Robin Foster. Foster's estimates are particularly valuable for the tree flora, with which he is very familiar because of his ecological studies on the island. Measures of abundance are usually: 1, rare; 2, infrequent; 3, occasional; 4, common; 5, abundant.

BCI habitats. Although all of BCI falls within the tropical moist forest life zone of the Holdridge Life-Zone System (see maps on pp. 58–59 and discussion on p. 60), specific habitats are diverse. The major habitats include forest (both old forest and young forest), man-made clearings, and the lakeshore. Within the forest, there are still other specific habitats, such as those along deep ravines, along trails, and in tree-fall areas. The lakeshore itself provides several different types of habitats, such as eroded banks, forest edge (where the forest lies adjacent to the water), clearing edge, and plant-choked marshes.

Phenological statements. The phenological behavior of a species is discussed wherever something can usefully be said. The sections on phenology (p. 29) explain the methods used. Any month listed in parentheses represents less than 5% of the flowering period. Phenological data often provide an additional character for the separation of two species, for even closely related species are often distinct phenologically.

Miscellaneous ecological and taxonomic discussion. Specific ecological data, such as observed visits to the species (by pollinators or feeders), are discussed with the species description. More general commentary is incorporated with the family description; in a few cases, where the comments deal with a single genus, they follow the heading for that genus.

Miscellaneous taxonomic information follows the ecological portion of the species text. Any reference to Standley refers to his 1933 work, unless otherwise indicated.



SOURCE: R. W. Rubinoff, *Environmental Monitoring and Baseline Data* (Washington, D.C.: Smithsonian Institution Press, 1974)

1. Tall House
2. Barbour House
3. Main Laboratory
4. Paper House
5. Animal House
6. Kodak House
7. Chapman House
8. Herbarium
9. Office
10. Cook House
11. Dormitory–Dining Hall
12. Smith House
13. ZMA House
14. Boys' House
15. Carpenter Sheds
16. Boat House
17. Toolshed

BARRO COLORADO ISLAND

Scale in meters

500 0 500

Trail

Stream

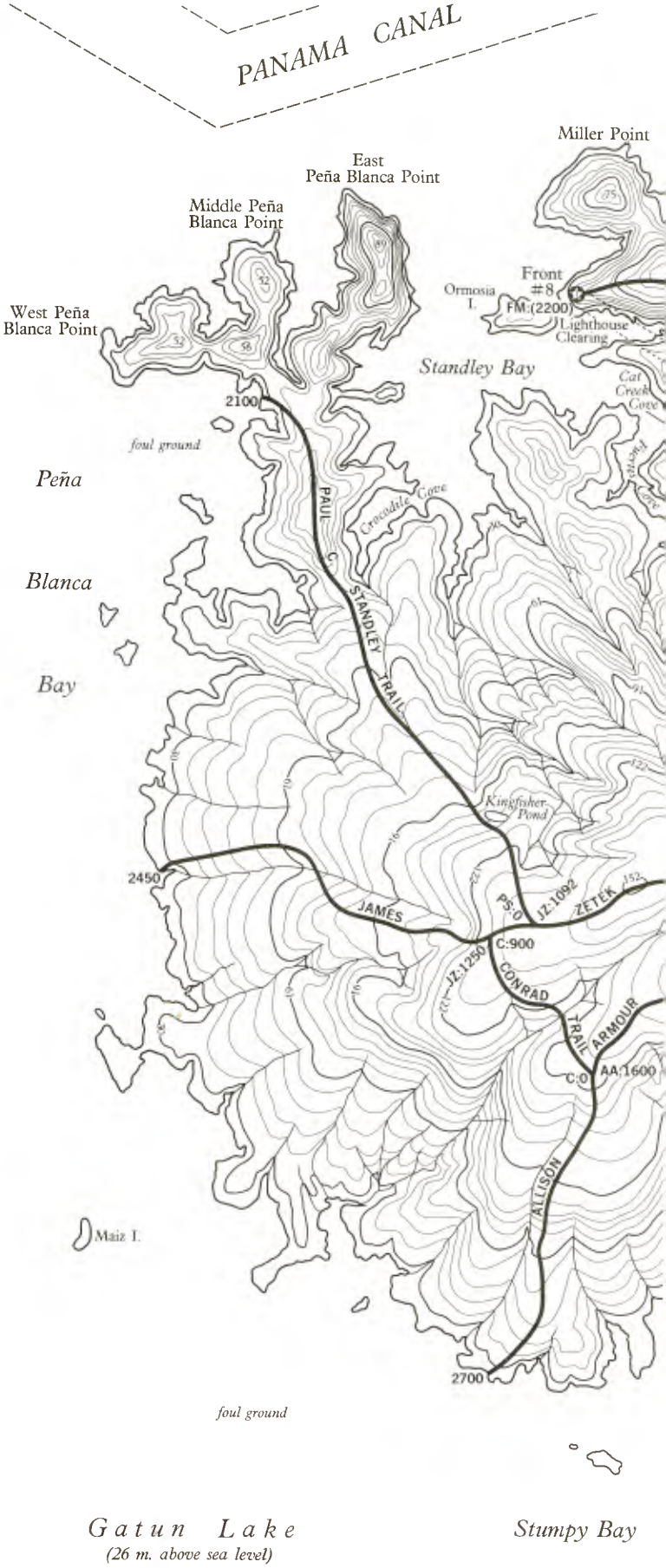
Lighthouse

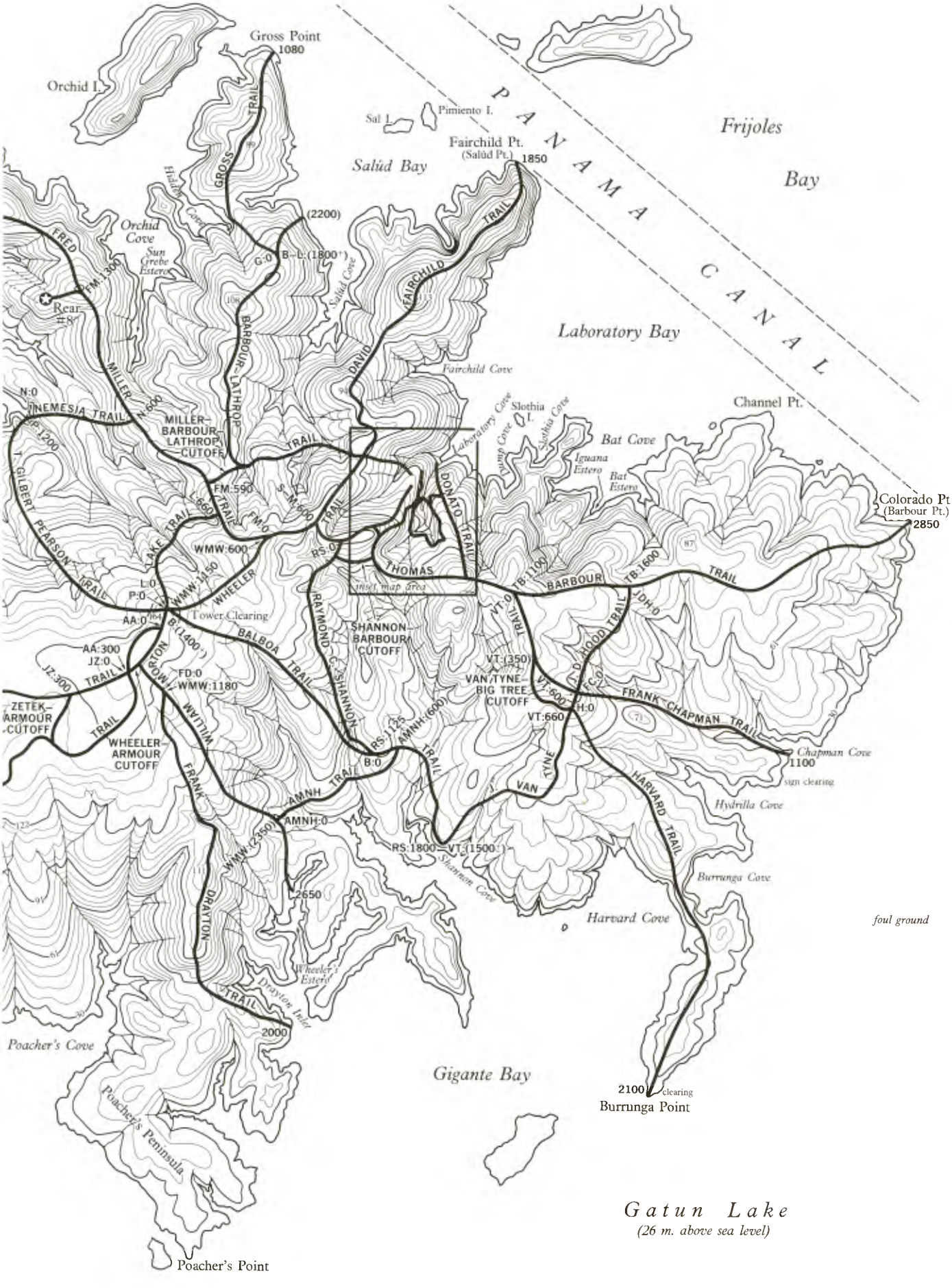
152 Elevation

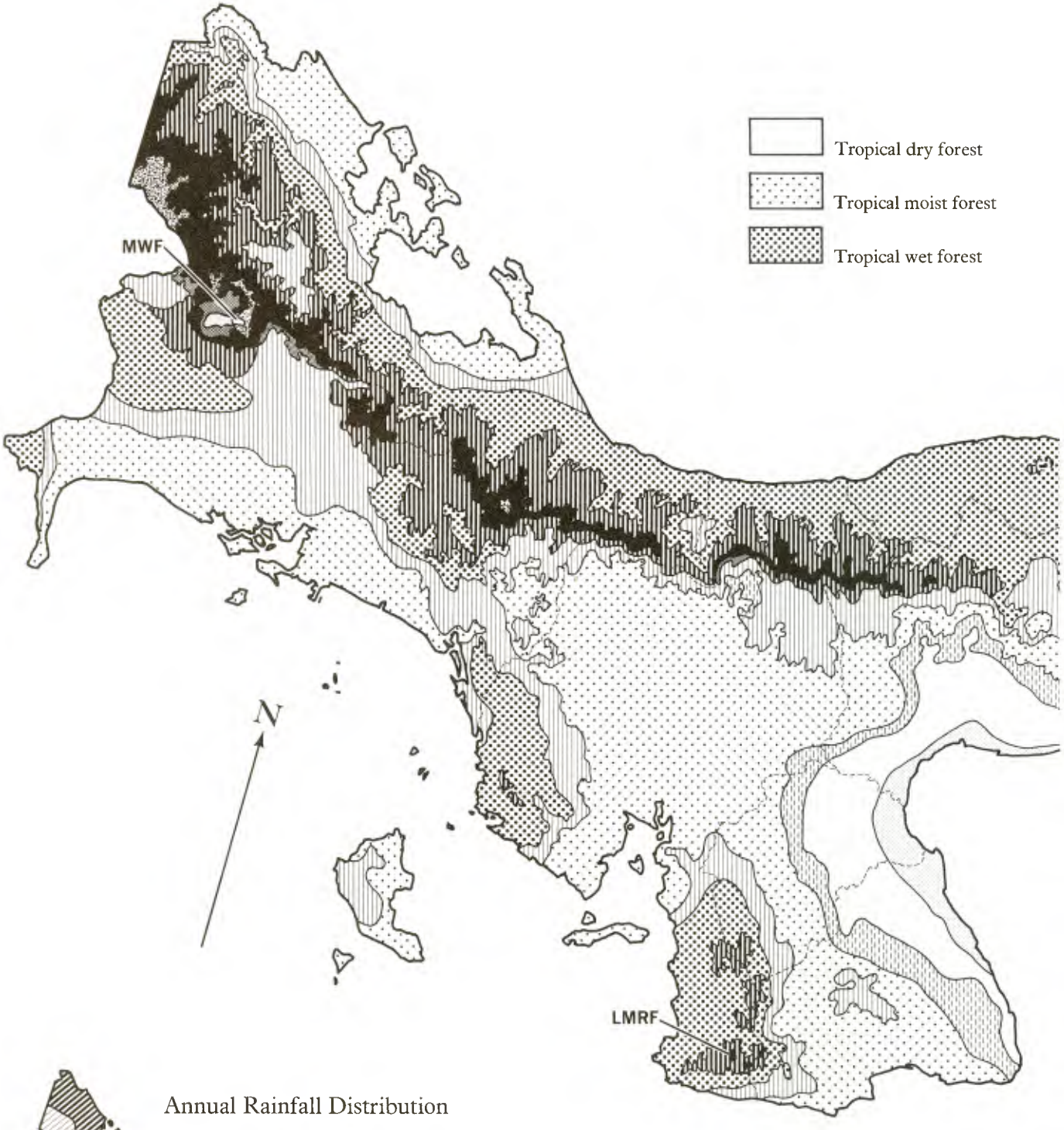
Contour interval 6.1 meters (converted from 20-foot intervals; rounded to nearest whole number)

AA:300 Trail name initials: meters from trail beginning (parentheses indicate approximate distance)

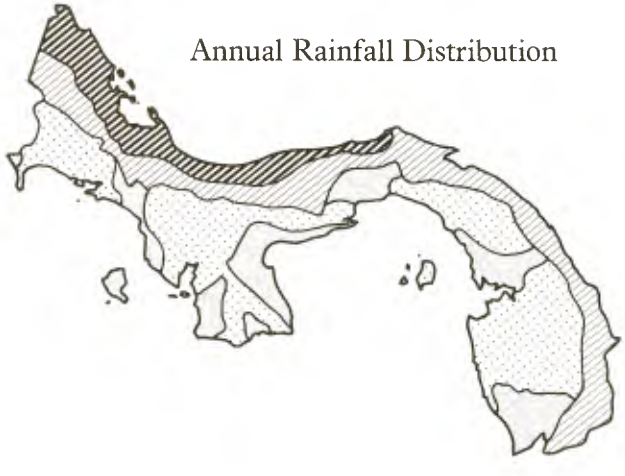
Adapted from 1927 survey by Panama Canal Company.




Gross Point
1080
Orchid I.
GROSS TRAIL
Sal I.
Pimiento I.
PANAMA CANAL
Frijoles
Bay
Fairchild Pt.
(Salûd Pt.)
1850
Salúd Bay
Orchid Cove
Sun Grebe Estero
(2200)
G:0
B–L:(1800')
FRED
FM:1300
Rear #8
FAIRCHILD TRAIL
Laboratory Bay
BARBOUR–LATHROP TRAIL
DAVID
Fairchild Cove
N:0
NEMESIA TRAIL
MILLER–BARBOUR–LATHROP CUTOFF
MILLER–N:600
GILBERT PEARSON TRAIL
FM:590
FM:0
S:M:600
LAKE TRAIL
WMW:600
RS:0
THOMAS
inset map area
DONATO TRAIL
Slothia Cove
Slothia I.
Laboratory Cove
Channel Pt.
Bat Cove
Iguana Estero
Bat Estero
Colorado Pt
(Barbour Pt.)
2850
TB:1100
TB:1600
BARBOUR TRAIL
L:0
P:0
WMW:1150
WHEELER TRAIL
AA:0
Tower Clearing
SHANNON–BARBOUR CUTOFF
RAYMOND–SHANNON TRAIL
VT:0
JDH:0
D. HOOD TRAIL
AA:300
JZ:0
JZ:300
B:(1400')
BALBOA TRAIL
FD:0
WMW:1180
VT:(350)
VAN TYNE–BIG TREE CUTOFF
VT:600
FC:0
H:0
VT:660
FRANK CHAPMAN TRAIL
ZETEK–ARMOUR CUTOFF
WHEELER–ARMOUR CUTOFF
RS:1125
AMNH:(600)
B:0
Chapman Cove
1100
sign clearing
Hydrilla Cove
VAN TYNE TRAIL
HARVARD TRAIL
AMNH TRAIL
AMNH:0
WMW:(2350)
RS:1800
VT:(1500')
Shannon Cove
Burrunga Cove
2650
Harvard Cove
foul ground
Wheeler's Estero
Drayton Inlet
2000
Poacher's Cove
Gigante Bay
2100
clearing
Burrunga Point
Poacher's Peninsula
Poacher's Point
Gatun Lake
(26 m. above sea level)



Annual Rainfall Distribution



Atlantic-Caribbean influence; moist (absence of a dry season of normal duration and intensity for the life zones present)

Atlantic-Caribbean influence; zonal (duration of dry and wet seasons normal or close to normal for the life zones present)

Pacific influence; wet-dry (alternation of wet and dry periods abnormally severe for the life zones present)

Pacific influence; zonal (duration of dry and wet seasons normal or close to normal for the life zones present)

Range and vegetation zones. For the species descriptions, overall range was determined by studies of herbarium specimens and recent monographs. (More details on range are given above, in the discussion of geographical affinities.)

The range of a species within Panama indicates the life zones and provinces in which the species is known to occur. Life zones are based entirely on the Holdridge Life-Zone System (Holdridge et al., 1971; Tosi, 1971). This system of classification is complex, and a thorough understanding requires close study of a detailed explanation. Such an explanation is best supplied in *Life Zone Ecology* by Holdridge (1967), and the life zones are best depicted by his Fig. 1, a two-dimensional diagram representing a three-dimensional set of life zones. The life zones are defined by mean annual values of the three major climatic factors of the environment—heat, precipitation, and moisture (Holdridge, 1967). The amount of moisture available for plant growth in a given site depends not only on the rainfall but also on the amount of moisture lost through evaporation and transpiration. Thus the same life zone may exist from sea level to the continental divide in Panama even though rainfall may be much greater nearer the coast. As the elevation increases, less water is lost through evapotranspiration, and the net amount available to plant populations remains the same. The general progression of life zones pertinent to species occurring on BCI is as follows: premontane dry forest, tropical dry forest, premontane moist forest, tropical moist forest, premontane wet forest, tropical wet forest, premontane rain forest, lower montane moist forest, lower montane wet forest, lower montane rain forest, and montane rain forest. This series of life zones in general progresses from very dry to very wet and, in Panama, also often from lower to higher elevation. Since tropical moist forest is intermediate to the two extremes, a few tropical moist forest species (but only the more ecologically variable) may occur in the extreme wet or dry situations. The average BCI species occurs in tropical moist forests elsewhere in Panama and less frequently in premontane wet forest and tropical wet forest. Since BCI lies in wetter-than-average tropical moist forest, relatively fewer of its species occur in premontane moist forest or tropical dry forest. Relatively few BCI species occur in premontane rain forest, since most such areas are at significantly higher elevations in Panama.

Species that otherwise occur in wetter areas, such as tropical wet forest or premontane rain forest, occur on BCI in comparatively large numbers and do not occur in drier parts of tropical moist forest, such as on the Pacific slope of the isthmus. At the same time, relatively few of the species typically found in drier areas get to BCI.

Life-zone determinations in this work are based principally on geographical information provided by the collector or taken from the *Mapa Ecologico de Panama* prepared by Tosi in 1970 (see pp. 58–59). Additional data are taken from Holdridge & Budowski (1956), Holdridge (1970), Tosi (1971), and Holdridge et al. (1971). Some of these works are particularly valuable for the larger forest trees, which, although conspicuous elements of the Panamanian flora, are not frequently collected. Provinces are listed in geographical order from west to east on the Atlantic slope and then on the Pacific slope. Locations in the provinces that overlap the continental divide are on the Pacific slope unless otherwise indicated.

In one case I have not followed the Life-Zone map: the northern end of the Navy Pipeline Road northwest of Gamboa in the Canal Zone is actually premontane wet forest, according to L. Holdridge (pers. comm.), though the map indicates that it is tropical moist forest. There are no doubt other errors in the map, but this one is particularly worth noting, since the area is so well collected and contains many species known from BCI.

Considerable criticism (both published and unpublished) has been leveled at the Holdridge Life-Zone System. The arguments against the system are perhaps best voiced by Meyer (1969, pp. 9-12). However, the fact remains that the system in general works quite well. In Panama, those areas indicated as a particular life zone on the map do look alike and have basically the same flora. Until someone produces a more accurate map, the Holdridge Life-Zone map of Panama will be used extensively, and will be quite helpful in understanding the ecological conditions under which a species will grow.

It is not surprising that most BCI species are found in other parts of Panama. In general, if a species is common on BCI it is found in most of the tropical moist forest areas of Panama; the more common (apparent) exceptions, such as absence from San Blas or Chiriquí provinces, are probably due to lack of collecting, and to a lesser extent the same can be said for parts of the Azuero Peninsula and other areas of western Panama. Recent but unstudied collections from tropical moist forest in the vicinity of the Burica Peninsula in lowland Chiriquí Province have produced many new province reports, confirming my belief that the absence of many species from tropical moist forest in Chiriquí is due simply to inadequate collecting.

There is, however, considerable variation within the tropical moist forest life zone, especially if we compare the Pacific slope with the Atlantic slope. Many species are restricted to one or the other slope, depending on ecological requirements.

Photographs. No attempt has been made to illustrate all of the species in the flora. Those photographs selected for publication—all are by the author—were chosen partly on the basis of quality but chiefly for their usefulness in the identification of species. Special consideration was given to those species that had not previously been illustrated elsewhere. Readers who have collected in tropical forests will appreciate the difficulty of obtaining exemplary photographs under conditions of insufficient—or excessive—sunlight.

Species Excluded

A total of 138 names have been excluded from the flora (see p. 911). Most of these are the result of misidentification by Standley at the time of the writing of the *Flora* (1933), but some reflect the different interpretations of later workers. Others are cultivated plants that no longer grow on the island. A few species, such as *Bidens pilosa, Porophyllum ruderale,* and *Lemna cyclostasa,* are species for which no specimens have been found from BCI. I believe that Standley reported some of these names merely because he thought they would be found there.

Maps

The map of the island on the front endsheet is also shown in the text (pp. 56–57). The back endsheet map of Panama shows province boundaries, some cities, and topographical features. The Holdridge Life Zones of Panama (see above), and annual precipitation in Panama, are shown in a series of maps on pages 58–59.

Over the course of the years there have been many modifications and extensions to the island's trail system. Some trails were abandoned while others were added or remade; still others have been diverted so many times by tree falls that they no longer follow the course they originally took.

One of the most significant modifications is the sharp curtailing of Gilbert Pearson Trail, which once began at the west edge of the Laboratory Clearing and ran more or less parallel to Snyder-Molino Trail and William Morton Wheeler Trail, then swung southwest along part of what is now Lake Trail to meet with the present Pearson Trail just west of the Tower Clearing. Other trails have been added to the system as it existed in 1927, and given the names Paul C. Standley, Nemesia, Balboa, Abraham Conrad, American Museum of Natural History (AMNH), Donato, Harvard, and A. Wetmore. Moreover, some of the existing trails have been modified. Frank M. Chapman Trail, which once had its end at Burrunga Cove, was extended south to Burrunga Point and renamed Harvard Trail. A new Chapman Trail was created farther north, to extend more or less east from Van Tyne Trail 660. The end of Fred Miller Trail had been allowed to become very overgrown, stopping at the cutoff to the Rear #8 Lighthouse Clearing (about Miller Trail 1300); it has been reopened recently. The ends of Gross Trail and Fairchild Trail are actually much farther east than the 1927 map indicates. Standley Trail, which once extended to a cove near West Peña Blanca Point, now ends in Peña Blanca Bay. The west (unnamed) fork of what is now J. D. Hood Trail has been abandoned, as has the trail extending between the end of Frank Drayton Trail and Allison-Armour Trail 2200. There are other, more minor, modifications incorporated on the current map, but they need not be mentioned here.

Other physical changes that have been made on the island include the razing of Fuertes House (which began with the assistance of thieves in 1970), Zetek House, Banks House, and the metal tower in what is still called the Tower Clearing, near the center of the island. The houses at the ends of the various trails were built for scientists—largely, I believe, during the time when James Zetek was manager of the island. Zetek was interested in termites, and the houses were variously treated to test the effectiveness of the chemicals against termites. Most were eventually eaten up and became very inhospitable, and were therefore razed. Fuertes House was situated at the end of Pearson Trail next to Fuertes Cove. Banks House was on Burrunga Point, and Zetek House and Drayton House (also called Termite House) were at the ends of the trails so named. Drayton House at this writing still stands, but it is badly infested with termites and will not survive much longer.

The farmers who settled BCI before it became a preserve pursued the typical temporary slash-and-burn techniques that are employed elsewhere in Panama today. Until evicted when the area was set aside as a preserve, they raised maize, manihot, bananas, plantain, pineapples, and the other plants typical of the isthmus.

Many features that were previously unnamed are given names on the endsheet map. Robin Foster and R. K. Enders have been especially helpful in providing names that are known to have been in use. In a normal area (i.e., a stretch of land not given over specifically to scientific study) such tiny bays, coves, and points would go unnamed, but on BCI it will be helpful to other workers to be able to refer to areas of study unequivocally. Egbert and Elizabeth Leigh, Ed Willis, Stan Rand, and Nick Brokaw were of great help in updating the trail system.

Classification and Family Sequence

The classification system used in this book for the vascular cryptogams is that of Scagel et al. (1965); for the phanerogams, that of the traditional Englerian system (De Dalla Torre & Harms, 1963). Genera are alphabetized within families; species within genera. The assignment of genera to families follows the *Flora of Panama,* except in a few cases (such as *Hampea*) that have recently (and persuasively) been transferred to other families.

The family numbers in the list that follows were assigned for convenience; they are used throughout the text and carried in the running heads, as well. The list also gives the number of BCI genera per family and the number of lesser taxa per genus (a species with two BCI varieties, for example, counts as two taxa).

ORDER OF SYSTEMATIC TREATMENT

Major groups and families	Number of genera	Number of lesser taxa
Division Lycopodophyta		
Order Selaginellales		
1. Selaginellaceae	1	6
Order Lycopodiales		
2. Lycopodiaceae	1	2
Division Pterophyta		
Order Marattiales		
3. Marattiaceae	1	1

Order Ophioglossales		
4. Ophioglossaceae	1	1
Order Filicales		
5. Schizaeaceae	2	3
6. Gleicheniaceae	2	3
7. Hymenophyllaceae	2	10
8. Parkeriaceae	1	1
9. Cyatheaceae	4	5
10. Polypodiaceae	27	71
Order Salviniales		
11. Salviniaceae	1	1
TOTAL CRYPTOGAMS	43	104
Division Coniferophyta		
Order Coniferales		
12. Araucariaceae	1	1
Division Gnetophyta		
Order Gnetales		
13. Gnetaceae	1	1
TOTAL GYMNOSPERMS	2	2
Division Anthophyta (=Angiospermae)		
Class Monocotyledoneae		
Order Pandanales		
14. Typhaceae	1	1
Order Alismatales		
15. Alismataceae	1	1
16. Hydrocharitaceae	2	2
Order Graminales		
17. Gramineae (Poaceae)	43	81
18. Cyperaceae	10	28
Order Palmales		
19. Palmae (Arecaceae)	12	18
Order Cyclanthales		
20. Cyclanthaceae	4	5
Order Arales		
21. Araceae	14	46
Order Commelinales		
22. Bromeliaceae	8	20
23. Commelinaceae	7	7
24. Pontederiaceae	2	3
Order Liliales		
25. Liliaceae	1	1
26. Smilacaceae	1	5
27. Haemodoraceae	1	1
28. Amaryllidaceae	4	4
29. Dioscoreaceae	1	7
30. Iridaceae	1	1
Order Scitaminales		
31. Musaceae	2	9
32. Zingiberaceae	4	10
33. Marantaceae	4	12
Order Orchidales		
34. Burmanniaceae	1	1
35. Orchidaceae	45	90
TOTAL MONOCOTS	169	353
Class Dicotyledoneae		
Order Piperales		
36. Piperaceae	3	32
37. Lacistemaceae	2	2
Order Urticales		
38. Ulmaceae	2	3
39. Moraceae	15	35
40. Urticaceae	5	5
Order Proteales		
41. Proteaceae	1	1
Order Santales		
42. Loranthaceae	4	7
43. Olacaceae	1	3
Order Aristolochiales		
44. Aristolochiaceae	1	3
45. Rafflesiaceae	1	1
Order Polygonales		
46. Polygonaceae	3	9
47. Amaranthaceae	6	8
48. Nyctaginaceae	3	3
49. Phytolaccaceae	4	4
50. Portulacaceae	1	1
51. Caryophyllaceae	1	1
Order Ranales		
52. Nymphaeaceae	1	2
53. Ceratophyllaceae	1	1
54. Menispermaceae	4	7
55. Annonaceae	7	13
56. Myristicaceae	1	2
57. Monimiaceae	1	2
58. Lauraceae	5	11
Order Rhoeadales		
59. Capparidaceae	2	2
Order Rosales		
60. Saxifragaceae	1	1
61. Chrysobalanaceae	2	5
62. Connaraceae	3	4
63. Leguminosae (Fabaceae)		
A. Mimosoideae	9	37
B. Caesalpinioideae	11	17
C. Papilionoideae	28	60
Order Geraniales		
64. Oxalidaceae	1	1
65. Humiriaceae	1	1
66. Erythroxylaceae	1	2
67. Rutaceae	2	10
68. Simaroubaceae	3	3
69. Burseraceae	4	6
70. Meliaceae	3	7
71. Malpighiaceae	10	20
72. Trigoniaceae	1	1
73. Vochysiaceae	1	1
74. Polygalaceae	2	3
75. Euphorbiaceae	19	33
Order Sapindales		
76. Anacardiaceae	5	7
77. Celastraceae	1	1
78. Hippocrateaceae	5	5
79. Staphyleaceae	1	1
80. Sapindaceae	6	26
Order Rhamnales		
81. Rhamnaceae	2	3
82. Vitaceae	2	6

Order Malvales		
83. Elaeocarpaceae	2	3
84. Tiliaceae	6	8
85. Malvaceae	5	10
86. Bombacaceae	7	9
87. Sterculiaceae	7	8
Order Parietales		
88. Dilleniaceae	4	9
89. Ochnaceae	2	2
90. Marcgraviaceae	2	2
91. Theaceae	1	1
92. Guttiferae (Clusiaceae)	11	15
93. Bixaceae	1	1
94. Cochlospermaceae	1	1
95. Violaceae	2	3
96. Flacourtiaceae	8	16
97. Turneraceae	1	1
98. Passifloraceae	1	11
99. Caricaceae	2	3
100. Begoniaceae	1	3
Order Opuntiales		
101. Cactaceae	2	3
Order Myrtales		
102. Lythraceae	3	3
103. Lecythidaceae	3	4
104. Rhizophoraceae	1	1
105. Combretaceae	2	7
106. Myrtaceae	5	14
107. Melastomataceae	14	35
108. Onagraceae	1	5
Order Umbellales		
109. Araliaceae	4	5
110. Umbelliferae (Apiaceae)	3	3
Order Primulales		
111. Theophrastaceae	1	1
112. Myrsinaceae	3	5
Order Ebenales		
113. Sapotaceae	2	6
114. Ebenaceae	1	1
Order Gentianales		
115. Loganiaceae	2	6
116. Gentianaceae	3	5
117. Menyanthaceae	1	1
118. Apocynaceae	15	23
119. Asclepiadaceae	8	11
Order Solanales		
120. Convolvulaceae	6	10
121. Boraginaceae	3	11
122. Verbenaceae	6	8
123. Labiatae (Lamiaceae)	3	5
124. Solanaceae	9	25
125. Scrophulariaceae	5	6
126. Bignoniaceae	21	29
127. Gesneriaceae	9	10
128. Lentibulariaceae	1	2
129. Acanthaceae	12	15
Order Rubiales		
130. Rubiaceae	37	67
Order Cucurbitales		
131. Cucurbitaceae	8	15
Order Campanulales		
132. Campanulaceae	1	1
133. Compositae (Asteraceae)	33	42
TOTAL DICOTS	490	910
TOTAL	704	1,369

KEY TO THE VASCULAR PLANTS OF BARRO COLORADO ISLAND

Plants ferns or fernlike, lacking seeds; reproduction by means of spores (vascular cryptogams):
- Leaves scalelike or acicular, minute ..... LYCOPODOPHYTA, p. 67
- Leaves foliaceous ..... PTEROPHYTA, p. 71

Plants not fernlike; reproduction by means of true seeds containing embryos (spermatophytes):
- Ovules naked, not included in an ovary of a flower (gymnosperms):
  - Xylem vessels present in wood; male cones compound (on BCI represented by a woody liana with opposite leaves, ovate leaf blades, and drupaceous fruits) ..... GNETOPHYTA (13. GNETACEAE), p. 115
  - Xylem vessels lacking in wood; male cones simple (on BCI represented by a cultivated tree with needlelike leaves) ..... CONIFEROPHYTA (12. ARAUCARIACEAE), p. 113
- Ovule or ovules enclosed by the ovary of a true flower (ANTHOPHYTA/angiosperms):
  - Leaves mainly with parallel veins, alternate; stipules lacking; blades often sheathing at base; flower parts usually in 3s or 6s, less frequently in 2s or 4s, never in 5s; stems lacking annular layers or central pith; vascular bundles closed and scattered ..... MONOCOTYLEDONEAE, p. 117
  - Leaves mainly with reticulate veins, alternate or opposite or whorled; stipules present or lacking; blades usually not sheathing at base; flower parts usually in 4s or 5s or in multiples of these; stems usually with annular layers and a central pith; vascular bundles arranged concentrically in stems ..... DICOTYLEDONEAE, p. 309

Lycopodophyta

KEY TO THE LYCOPODOPHYTA

Leaves distichous, the stem with its leaves forming a flat plane; cones ± 4-angled ..... 1. SELAGINELLACEAE
Leaves spiraled, the stem, including its leaves, terete; cones terete ..... 2. LYCOPODIACEAE

1. SELAGINELLACEAE

Heterosporous annuals or perennials with adventitious roots. Leaves 1-veined, usually dimorphic in 4 ranks, with a minute ligule at base of each leaf. Strobili usually 4-sided, consisting of imbricated megasporophylls at base and microsporophylls at apex; sporangia 1-chambered, containing (in axils of sporophylls) either microspores or megaspores; prothallia very small, unisexual.

Members of the family are distinguished by their minute dimorphic leaves, usually all held in a single plane such that the plant often looks like a single, lacy, highly dissected, compound leaf. The four-sided, cone-like strobili are also a distinguishing character of the Selaginellaceae.

Dispersal may be in part by rain water, which washes away the megacarps (van der Pijl, 1968).

One genus, with about 700 species; tropical, subtropical, and temperate regions.

SELAGINELLA Beauv.

Selaginella arthritica Alston, Arch. Bot. (Forlì) 11:43. 1935

S. conduplicata sensu Spring.

Terrestrial, usually 15–40 cm tall, glabrous; lower parts of stems in adult plants usually creeping, densely rooted, and leafless, the stems becoming erect and sparsely leafy and flexuous near apex, at least the larger stems swollen and markedly articulate, the lateral branches sparse, only the lower few of noticeable length. Median leaves auriculate, appearing affixed well above base, acute at apex, entire; lateral leaves ovate-oblong, acute to blunt at apex, not or weakly auriculate, to ca 5 mm long; lower stem leaves auriculate. Cones 1 mm wide, mostly 5–15 mm long, usually solitary, rarely 2–4 at apex of ultimate branches, sharply square; megaspores few, smooth, light brown. *Croat 8614.*

KEY TO THE SPECIES OF SELAGINELLA

Plants ± erect, usually more than 20 cm tall; main stem not branched from near base:
  Stems reddish at base; leaves minutely and evenly denticulate ..... *S. haematodes* (Kunze) Spring.
  Stems not reddish; leaves entire:
    Plants usually less than 40 cm tall, usually creeping; stems glabrous and markedly articulate, usually with few lateral branches (less than 4); plants abundant; fertile parts ca 1 mm wide, sharply square ..... *S. arthritica* Alston
    Plants usually 1 m or more tall, erect, then arching, stems pubescent, not markedly articulate, usually with many lateral branches; plants rare; fertile parts ca 2 mm wide, irregular, ± terete ..... *S. exaltata* (Kunze) Spring.
Plants scandent or decumbent, usually less than 20 cm tall; main stem usually branched from near base:

Fig. 1. *Selaginella haematodes*

Fig. 2. *Selaginella mollis*

Fig. 3. *Lycopodium dichotomum*

Fig. 4. *Lycopodium dichotomum*

Leaves conspicuously ciliate (at least the base of the lateral leaves):
Both lateral and stem leaves auriculate, usually appearing affixed well above base; lateral leaves usually more than 2.5 mm long; plants usually long-creeping ..... *S. horizontalis* (Presl) Spring.
Leaves not auriculate, clearly basifixed; lateral leaves less than 2 mm long; plants short, not creeping ..... *S. mollis* A. Braun
Leaves entire or merely short-toothed, not ciliate:
Stems markedly articulate, never flagelliform at apex of main stem; largest lateral leaves 3.5–5 mm long, entire; median leaves markedly auriculate, appearing affixed well above base ..... *S. arthritica* Alston
Stems not articulate, usually flagelliform at apex; largest lateral leaves usually less than 2 mm long, inconspicuously toothed; median leaves not auriculate, basifixed ..... *S. flagellata* Spring.

Very abundant throughout the forest, especially along trails.

Juvenile forms often have long-creeping, sparsely leafy stems and much narrower, erect, leafy portions.

Nicaragua to Panama; to 1,700 m elevation. In Panama, known from tropical moist forest in the Canal Zone (BCI only), Bocas del Toro (Shepherd Island), and Darién, and from tropical wet forest in Panamá (Cerro Trinidad).

Selaginella exaltata (Kunze) Spring., Bull. Acad. Roy. Sci. Bruxelles 10:234. 1843

Terrestrial, to 1 m or more tall, erect or frequently arching and scandent; main stem articulate, glabrous or pubescent, sparsely leafy, the smaller stems inarticulate, more closely leafy, usually with short, stiff trichomes. Median leaves asymmetrical, sharply long-acuminate, decurrent at base, entire; lateral leaves ± oblong, sharply acuminate, basifixed, 2–4 mm long, entire; leaves on main and secondary stems sparsely spaced, to 1 cm long, markedly auriculate. Cones terete to squarish at apices of ultimate branches; megaspores prominently white-ruffled. *Shattuck 1158, Croat 16193.*

Rare, in ravines in the old forest.

Standley reported *S. conduplicata* Spring., a synonym of *S. arthritica.* This report may have been based on a misdetermination of *Shattuck 1158,* which is this species.

Panama to Peru. In Panama, known from tropical moist forest in the Canal Zone, San Blas, and Darién, from premontane wet forest in Colón, and from premontane rain forest in Darién.

Selaginella flagellata Spring., Bull. Acad. Roy. Sci. Bruxelles 10:228. 1843

Terrestrial, small and creeping, glabrous; stems moderately weak, not articulate, the lower part leafy, the apical part long-flagellate, sparsely short-branched. Median leaves abruptly and sharply long-acuminate, basifixed and decurrent, not auriculate, the margins inconspicuously toothed and often appearing hyaline; lateral leaves ± ovate-oblong, usually less than 2 mm long, acute to weakly acuminate, not auriculate, the margins inconspicuously toothed. Cones ± inconspicuous, merging with leaves; megaspores minute, white, smooth. *Croat 4098, 6467.*

Infrequent in the forest, usually on trails, sometimes growing on rocks.

Mexico to Bolivia and French Guiana. In Panama, known only from tropical moist forest in the Canal Zone and Panamá.

Selaginella haematodes (Kunze) Spring. in Mart., Fl. Brasil. 1(2):126. 1840

Terrestrial, erect, to 80 cm tall and to 35 cm wide, unbranched in lower half, reddish near base, not articulate, sparsely leafy, regularly branched from near middle, the branches 12–25 cm long, gradually diminished in length toward apex. Leaves uniform, reddish, basifixed, ovate-oblong, usually acute; median leaves gradually long-acuminate, basifixed, minutely toothed; lateral leaves ovate-oblong, acute at apex, basifixed, minutely toothed. Cones numerous, solitary at branch apices, mostly to ca 1 cm long, ± square, the bracts long-acuminate and ± spreading; megaspores minute, white, smooth. *Croat 4111.*

Locally abundant along trails near streams; less frequent elsewhere in the forest.

Easily distinguished by the reddish stem, large size, and triangular blade.

Panama to Bolivia. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darien, and from premontane wet and tropical wet forests in Panamá.

See Fig. 1.

Selaginella horizontalis (Presl) Spring., Bull. Acad. Roy. Sci. Bruxelles 10:226. 1843
S. fendleri Baker; *S. sylvatica* Baker

Terrestrial, usually long-creeping and ± regularly short-branched; stems obscurely articulate, lacking flagellate apices, glabrous, prominently rooted along their length, the roots produced from bottom side of stem. Median leaves acuminate, auriculate, and affixed well above base, markedly ciliate at base; lateral leaves ± oblong, 3–4 mm long, acute at apex, auriculate at base, the basal part markedly long-ciliate. Cones short, inconspicuous, solitary at apices of ultimate branches, squarish, the bracts long-tapered, spreading, minutely toothed; megaspores minute, alveolate, light yellow-brown. *Croat 6933, 12670.*

Abundant in the forest, usually along trails; also found in shaded places in clearings.

Costa Rica to Colombia. In Panama, known from tropical moist forest in the Canal Zone and Panamá.

Selaginella mollis A. Braun, Ann. Sci. Nat. Bot., sér. 5, 3:276. 1865

S. schrammii Hieron.

Terrestrial, creeping or appressed, minute, usually less than 10 cm long, glabrous except for long cilia on lower part of leaves; stems not flagellate at apex, leafy throughout at base, short-branched almost throughout, the branches nearly equal in length. Median leaves not much smaller than lateral leaves, ± ovate, abruptly acuminate, short-toothed near apex, ciliate toward base, not auriculate, basifixed; lateral leaves ± oblong, usually acute at apex, not auriculate, basifixed, to ca 2 mm long, prominently long-ciliate at least near base. Cones inconspicuous, constituting a gradual continuation of branch apices, the bracts short-toothed; megaspores minute. *Croat 10759.*

Rare, in the forest, usually on steep shaded banks.

Mexico to Panama and Colombia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Panamá and from premontane wet forest in Panamá.

See Fig. 2.

2. LYCOPODIACEAE

Homosporous perennials; stems and roots dichotomously branched. Leaves spiraled, narrowly linear-lanceolate, 1-veined, usually imbricate. Sporangia adaxial at base of sporophylls, either similar to foliage leaves and at apex of stems or imbricated into distinct strobili; sporangia pouch-shaped, dehiscing vertically across summit; spores numerous, yellowish; prothallia monoecious, mostly saprophytic.

Recognized by their acicular, spirally arranged leaves and frequent dichotomous branching.

As in all cryptogamic families, the plants are dispersed chiefly by wind or water. Some Lycopodiaceae are dispersed by bulbils (Ridley, 1930).

Two genera and about 450 species; tropics to arctic regions.

LYCOPODIUM L.

Lycopodium cernuum L., Sp. Pl. 1103. 1753

Terrestrial, scandent or erect, to ca 1 m tall, creeping, weakly rooted, dichotomously branched; stems mostly less than 4 mm diam, the primary stems sparsely leafy throughout much of their length, the upper parts and secondary stems more densely leafy. Leaves acicular, spiraled, 2–4 mm long. Cones terete, at most apices, often pendent on recurved apices, mostly 4–9 mm long, ca 2 mm diam; sporophylls lanceolate-deltoid, to ca 2 mm long including the attenuate apex, closely imbricated, the margins irregularly lacerate. *Wilson 50, Croat 6448.*

Locally abundant along steep shore banks, especially along Old French Lock Site.

Probably native to Africa; widespread in the New World. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, and Veraguas, from tropical wet forest in Colón and Panamá, from premontane wet forest in Colón, Coclé, and Panamá, from premontane rain forest in Chiriquí and Panamá, and from lower montane rain forest in Chiriquí.

Lycopodium dichotomum Jacq., Enum. Stirp. Plerar. Vindob. 314. 1762

Epiphytic, usually ± erect, 5–20 cm tall; stems densely leafy, obscured, branching dichotomously a few times. Leaves acicular, spiraled, ca 10 mm long and 1 mm broad, moderately thick. Cones lacking; sporangia solitary in upper leaf axils, ± reniform, with a very short stalk in the sinus. *Croat 8029.*

An occasional epiphyte in the forest, usually high in the canopy on branches that are laden with other epiphytes. Individual plants never abundant locally.

United States and Mexico south to Panama, Colombia, Venezuela, and Ecuador. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién, from premontane wet forest in Coclé (El Valle), and from tropical wet forest in Chiriquí and Colón.

See Figs. 3 and 4.

KEY TO THE SPECIES OF LYCOPODIUM

Leaves less than 5 mm long, sparse on stem, most of the stem exposed; sporangia aggregated into distinct cones at branch apices; plants terrestrial, often vinelike ..... *L. cernuum* L.

Leaves ca 1 cm long, very dense, obscuring stem; sporangia solitary in upper leaf axils; plants epiphytic in trees, mostly short and erect ..... *L. dichotomum* Jacq.

Pterophyta

KEY TO THE PTEROPHYTA

Genera in this key for which family is not indicated are in the Polypodiaceae, family 10.

Plants free-floating, not attached by roots, with 2 opposite entire leaves floating on the water .....
..... 11. SALVINIACEAE (*Salvinia radula* Baker)
Plants attached by roots, not free-floating (aquatic or not):
  Leaves translucent, usually consisting of a single layer of cells; sporangia sessile on a threadlike stalk emerging from a bilabiate, tubular, or urceolate indusium, the indusia arising along margins of leaflets; plants often minute, usually forming close, ± appressed mats.....
..... 7. HYMENOPHYLLACEAE (in part)
  Leaves and sporangia not as above:
    Plants free-climbing vines, never epiphytic, the stems not appressed to trees:
      Leaves palmately lobed at least at base, not sessile; sporangia borne on protuberances at margin of leaflets ..... 5. SCHIZAEACEAE (*Lygodium*)
      Leaflets pinnatifid, sessile; sporangia borne on lower surface of segments .....
..... 6. GLEICHENIACEAE
    Plants not free-climbing vines (if vinelike, the stems appressed to trees):
    • Leaves simple and not deeply lobed:
      Plants terrestrial; leaves dimorphic:
        Plants less than 10 cm tall; sterile leaf 1 (rarely 2), ovate; fertile leaf 1, slender, nearly all sporangial tissue ..... 4. OPHIOGLOSSACEAE (*Ophioglossum reticulatum* L.)
        Plants more than 20 cm tall; sterile leaves usually 4 or more, narrowly oblong; fertile leaves with sporangia restricted to a narrow band along the margin .....
..... *Dictyoxiphium panamense* Hook.
      Plants epiphytic; leaves dimorphic or not:
        Sporangia arranged in distinct rounded sori on surface of leaves..... *Polypodium* (in part)
        Sporangia not in distinct rounded sori:
          Sporangia forming an anastomosing pattern over entire underside of leaf; blades usually less than 15 cm long, oblanceolate; rhizome usually closely appressed
..... *Anetium citrifolium* (L.) Splitg.
        Sporangia not as above:
          Leaves more than 6 cm wide; sori in narrow lines paralleling the lateral veins....
..... *Asplenium serratum* L.
          Leaves less than 4 cm wide; sori not as above:
            Leaves dimorphic, with sporangia densely covering the reduced fertile leaf; rhizome scales conspicuous, reddish-brown, very thin, many times broader than thick; plants frequently sterile ..... *Elaphoglossum*
            Leaves monomorphic, with sori in rows along margins of leaves; rhizome scales not as above, filiform, not conspicuous:
              Leaves mostly more than 1 cm wide, widest at middle; sori frequently with short interruptions, more than 1 mm wide .....
..... *Ananthacorus angustifolius* (Sw.) Und. & Max.
              Leaves less than 5 mm wide, linear; sori usually continuous, less than 1 mm wide ..... *Vittaria*

- Leaves simple and deeply lobed *or* leaves compound:
  - Leaves simple and deeply lobed:
    - Leaves ± regularly pinnatifid:
      - Leaves monomorphic; sori in round dots on lower surface of leaflets ..... *Polypodium* (in part)
      - Leaves dimorphic; sori immersed in margin ..... 7. HYMENOPHYLLACEAE (*Trichomanes diversifrons* (Bory) Mett.)
    - Leaves not regularly pinnatifid:
      - Plants aquatic; leaves dimorphic, the segments of the fertile leaves linear, the sterile leaves 2–4-pinnatifid, pentagonal in outline, very thin ..... 8. PARKERIACEAE (*Ceratopteris pteridoides* (Hook.) Hieron.)
      - Plants epiphytic or terrestrial; leaves monomorphic, dichotomously or pinnately lobed:
        - Sporangia borne in small, pectinate-pinnate, ± reniform clusters from tips of teeth on each blade division .... 5. SCHIZAEACEAE (*Schizaea elegans* (Vahl) Sw.)
        - Sporangia borne over entire blade surface or continuous along margins:
          - Plants epiphytic; blades ± dichotomously branched, the lobes mostly ca 1 cm wide; leaf tissue extending to base of leaf; sporangia in ± continuous marginal rows near apex of lobes ..... *Dicranoglossum panamense* (Christensen) Lell.
          - Plants terrestrial; blades pinnately lobed, the lobes usually more than 5 cm wide; leaf tissue not extending to base of leaf; sporangia scattered over blade surface ..... *Tectaria euryloba* (H. Christ) Max.
  - Leaves compound:
    - Leaves 1-pinnate, the leaflets regularly and deeply pinnatifid *or* the leaves more than 1-pinnate:
      - Leaves 1-pinnate, the leaflets regularly and deeply pinnatifid on both sides:
        - Lobes of leaflets markedly asymmetrical, especially at base ..... *Ctenitis protensa* (Afz.) Copel. var. *funestra* (Kunze) Proct.
        - Lobes of leaflets ± symmetrical:
          - Sori indusiate; upper side of costae with acicular scales ..... *Thelypteris* (in part)
          - Sori exindusiate; upper side of costae lacking acicular scales ..... *Dryopteris sordida* Max.
      - Leaves more than 1-pinnate:
        - Leaves dimorphic, the fertile leaves reduced; plants closely appressed, hemiepiphytic climbers, the climbing rhizomes with conspicuous scales:
          - Sterile leaves to 3-pinnate, all but the uppermost leaflets divided more than halfway to midrib; segments acute at apex, sharply toothed, the lowermost often free; rhizome scales fine, ± curly, spreading; sori indusiate, round, discrete ..... *Maxonia apiifolia* (Sw.) Christensen
          - Sterile leaves 2-pinnate or 2-pinnate-pinnatifid, most leaflets divided less than halfway to midrib; segments nearly rounded at apex, entire to bluntly toothed, the lowermost usually not free; rhizome scales coarse, stiff, appressed or nearly so; sori exindusiate, apparently continuous along margins or over entire surface ..... *Polybotrya villosula* H. Christ
        - Leaves monomorphic; plants terrestrial:
          - Plants tree ferns, the adults with a definite trunk (trunk may be short in *Cnemidaria*); leaves armed, at least at base ..... 9. CYATHEACEAE (except *Metaxya*)
          - Plants not tree ferns; leaves usually unarmed:
            - Lower surface of leaflets white-waxy; sporangia scattered over surface; plants growing on exposed banks ..... *Pityrogramma calomelanos* (L.) Link
            - Lower surface of leaflets not white-waxy; sporangia not scattered over surface; habitats various:
              - Leaflets markedly asymmetrical, especially at base, toothed but not equally and deeply dissected on both sides (in *Ctenitis*, the leaflets deeply lobed but asymmetrical):
                - Plants epiphytic; sori exindusiate; leaflets mostly deeply, irregularly lobed on both sides ..... *Ctenitis protensa* Afz. (Copel.) var. *funestra* (Kunze) Proct.
                - Plants terrestrial; sori indusiate; leaflets often toothed on 1 side but never deeply lobed on both sides ..... *Adiantum* (in part)
              - Leaflets ± symmetrical and regularly pinnatifid:
                - Lobes of leaflets entire; plants regularly dichotomously branched, usually vinelike; sori round, arranged in a row along midrib of lobe ..... 6. GLEICHENIACEAE

Lobes of leaflets toothed at least near apex; plants not both regularly dichotomously branched and vinelike; sori various:
Leaves not lacy, broadly dissected, the terminal leaflet more than 8 cm long; sori elongate, along margins of leaflets, with a narrow, continuous indusium open on 1 side ... *Pteris* (except *P. grandifolia*)
Leaves lacy, finely dissected, the terminal leaflet less than 4 cm long; sori round:
Plants tree ferns with a conspicuous trunk; petioles armed with spines at least at base ..... 9. CYATHEACEAE (*Trichopteris*)
Plants not tree ferns; petioles unarmed:
Spores borne in cuplike indusia on margin of leaflets, the indusia commonly in toothed depressions; leaves 3- or 4-pinnate-pinnatifid ..... *Dennstaedtia cicutaria* (Sw.) Moore
Spores borne in ± round indusiate or exindusiate sori on surface of leaflets, not on margins in cuplike indusia; leaves 2- or 3-pinnate-pinnatifid, never 4-pinnate-pinnatifid:
Rachis pubescent, with jointed trichomes on upper side; underside of leaflets scaly ..... *Ctenitis sloanei* (Poepp.) Mort.
Rachis glabrous except for dense pubescence along ridge on upper side; underside of leaflets hispid, with short-stalked glands ..... *Thelypteris torresiana* (Gaud.) Alston

◆ Leaves 1-pinnate, the leaflets not regularly pinnatifid (i.e., not regularly and deeply lobed on both sides):
Leaves dimorphic, the fertile leaf much reduced:
Leaflets exactly opposite, caudate-acuminate, ± entire, the veins numerous, close and parallel, branched only near base; plants terrestrial ..... 3. MARATTIACEAE (*Danaea nodosa* (L.) J. Sm.)
Leaflets not as above; plants epiphytic or terrestrial:
Plants terrestrial; sterile leaflets shallowly lobed, usually more than 10 cm long, the smaller veins anastomosing ..... *Bolbitis cladorrhizans* (Spreng.) Ching
Plants epiphytic:
Rachis narrowly winged; leaflets usually less than 6 cm long, usually more than 10 pairs of leaflets per leaf ..... *Lomariopsis vestita* Fourn.
Rachis not winged; leaflets usually more than 6 cm long, usually less than 6 pairs of leaflets per leaf ..... *Bolbitis nicotianifolia* (Sw.) Ching
Leaves monomorphic:
Sporangia on margins of leaves:
Leaflets asymmetrical about midrib ..... *Adiantum* (in part)
Leaflets ± symmetrical about midrib:
Leaflets thin, translucent; sporangia in tubular indusia protruding from leaflet margins ..... 7. HYMENOPHYLLACEAE (*Trichomanes pinnatum* Hedw.)
Leaflets and sporangia not as above:
Sori ± round, interrupted along margins of leaflets ..... *Nephrolepis*
Sori continuous along margins of leaflets:
Rachis dark brown or purplish; leaflets coarsely toothed near apex, the lateral veins frequently 1-forked but never anastomosing frequently ..... *Saccoloma elegans* Kaulf.
Rachis light in color; leaflets ± entire near apex, the lateral veins anastomosing several times ..... *Pteris grandifolia* L.
Sporangia or sori dispersed over surface of blade:
Plants massive aquatics, growing in dense clusters with the sporangia completely covering at least part of all the uppermost leaflets ..... *Acrostichum*
Plants not as above, the sporangia arranged in distinct sori:
■ Sori ± round:
Leaflets ± entire (except possibly at apex):
Leaflets markedly unequal and auriculate on lower proximal edge, overlapping rachis; leaflets generally less than 15 cm long ..... *Cyclopeltis semicordata* (Sw.) J. Sm.
Leaflets ± equal at base or at least not auriculate; leaflets generally more than 15 cm long:
Plants epiphytic; sori in rows, each row in an areole between major lateral veins; leaflets ± entire at apex ..... *Polypodium triseriale* Sw.
Plants terrestrial; sori not in rows, ± irregularly clustered near midrib on major lateral veins; leaflets regularly toothed near apex ... 9. CYATHEACEAE (*Metaxya rostrata* (Willd.) Presl)

Leaflets not entire:
Leaflets ± regularly toothed and equal in shape ..... *Thelypteris poiteana* (Bory) Proct.
Leaflets irregularly lobed or sinuate, at least the lowermost with a larger basal lobe ..... *Tectaria incisa* Cav.
■ Sori linear or at least several times longer than wide (not in dots):
Sori in 2 continuous lines along midrib of each leaflet ..... *Blechnum*
Sori not in 2 continuous lines along leaflet midrib:
Leaflets more than 20 cm long and 6 cm wide; margins entire; plants usually more than 2 m tall ..... *Hemidictyum marginatum* (L.) Presl
Leaflets usually less than 20 cm long or, if longer, much less than 6 cm wide; margins usually toothed; plants usually less than 1.5 m tall:
Sori short, ± equal, arranged in short rows perpendicular to and between lateral veins; plants generally aquatic ..... *Thelypteris serrata* (Cav.) Alston
Sori short or long, often markedly unequal in length, arranged in rows parallel to lateral veins; plants not aquatic:
Leaflets mostly less than 6 cm long, frequently blunt or rounded and toothed at apex; open side of all indusia facing apex of leaflet ..... *Asplenium* (in part)
Leaflets usually more than 6 cm long, usually gradually tapered to acuminate apex; open face of at least some indusia facing away from apex of leaflet (in *Asplenium delitescens,* most facing toward apex):
Leaflets usually more than 2.5 cm wide, obtuse to rounded at base on both sides; sori often unequal, the longer ones interspersed with the shorter ..... *Diplazium grandifolium* Sw.
Leaflets usually less than 2.5 cm wide, the base oblique, the lower proximal edge usually acute; sori ± equal:
Terminal leaflet of nearly same shape as lateral leaflets; plants epiphytic; rhizome scales clathrate (latticed) ..... *Asplenium falcinellum* Max.
Terminal leaflet unlike lateral leaflets, pinnatifid; plants terrestrial; rhizome scales fibrous, not clathrate ..... *Asplenium delitescens* (Max.) A. R. Smith

3. MARATTIACEAE

Homosporous, terrestrial herbs; stem a dorsiventral rhizome. Leaves usually large, circinate in venation, pinnately compound (in ours); secondary veins on the leaflets free, closely parallel. Fertile leaves moderately contracted; sorus a double row of sporangia extending from midrib to margin, joined to form a synangium, each sporangium opening by a terminal pore; prothallia growing on ground, green with mycorrhiza.

Recognized by their pinnately compound leaves, the leaflets opposite, and the secondary veins closely parallel.

Six genera and over 200 species; tropics and subtropics.

DANAEA J. Sm.

Danaea nodosa (L.) J. Sm., Mem. Acad. Roy. Sci. (Turin) 5:420. 1793

Terrestrial, usually 1.5–2 m tall; rhizome horizontal. Leaves 1-pinnate, dimorphic; petioles to ca 1 m long, sparsely to moderately scaly, prominently ridged above; leaflets exactly opposite; sterile leaflets usually narrowly oblong, long-acuminate, obtuse to acute and often slightly inequilateral at base, 10–40 cm long, 4–5.5 cm wide, the margin entire to undulate or faintly serrulate near apex, the midrib sparsely scaly, the scales irregular and deeply lacerate, the lateral veins 1-forked at base; fertile leaflets much shorter and narrower, 1.5–2.5 cm broad. Sporangia in 2 rows, continuous, borne along the veinlets, almost completely covering the fertile leaflets beneath. *Croat 12301.*

Infrequent, on steep moist creek banks in ravines.

Mexico to Brazil; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Veraguas, and Panamá (San José Island), from premontane wet forest in Panamá (Chimán) and Veraguas, and from tropical wet forest in Panamá.

See Fig. 5.

4. OPHIOGLOSSACEAE

Homosporous, terrestrial herbs; stems short, lacking scales. Leaves solitary or few, with dimorphic segments; blades splitting into a dorsal and a ventral part, the dorsal part sterile, green, with reticulate venation, the ventral part fertile, arising from dorsal part, spikelike, bearing a row of large immersed sporangia in each side. Sporangia opening by transverse slits; prothallia subterranean, saprophytic.

Fig. 5. *Danaea nodosa*

Fig. 6. *Lygodium radiatum*

Fig. 7. *Lygodium venustum*

Recognized by their peculiar leaves, a spikelike fertile segment arising from each green, fan-shaped blade.

Four genera and 70 species; temperate and tropical areas.

OPHIOGLOSSUM L.

Ophioglossum reticulatum L., Sp. Pl. 1063. 1763

Small terrestrial plant, consisting of a single succulent stem bearing 1 sterile leaf (rarely 2) and 1 fertile stalk. Sterile leaf blade arising 2–9 cm above ground, ovate, acute to rounded at apex, cuneate at base, ca 1–4 cm long. Sporangia borne distally on a long, slender, solitary stalk extending 5–20 cm above sterile leaf, the sporangia sessile, thick-walled, lacking annuli. *Dressler 2874.*

Collected once in the Laboratory Clearing. The species has been seen fertile only during the rainy season.

Mexico to Argentina; West Indies; Old World. In Panama, known only from BCI.

5. SCHIZAEACEAE

Homosporous, terrestrial ferns, vines, or herbs; rhizomes creeping or ascending; rachis monopodial, the alternate branches dwarfed, each with 1 pair of leaflets and an abortive bud. Leaves variously palmately or dichotomously lobed; veins usually free. Sporangia biseriate on marginal spikes (each sporangium subtended by an outgrowth serving as an indusium); annuli distal, complete, opening by longitudinal slit; spores tetrahedral; prothallia green, flat.

Distinguished by their vinelike habit (except *Schizaea*), palmately or dichotomously lobed leaves, and marginal, spikelike sori.

Four to six genera and 150 species; mostly tropics, a few species in subtropical or temperate regions.

LYGODIUM Sw.

Lygodium radiatum Prantl, Unters. zur Morph., Schiz. 66. 1881

Slender vine, glabrous throughout; stems slender. Leaves opposite, deeply palmate, with 3–7 lobes (fertile leaves usually 3–5-lobed); petioles slender, mostly 2.5–5.5 cm long; lobes long and narrow, acute to acuminate at apex (rounded and mucronate on some juveniles), 8–25 cm long, 7–25 mm wide, about equal in length on each leaf, serrate. Sporangia borne in small conelike groups exserted along leaf margins, each sporangium solitary, sessile, subtended by a cup-shaped involucre. *Croat 12803.*

Occasional, in the forest or at the edges of clearings, climbing to a height of 20 m.

Panama and Colombia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, San Blas, Panamá, and Darién and from tropical wet forest in Panamá and Colón.

See Fig. 6.

Lygodium venustum Sw., J. Bot. (Schrader) 1801(2):303. 1803

L. polymorphum (Cav.) H.B.K.

Slender vine; stems, petioles, and upper midrib of leaves densely pubescent. Leaves alternate, sessile or with slender petioles to 7 mm long, unequally palmate, with 3–5 lobes, the central lobe longest, 4–10 cm long, the lateral lobes 1–3 cm long, all lobes ± crenate, moderately to sparsely pubescent. Sporangia sessile, borne in narrow, pubescent, conelike clusters along margins. *Croat 7216.*

Abundant in old clearings; less frequent in the forest along margins of clearings.

Mexico to Peru; West Indies. In Panama, known principally from tropical moist forest in the Canal Zone, Colón, Chiriquí, Herrera, Coclé, Panamá, and Darién; known also from tropical dry forest in Panamá (Taboga Island), from premontane moist forest in Panamá (Saboga Island), and from premontane wet forest in Chiriquí and Panamá (Chimán).

See Fig. 7.

SCHIZAEA J. Sm.

Schizaea elegans (Vahl) Sw., J. Bot. (Schrader) 103. 1801

Erect, terrestrial herb, 20–60 cm tall; rhizome erect, with rufous scales. Petioles 20–40 cm long, darkened at base, sparsely covered with long, flattened or acicular scales, glabrate toward apex; blades dichotomously divided or lobed, the veins repeatedly dichotomous, each leaf segment fan-shaped, narrowly incised at apex, gradually tapered to base. Sporangia sessile on branches of compact, pectinate-pinnate, ± reniform distal segments of blade. *Foster 2795.*

Known from a single collection from the end of Chapman Trail. Elsewhere in Panama the species has been found in fertile condition essentially all year.

Mexico to Brazil and Bolivia; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Herrera, and Panamá and from premontane wet forest in Panamá.

KEY TO THE SPECIES OF SCHIZAEACEAE

Plants erect herbs, less than 60 cm tall; sporangia arranged in pectinate-pinnate, ± reniform structures, only on distal segments of blades ..... *Schizaea elegans* (Vahl) Sw.

Plants scandent herbs, usually long vines; sporangia arranged along lateral margins of all leaflets:

Leaflets divided into nearly equal lobes ..... *Lygodium radiatum* Prantl

Leaflets with median lobe much longer than lateral lobes ..... *Lygodium venustum* Sw.

KEY TO THE SPECIES OF GLEICHENIACEAE

Veins of leaf segments 1-forked; leaflet midribs normally covered with brown scales below; leaf segments 8–16 times longer than wide ..... *Gleichenia bifida* (Willd.) Spreng.
Veins of leaf segments 2–5-forked; leaflet midribs not covered with brown scales below; leaf segments less than 5 times longer than wide:
A pair of accessory pinnae at all but ultimate nodes ..... *Dicranopteris flexuosa* (Schrad.) Und.
Accessory pinnae lacking, or (rarely) only at lower nodes .... *Dicranopteris pectinata* (Willd.) Und.

6. GLEICHENIACEAE

Homosporous, terrestrial herbs, often vinelike; rhizomes long-creeping. Leaves 2-pinnate or more compound (in ours; sometimes pinnate elsewhere), often pseudodichotomous by abortion of terminal bud, usually coriaceous; veins free. Sori exindusiate; sporangia few on lower blade surface, in 2 rows along major divisions, each sporangium with a complete transverse medial annulus opening by a longitudinal slit; prothallia green, flat, costate.

Recognized by their vinelike habit and their dichotomously branched, pinnately compound leaves, the sporangia borne along the segments of the pinnatifid pinnae.

Five or six genera and 130–160 species; tropical, subtropical, and subtemperate areas of the Southern Hemisphere.

DICRANOPTERIS Bernh.

Dicranopteris flexuosa (Schrad.) Und., Bull. Torrey Bot. Club 34:254. 1907

Similar to *D. pectinata*, but with a pair of reduced accessory pinnae at most leaf nodes; the plant glabrous throughout; the veins of the leaflets 2–4-forked, darker, not at all raised. *Kenoyer 4.*

Found in same habitats as *D. pectinata.* Collected once by Kenoyer, and possibly no longer present on the island.

Southern Mexico to Colombia and along the Andes to Brazil and Peru, mainly at lower elevations; West Indies. In Panama, known principally from tropical moist forest in the Canal Zone, Veraguas, Herrera, Panamá, and Darién, but also from premontane wet forest in Panamá (Cerro Campana).

Dicranopteris pectinata (Willd.) Und., Bull. Torrey Bot. Club 34:260. 1907

Free-climbing, vinelike, dichotomously branched herb; rhizome long-creeping, 3–5 mm diam, scabrous from persistent bases of articulate trichomes; primary leaf axes at first erect, eventually arching. Leaflets paired at ultimate nodes, deeply pinnatifid, oblong-lanceolate, mostly 10–25 cm long, 1.5–6 cm wide, sessile, glaucous beneath, glabrate, sometimes with a few brown, stellate scales below; lobes 3–6 mm wide, firm, the veins 3–5-forked, somewhat raised; leaf nodes in lower dichotomies rarely with a pair of reduced accessory pinnae. Sori round, exindusiate, in 2 rows, 1 row on each side of midrib on underside of lobes, each sorus bearing more than 6 sporangia. *Croat 4829.*

Locally abundant on steep, eroding banks on the shore, particularly on the northern shore of Orchid Island and on Gross Point.

For a description of branching in this genus, see Underwood (1907).

Mexico to Brazil, the Guianas, and Bolivia; West Indies. In Panama, known principally from tropical moist forest in the Canal Zone, San Blas, Herrera, Panamá, and Darién; known also from tropical dry forest in Panamá (Taboga Island) and from tropical wet forest in Colón.

GLEICHENIA J. Sm.

Gleichenia bifida (Willd.) Spreng., Syst. Veg. 4:27. 1827

Erect or subscandent, dichotomously branched herb; rhizome creeping, scaly; stems, midribs of leaflets above and below, and lobes of leaflets below ± densely covered with brown arachnoid scales, some scales lanceolate with long-ciliate margins. Leaflets paired at ultimate nodes, deeply pinnatifid, oblong, tapered to long-caudate-acuminate apices, 25–45 cm long, 2–8 cm wide, sessile; lobes sometimes of irregular lengths, mostly 2–4.5 cm long, 2–3 mm wide, moderately thin, the veins 1-forked. Sori round, in 2 rows, 1 row on each side of midrib on underside of lobes, each sorus usually bearing 4 or fewer sporangia. *Croat 11762.*

Locally abundant on steep, eroding banks on the shore, on the north side of the island, often growing with the more abundant *Dicranopteris pectinata* and often preferring the more shaded areas.

Mexico to South America below 2,000 m; West Indies. In Panama, known from tropical moist forest in the Canal Zone and Darién, but probably more common in premontane wet forest in Colón, Chiriquí, Coclé, and Panamá.

7. HYMENOPHYLLACEAE

Homosporous epiphytic or terrestrial herbs; stems usually rhizomes with distichous scales, less commonly erect and radially symmetrical. Leaves usually small; leaflets usually 1 cell thick, lacking stomata, usually coiled in bud; veins usually free. Involucres consisting of urceolate, tubular, or bivalvate marginal extensions of blade (the indusia); sporangia borne on all surfaces of free-ending vein extensions (the receptacles) within the involucre; sporangia opening by a ± longitudinal slit; spores tetrahedral or becoming globose; prothallia filamentous or thallose.

KEY TO THE TAXA OF HYMENOPHYLLACEAE

Involucre valvate, not at all tubular ..... *Hymenophyllum brevifrons* Kunze
Involucre tubular ..... *Trichomanes*

Recognized by their lacy, generally transparent leaves and by their tubular, urceolate, or bivalvate marginal indusia.

Three genera and about 650 species; all tropical and temperate regions of the world.

HYMENOPHYLLUM J. Sm.

Hymenophyllum brevifrons Kunze, Bot. Zeitung (Berlin) 5:185. 1847

Epiphyte; rhizome slender, creeping, branched, with numerous, short, filiform, reddish-brown scales, these ultimately deciduous. Leaves simple, deeply and irregularly divided, translucent, glabrous, usually drying brown and curled; petioles ca 1 cm long; blades ± ovate in outline, ca 1 cm or more long; ultimate lobes usually emarginate, never toothed; veins thick, dichotomously branching several times in lobes. Sori usually near apex of blade, marginal, the indusia bivalved throughout (or at least to middle). *Shattuck 1013.*

Probably rare; collected once by Shattuck on Zetek Trail.

An inconspicuous plant, usually growing interspersed with mosses. It could easily be overlooked and is possibly more abundant than meets the eye.

Guatemala to Panama and the Guianas. In Panama, known from tropical moist forest in the Canal Zone and Panamá and from premontane wet forest in Panamá.

TRICHOMANES L.

Many of the smaller, inconspicuous species are easily overlooked and possibly more abundant than they appear. See the genus key for distinguishing characters of *T. curtii* Ros., which has not been identified from BCI but is likely to occur.

Trichomanes diversifrons (Bory) Mett., Sadeb. Nat. Pfl. 1(4):108. 1899

Terrestrial, mostly 20–30 cm tall; rhizome stout, erect; petiole bases closely spaced; rhizome and petioles bearing stiff, dark, threadlike, seemingly jointed scales. Leaves simple, dimorphic; petioles on sterile leaves 3–5 cm long; sterile blades deeply pinnatifid, oblong-lanceolate, tapered to very long filiform apex, 3.5–5 cm broad, glabrous above, with short-jointed filiform scales on underside of veins (particularly midrib); lobes mostly to 5 mm broad, acute at apex, ± uncinate-serrate, the veins anastomosing, the lowermost lobes reduced; sporophylls linear, denticulate, ca 15 cm long and 6 mm wide, on a petiole 9–18 cm long. Sori immersed into margin; sporangia sessile on a filiform, exserted receptacle. *Croat 10813.*

Occasional, on steep creek banks in ravines, usually in dark places.

Throughout American tropics. In Panama, known from tropical moist forest in the Canal Zone, San Blas, Veraguas, and Darién; known also from premontane wet forest in Colón (Santa Rita Ridge), from tropical wet forest in Colón and San Blas, and from premontane rain forest in Darién (Cerro Pirre).

Trichomanes ekmanii Wessels-Boer, Acta Bot. Neerl. 11:319. 1962

Epiphyte; rhizome slender, creeping, scaly, the petiole bases well spaced. Leaves simple; petioles 3–7 mm long, sparsely scaly; blades obovate or oblong to orbicular, rounded to irregularly lobed especially in upper part, rounded or tapered at base, to 2(3) cm long and 1(1.5) cm wide, the midrib distinct, the lateral veins pinnately arranged, and cross-veins lacking; false vein continuous, submarginal. Sori 4–9 per leaf, together near apex or solitary on apical lobes; indusium wholly immersed in margin, lacking lips and not dark-edged, the tube cylindrical and broadly expanded at apex. *Croat 16515.*

Distribution on BCI unknown. Found in wet forests on roots and bases of trees and on fallen logs.

Throughout Central America and northern South America; Greater Antilles. In Panama, known only from tropical moist forest in the Canal Zone.

Trichomanes godmanii Hook. in Baker, J. Linn. Soc., Bot. 9:337. 1866

Tiny epiphyte; rhizome slender, creeping, with fine scales. Leaves simple, glabrous; petioles 4–10 mm long; blades orbicular or obovate, rounded at apex, tapered to obtuse or acute base, 5–20 mm long and wide, entire or slightly lobed, with a distinct costa and pinnate veins in lower blade and flabellate venation above; false veinlets distinct, reticulate; false vein submarginal. Sori 1–9 in upper part of leaf; indusium wholly immersed in margin, lacking lips and not dark-edged, obconic with the mouth expanded, the receptacle long-exserted. *Croat 16202.*

Fairly common; seen densely covering all sides of base of *Scheelea zonensis* (19. Palmae) trunk.

Throughout Central America; Cuba. In Panama, known only from tropical moist forest in the Canal Zone and Panamá.

Trichomanes kapplerianum Sturm in Mart., Fl. Brasil. 1(2):276. 1859

T. hookeri Presl var. *minor* (Jenm.) Domin

Tiny epiphyte; rhizome slender, creeping, scaly. Leaves simple; petioles very short; young blades often orbicular, cordate; mature blades ovate to oblong, irregularly lobed, ± rounded at apex, rounded to narrowly acute at base,

KEY TO THE SPECIES OF TRICHOMANES

Plants terrestrial; leaves often more than 20 cm long:
- Leaves dimorphic, simple, the sterile leaves pinnatifid, the fertile leaves linear; sori immersed in margin ..... *T. diversifrons* (Bory) Mett.
- Leaves ± monomorphic, 1-pinnate; sori along margins of leaflets except near apex ..... *T. pinnatum* Hedw.

Plants epiphytic; leaves less than 10 cm long:
- All leaves pinnately lobed, most more than 3 cm long, the costa extending to apex of blade:
  - Trichomes frequent on blade surface and margins, all trichomes stellate; indusia bell-shaped, immersed, the lips not dark-edged ..... *T. polypodioides* L.
  - Trichomes only on margins of blades, the blades otherwise glabrous, the trichomes simple or bifid; indusia tubular, partly exserted, the lips dark-edged ..... *T. krausii* Hook. & Grev.
- At least some leaves not pinnately lobed, most less than 3 cm long, the costa only rarely extending to the apex:
  - Leaves bearing marginal trichomes but lacking a submarginal false vein; indusia at least partly exserted, with 2 distinct dark-edged lips:
    - Leaves less than 8 mm long, usually bearing a single terminal sorus ..... *T. ovale* (Fourn.) Wessels-Boer
    - Leaves more than 1 cm long, usually bearing several to many sori:
      - Sori often 6 or more per leaf; indusia exserted, not between lobes or in sinuses (species not known from BCI but to be expected) ..... *T. curtii* Ros.
      - Sori rarely as many as 5 or 6 per leaf; indusia half immersed, between lobes ..... *T. punctatum* Poir. subsp. *sphenoides* (Kunze) Wessels-Boer
  - Leaves lacking marginal trichomes but bearing a submarginal false vein; indusia wholly immersed, without lips and not dark-edged:
    - Venation reticulate; mature fertile leaves ± orbicular ..... *T. godmanii* Hook.
    - Venation lacking cross-veins; mature fertile leaves elongate:
      - Submarginal vein continuous; young leaves ± elongate ..... *T. ekmanii* Wessels-Boer
      - Submarginal vein discontinuous; young leaves often orbicular or cordate ..... *T. kapplerianum* Sturm

5–30 mm long, 5–15 mm wide, bearing a distinct midrib, pinnate lateral veins in lower part of blade, flabellate venation above; false vein discontinuous, submarginal. Sori usually 3–7, together near apex or on small lobes; indusium wholly immersed in margin, lacking lips and not dark-edged, the mouth expanded; receptacle exserted. *Wilson 87.*

Distribution on BCI not known. Forming mats on tree trunks and moist rocks.

Costa Rica to the Guianas and Amazon basin; Lesser Antilles. In Panama, known only from tropical moist forest on BCI and in Bocas del Toro.

Trichomanes krausii Hook. & Grev., Icon. Fil. t. 149. 1831

Tiny epiphyte; rhizome slender, creeping, scaly. Leaves simple, very thin, somewhat lacy; petioles mostly very short; petioles and lower midribs densely scaly; blades oblong or lanceolate-oblong, irregularly pinnatifid, glabrous except on margins, the segments weakly lobed, 2–4.5 (9) cm long, 1–2.5 cm wide; lobes ± linear, irregular, 1–3 mm broad, separated by broad, open sinuses, a large dark stellate scale on a tooth in the sinus, some of the marginal scales simple or bifid; midrib of lobes extending to apex, almost lacking connected lateral veins; false veinlets few, partly parallel to margin. Sori several, solitary in upper lobes; indusium partly immersed, its lips semiorbicular, dark-edged. *Croat 8789.*

Distribution on BCI uncertain. Found on moist, shaded rocks, twigs, and tree trunks to 1,350 m elevation.

Throughout tropical and subtropical America. In Panama, known from tropical moist forest in the Canal Zone and Darién, from premontane wet forest in Panamá, and from tropical wet forest in Chiriquí.

Trichomanes ovale (Fourn.) Wessels-Boer, Acta Bot. Neerl. 11:296. 1962

T. sphenoides Kunze var. *minor* Ros.

Tiny epiphyte, the blades usually ± appressed. Leaves simple, minute; petioles very short; blades variable, orbicular, ovate, or lanceolate, usually rounded or cordate and broadest at base, 3–8 mm long, 2–6 mm wide, ± entire, with bifid or stellate trichomes on margin; midrib on fertile leaves and some sterile leaves running to apex, the lateral veins pinnate, partly free. Sorus solitary at apex (rarely 2 or 3); indusium partly immersed, at least the lips exserted, the lips dark-edged, small, narrowly winged with stellate scales and with a few rows of brown cells. *Croat 14999.*

Distribution on BCI not known. Found on moist, deeply shaded rocks and tree trunks.

Probably throughout the American tropics, but seldom seen because of its small size. In Panama, known only from tropical moist forest in the Canal Zone and Panamá.

Trichomanes pinnatum Hedw., Fil. Gen. et Sp. t. 4, f. 1. 1799

Terrestrial, usually 25–50 cm tall; rhizome erect, short, bearing brown, threadlike scales. Leaves 1-pinnate,

6–30(40) cm long, often with a long leafless tail at apex, the tail sometimes rooting and producing another plant; petiole and rachis with moderate to sparse, long, threadlike scales; pinnae lanceolate-oblong, blunt to obtuse at apex, obtuse to truncate or subcordate at base (sterile pinnae imbricate at base), 3–6 cm long, 1–1.5 cm wide, minutely and sharply serrate, glabrous except on midrib below, with many lateral, 1–4-forked veins; fertile leaflets somewhat narrower and more widely spaced along rachis. Sori along margin except very near apex; indusium ± tubular, stalked; receptacle exserted, about as long as tube. *Croat 5046.*

Occasional, in ravines on steep banks.

Throughout the American tropics. In Panama, known only from tropical moist forest in the Canal Zone and Panamá and from tropical wet forest in Panamá.

Trichomanes polypodioides L., Sp. Pl. 1098. 1753

Small epiphyte; rhizome slender, creeping, scaly. Leaves simple, very thin, irregularly pinnatifid, the segments lobed, 3–12 cm long, 1.5–2.5 cm wide, oblong to ovate in outline with light-brown, stellate scales on margin and surface; midrib extending to apex with lateral veins at each lobe, these sometimes 1- or 2-forked. Sorus solitary, mostly at apex of lobes or rarely in sinuses; indusium immersed, lacking dark-edged lips but with stellate trichomes on margin, the receptacle long-exserted, often many times longer than involucre. *Croat 11232.*

Distribution on BCI not known. Found on moist tree trunks.

Throughout the American tropics. In Panama, known from tropical moist forest in the Canal Zone (BCI only), Colón, and Panamá, from premontane wet forest in Chiriquí and Panamá, and from tropical wet forest in Panamá (Campo Tres).

Trichomanes punctatum Poir. subsp. **sphenoides** (Kunze) Wessels-Boer, Acta Bot. Neerl. 11:301. 1962

Tiny epiphyte; rhizome creeping, slender, densely scaly, the scales dark reddish-brown, threadlike, deciduous. Leaves simple, entire or with short lobes, sometimes split when dry; petioles very short, scaly; blades round-oblong, ovate or obovate, rounded at apex, acute to subcordate at base, 5–20 mm long, 5–15 mm wide, with stellate scales on margin, midrib lacking, the veins very densely flabellate, the margin entire or with a few ± linear lobes or regularly crenate. Sori few to several, arising from between the lobes; indusium about half immersed, the involucres contracted at neck, the lips circular, narrowly dark-edged, as broad as tube. *Croat 14021.*

Distribution on the island is uncertain.

Very similar to *T. curtii* Ros. (not known from BCI; see the key to the genus).

Throughout Central America and northwestern South America; Greater Antilles. In Panama, known from tropical moist forest on BCI and in Bocas del Toro, Colón, Coclé, and Panamá.

8. PARKERIACEAE

Homosporous, aquatic or subaquatic annuals; rhizomes short, ± erect. Leaves alternate, dimorphic, pinnately decompound, the fertile blades erect, repeatedly pinnate-pinnatifid, larger than sterile blades and more finely dissected, the leaflets longer and narrower; veins areolate, included; veinlets absent. Sporangia borne in 1 or 2 sparse rows usually along the margin, globose, ± sessile, thin-walled, protected by continuous revolute margins; annulus complete or vestigial; spores triplanate.

Recognized by their aquatic habitat, by their decompound, dimorphic leaves, and by sporangia that develop only when the plants are emergent or floating on the surface of the water (Schulthorpe, 1967).

One genus, with 2 species; tropics and subtropics.

CERATOPTERIS Brongn.

Ceratopteris pteridoides (Hook.) Hieron., Bot. Jahrb. Syst. 34:561. 1905

Plant floating or partly submerged, usually anchored in soil, the roots borne on the stipe. Leaves very thin, simple, dimorphic, usually glabrous; sterile leaves ± pentagonal, to 25 cm long, about as broad, expanded at about the middle and deeply divided (appearing 2–4-pinnatifid), the ultimate segments mostly 3–10 mm broad, blunt to rounded at apex; leaves of floating plants usually with bulbous stipes; fertile blades to 40 cm long, divided as in sterile blades but with segments more than 2 mm wide, the margins evenly and narrowly revolute. Sporangia large, globose, borne in 1 row along each margin. *Shattuck 606.*

Collected once by Shattuck; not collected on BCI in recent years, but probably still occurs there. Seen fertile in July.

Florida, Panama, the Guianas, and Brazil; Greater Antilles. In Panama, known from tropical moist forest in the Canal Zone on the Atlantic slope and from Bocas del Toro.

9. CYATHEACEAE

Mostly arborescent, homosporous; rhizomes usually simple, decumbent or erect, scaly. Leaves borne at apex, articulate or not, 1–4-pinnate, usually very large, lanceolate-oblong to deltoid-ovate in outline. Sori indusiate or exindusiate, ± globose, borne on veins of underside of blades; sporangia numerous, crowded, radial, in several ranks, the annulus oblique; spores triplanate.

Except for the atypical *Metaxya rostrata,* members of the family on BCI are characterized by being arborescent with large, graceful, compound leaves. They are most readily confused with large, compound-leaved members of the Polypodiaceae (10), but can be distinguished from them by having sporangia with an oblique annulus.

Nine genera and 750 species; tropical regions.

KEY TO THE SPECIES OF CYATHEACEAE

Leaves 1-pinnate ..... *Metaxya rostrata* (Willd.) Presl
Leaves 2- or 3-pinnate-pinnatifid:
  Sori along margins of pinnatifid lobes of leaflets; leaflets nearly glabrous; lobes divided about halfway to midrib, often 8 mm or more broad ..... *Cnemidaria petiolata* (Hook.) Copel.
  Sori clustered at base of lobes or covering most of the lower surface; leaflets with at least the midrib pubescent; lobes divided nearly to base, usually less than 3 mm wide:
    Leaflets pubescent over all of upper surface with sparse, conspicuous, long trichomes; pubescence of rachis and pinnular rachis conspicuous, erect, 1–3 mm long ..... *Trichopteris trichiata* (Max.) Tryon
    Leaflets glabrous on upper surface or with few trichomes on midrib of segments; pubescence of rachis and pinnular rachis inconspicuous, appressed or very sparse:
      Petiole, rachis, and pinnular rachis armed with spines; leaflets lacking stellate trichomes on lower surface; sori exindusiate ..... *Trichopteris microdonta* (Desv.) Tryon
      Petiole, rachis, and pinnular rachis unarmed; leaflets bearing purplish stellate trichomes on lower surface; sori indusiate ..... *Nephelea cuspidata* (Kunze) Tryon

CNEMIDARIA Presl

Cnemidaria petiolata (Hook.) Copel., Gen. Fil. 97. 1947
Hemitelia petiolata Hook.

Small, spiny tree fern, 1.5–3.5 m tall, often fertile when trunk is still very short; trunk to 5 cm diam, conspicuously ribbed and with persistent petiole bases much of its length; leaf scars prominent, the cluster of new leaf crosiers densely scaly. Juvenile plants bearing leaves 1-pinnate, the leaflets with rounded, sharply serrate lobes; mature plants bearing leaves 2-pinnate-pinnatifid, to ca 2 m long, arch-ascending; petioles 50–75 cm long, with lanceolate-linear, brown to reddish-brown scales ca 1 cm long on upper side usually near base, armed throughout but especially on lower side with short spines to ca 5 mm long; rachis pubescent with stiff trichomes on upper surface, sometimes also on upper midrib of leaflets; leaflets usually 5–15 cm long, 1–3 cm wide at base, tapering to acuminate apex, ± regularly lobed approximately halfway to midrib, less so near apex, nearly glabrous; upper leaflets reduced, ultimately confluent. Sori marginal, round, bordering entire leaflet, at least part of the cup-shaped indusium persisting. *Croat 4143.*

Common in the forest, especially in ravines. May be found in fertile condition throughout the year.

Panama and Colombia. In Panama, common in some areas of tropical moist forest on the Atlantic slope at least in the Canal Zone, Colón, and San Blas; known also from tropical moist forest in Panamá and tropical wet forest in Colón and along the Darién–San Blas border.

See Figs. 8 and 9.

METAXYA Presl

Metaxya rostrata (H. & B. ex Willd.) Presl, Tent. Pterid. 60. 1836
Alsophila rostrata Mart.

Terrestrial, lacking a trunk; rhizome with a single siphonostele, densely pubescent with long yellowish trichomes (also a few at base of petiole). Leaves 1-pinnate, to ca 2 m long but arch-ascending, the apex usually drooping; petioles ca 50 cm long; rachis yellowish, dull; leaflets linear-oblong, caudate-acuminate, acute to obtuse and sometimes inequilateral at base, 10–32 cm long, 2–3.5 cm wide, the veins free or forked once usually near midrib, the margin entire except crenate near apex. Sori ± round, on veins in an irregular pattern on either side of midrib. *Croat 9527.*

Rare, seen only twice; probably restricted to ravines. Apparently fertile throughout the year.

Easily confused in sterile condition with *Saccoloma elegans* (10. Polypodiaceae), which has marginal sori, but distinguished by having the margins entire (except near apex), the veins rarely forked (except near base), the rachis yellowish and dull, and the rhizome clothed with dense yellow trichomes.

Guatemala to Peru, Bolivia, and Brazil; West Indies. In Panama, known from tropical moist forest on the Atlantic slope in the Canal Zone, Bocas del Toro, and Colón; known also from tropical moist and premontane wet forests in Panamá.

See Fig. 10.

NEPHELEA Tryon

Nephelea cuspidata (Kunze) Tryon, Contr. Gray Herb. 200:40. 1970
Cyathea punctifera H. Christ

Graceful tree fern, to 7(15) m tall; trunk to 20(40) cm diam; trunk and petioles with a few spines to 1 cm long, the spines embedded in a dense layer of irregularly serrate scales and adventitious roots. Leaves 2-pinnate-pinnatifid, to ca 3 m long and 1.5 m or more wide; petiole and rachis atropurpureous, with short, dense, almost granular scales (easily scraped off) especially on underside, the petiole to 50 cm long; pinnular rachis and costules densely pubescent with purplish ascending trichomes; pinnae to ca 1 m long and 30 cm wide; leaflets pinnatifid to near midrib, to 11.5(15) cm long and to 2.5(3.5) cm wide, tapered to a

Fig. 8. *Cnemidaria petiolata*

Fig. 9. *Cnemidaria petiolata*

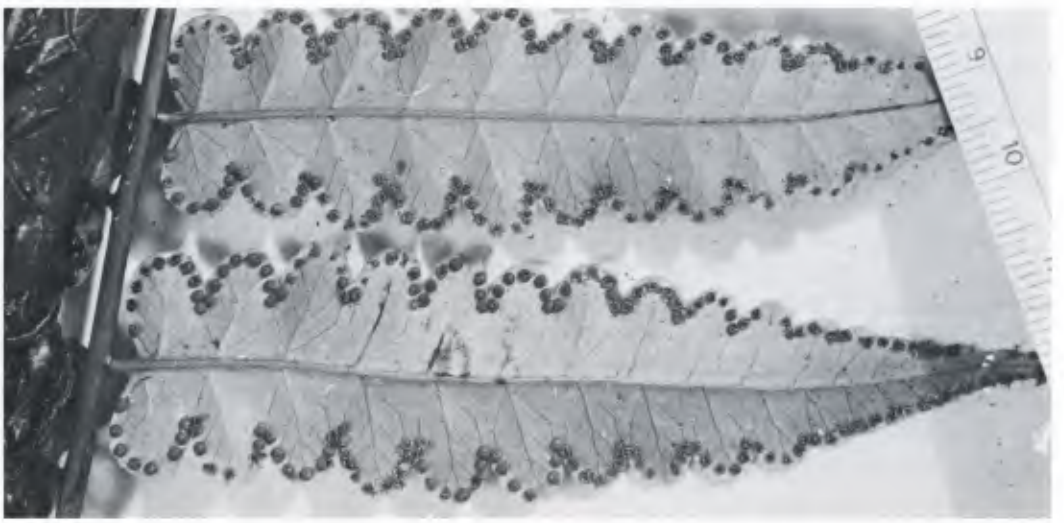


Fig. 10. *Metaxya rostrata*

Fig. 11. *Nephelea cuspidata*

long, bluntly acuminate apex, the lobes 2–3 mm wide, somewhat falcate, entire to minutely crenate; veins mostly 1-forked near base, the major veins sparsely pubescent beneath with purplish, mostly stellate scales. Sori round, usually 4–6, clustered in proximal half of lobes; indusium globose to urn-shaped, dark brown, completely enclosing sporangia, breaking into irregular segments at maturity, deciduous to persistent, scarious. *Croat 6529.*

Rare on the island, restricted to deep ravines. Seasonal behavior undetermined. Seen fertile in April, August, and September.

Nicaragua to Peru, Bolivia, Paraguay, and Brazil. In Panama, known only from tropical moist forest on BCI and in Darién.

See Fig. 11.

TRICHOPTERIS Presl

Trichopteris microdonta (Desv.) Tryon, Contr. Gray Herb. 200:46. 1970

Alsophila microdonta Desv.

Tree fern, 1–5 m tall, slender, the trunk only a few cm diam. Leaves few, 2-pinnate-pinnatifid; petioles to ca 1 m long, lustrous, purplish near base, becoming light brown, glabrate, sparsely scaly near base and bearing numerous distant, narrowly conical spines, these curved and to 1 cm long; scales to ca 1.5 cm long and 2 mm wide, brown, very long-caudate-acuminate; leaves ovate-oblong, abruptly acuminate, to 1.5 m long and 1.2 m broad, the primary rachis brown or yellowish-brown, armed throughout; pinnae petiolate, narrowly oblong, acuminate, 30–60 cm long, 10–25 cm wide; secondary rachis yellowish-strigose above, thinly scurfy-hirtellous below (glabrate in age), distantly aculeate with spines to ca 4 mm long; leaflets ± sessile, ± oblong, long-attenuate, 5–13 cm long, 1.5–3 cm wide, the costa densely yellowish-strigose above, scurfy-hirtellous and with a few minute, mostly caducous scales below, the segments of 19–25 pairs, linear, ± acute, 8–18 mm long, 2–4 (5) mm wide, crenate-serrate, the costules distantly hispid above, thinly scurfy-hirtellous below. Sori in 6–11 pairs, the paraphyses very numerous, equaling sporangia. *Kenoyer 7, Munch s.n.*

Apparently rare, in ravines; more common elsewhere in the Canal Zone.

Mexico to Peru and Brazil, principally at low elevations; West Indies (Isle of Pines). In Panama, known only from tropical moist forest in the Canal Zone.

Trichopteris trichiata (Max.) Tryon, Contr. Gray Herb. 200:44. 1970

Alsophila trichiata Max.

Graceful tree fern, to 3.5 m tall. Leaves 2- or 3-pinnate-pinnatifid on lower parts of large leaves, to 3.5 m long and 2 m wide at the middle; petioles densely pubescent with moderately stiff trichomes, sparsely armed throughout with short spines; rachis with short, soft, villous pubescence interspersed with long, stiff, jointed trichomes; pinnae lanceolate to oblong-lanceolate, 50–90 cm long, to 30 cm wide, abruptly acuminate and confluent toward apex; leaflets sessile, linear-lanceolate, attenuate-caudate, pinnatifid to beyond the middle, mostly to 9 (15) cm long, to 2 cm wide, both surfaces pubescent especially on veins, the segments 5–10 mm long, 1.5–3 mm wide, usually bidentate at apex. Sori exindusiate, round, on veinlets on proximal two-thirds of lobes, consisting of moderately few sporangia; paraphyses few, scarcely exceeding sporangia. *Croat 11729.*

Apparently rare; collected once on Gross Point Peninsula (*Croat 11729*) and twice elsewhere by Shattuck (*740, 1149*). Probably fertile throughout the year.

The generic name *Trichipteris,* used by some authors, is an orthographic error.

Costa Rica to Ecuador and Venezuela, from near sea level in Costa Rica to ca 1,000 m in Ecuador. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién and from premontane wet forest in the Canal Zone and Panamá.

10. POLYPODIACEAE

Terrestrial or epiphytic (rarely aquatic), homosporous; rhizomes creeping to erect. Leaves pendent to spreading or erect, usually petiolate; blades uniform to strongly dimorphic, simple to multiply pinnate or pinnatifid or further compounded, coiled in bud. Sori various in shape and arrangement on veins on underside of blades, usually in lines or clusters, sometimes over the whole surface; indusia various or lacking, developing from veins or margins of blades; sporangia long-stalked, bearing an incomplete vertical annulus, opening transversely; prothallia green.

About 150 genera and 6,000 species; worldwide. A very diverse family, frequently split into a variety of subfamilies or separate families.

All genera of the Polypodiaceae are keyed out in the key to the Pterophyta (p. 71).

ACROSTICHUM L.

Acrostichum aureum L., Sp. Pl. 1069. 1753

Helecho de manglar

Massive aquatic, to 3 m tall with a stout, scaly rhizome. Leaves 1-pinnate; petioles stout, ribbed, much shorter than the rachis, with large ligulate scales at base; leaflets narrowly oblong, rounded to acute or mucronate at apex, stiff, to 25 cm long and 4 cm wide, revolute and entire, mostly 2–6 cm apart near apex, the veins prominent but glabrous and scarcely if at all raised below. Sporangia covering all or part of underside of uppermost leaflets. *Croat 5288.*

Common in dense stands, chiefly on the south and west shores of the island. No doubt an important element in hydrarch succession along the southern shore, where it forms dense stands in association with *Annona glabra* (55. Annonaceae).

KEY TO THE SPECIES OF ACROSTICHUM

Leaf veins glabrous, scarcely if at all raised ..... *A. aureum* L.
Leaf veins at least partly pubescent, standing up sharply ..... *A. danaifolium* Langsd. & Fisch.

Throughout tropical America. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Panamá, and Darién and from tropical wet forest in Colón (Miguel de la Borda).

See fig. on p. 12.

Acrostichum danaifolium Langsd. & Fisch., Icon. Fil. 5, t. 1. 1810

Very similar to *A. aureum,* but the fertile leaves having more of their leaflets fertile; and the leaflets 1–4 cm apart near apex, pubescent at least on the veins, and the veins beneath raised. *Croat 6165.*

Found with *A. aureum* along the shore of the island.

Throughout tropical America. In Panama, known only from BCI and the Pacific slope of the Canal Zone and in Panamá.

ADIANTUM L.

The genus *Adiantum,* distinguished by its oblique leaflets and indusiate marginal sori, provides the dominant terrestrial fern flora on the island.

Adiantum decoratum Max. & Weath., Amer. J. Bot. 19:165. 1932

Terrestrial, to 70 cm tall; rhizome ± erect, with dense linear scales. Leaves 2-pinnate; petiole, rachis, and pinnular rachis with long, conspicuous, ± dense, filiform scales; petioles as long as or longer than blades; leaflets asymmetrical (the midrib nearly submarginal), ± oblong, blunt at apex, truncate and parallel to rachis at base, to 2.5 cm long and 8 mm wide, glabrous, usually glaucous beneath, the sterile margins irregularly, finely serrate. Sori interrupted along upper and distal margins. *Shattuck 282.*

Rare, in the forest.

Mexico to Panama. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Los Santos, Panamá, and Darién and from premontane wet forest in Panamá (Cerro Azul).

Adiantum fructuosum Spreng., Syst. Veg. 4:113. 1827

Terrestrial, rarely taller than 50(80) cm. Leaves usually several, closely clustered on a short-creeping, scaly rhizome, usually 1-pinnate (often 2-pinnate elsewhere);

KEY TO THE SPECIES OF ADIANTUM

Leaflets borne on slender stalks more than 7 mm long:
  Leaflets ± reniform, rounded at apex, usually less than 4 cm long on stalks less than 2.5 cm long ..... *A. lunulatum* Burm.
  Leaflets ± ovate, acuminate, usually more than 5 cm long on a stalk more than 3 cm long ..... *A. seemannii* Hook.
Leaflets not borne on stalks more than 7 mm long:
  Sori continuous along margins:
    Leaflets more than 5 cm long, narrowly triangular; sori continuous along upper and lower margins ..... *A. lucidum* (Cav.) Sw.
    Leaflets less than 3 cm long, ± falcate; sori continuous on upper margin, sometimes with a shorter segment on the distal edge, lacking on lower margin ..... *A. pulverulentum* L.
  Sori interrupted along margins:
    Rachis bearing long, conspicuously spreading, threadlike scales, clearly visible to the naked eye, these interspersed with shorter, fine scales:
      Leaflets pubescent beneath ..... *A. humile* Kunze
      Leaflets glabrous beneath ..... *A. decoratum* Max. & Weath.
    Rachis lacking clearly visible scales or bearing scales ± appressed, not spreading, and less conspicuous:
      Sterile leaflets unevenly and coarsely serrate on upper and distal margins, the apex usually blunt to rounded ..... *A. fructuosum* Spreng.
      Sterile leaflets evenly and usually finely serrate or biserrate:
        Leaflets not glaucous beneath, the sterile ones usually acute to acuminate ..... *A. obliquum* Willd.
        Leaflets glaucous beneath (fertile leaflets sometimes pubescent on inner margin), the sterile ones usually blunt at apex:
          Leaflets pubescent beneath (often nearly glabrous on juvenile or sterile leaflets), usually not tapered much to apex ..... *A. humile* Kunze
          Leaflets usually glabrous beneath, usually much broader at base than apex ..... *A. petiolatum* Desv.

petiole and rachis dark brown, with fine, short threadlike scales persisting at least on rachis; leaflets nearly oblong, blunt to acute at apex, 1–3 cm long, glabrate beneath (elsewhere sometimes with filiform scales), midrib very near lower margin, the lower edge ± straight, the proximal edge paralleling the rachis, the upper and distal edges of sterile leaflets unevenly and coarsely serrate. Sori interrupted along upper and distal margins. *Croat 8576.*

Occasional, in the forest.

Distinguished by its small, coarsely serrate leaflets. The species is easily confused with and possibly not separable from *A. tetraphyllum* H. & B. ex Willd., which has a long-creeping rhizome with the petiole bases not closely crowded as in *A. fructuosum.* Moreover, in *A. tetraphyllum* the sterile apices of the leaflets are acute and turned toward the apex of the pinnae, whereas in *A. fructuosum* they are mostly straight and obtuse.

Mexico to Brazil; West Indies. In Panama, known from tropical moist forest in the Canal Zone, San Blas, Panamá, and Darién, from premontane wet forest in Panamá and Coclé, and from tropical wet forest in Colón.

See Fig. 12.

Adiantum humile Kunze, Linnaea 9:80. 1834

A. killipii Max. & Weath.

Terrestrial, usually less than 50 cm tall. Leaves 2-pinnate; petioles shiny and atropurpureous; rachis similar but usually covered with two types of scales—small, fine, ± appressed scales and longer, subulate-filiform scales; leaflets asymmetrical, mostly 1–3 cm long, acute at base, the lateral leaflets ± oblong or sometimes broader at the base with apex usually rounded and the proximal edge nearly paralleling the rachis, the lower surface usually glaucous and usually bearing numerous to few simple trichomes and sometimes filiform scales; sterile leaflets finely and evenly serrate. Sori interrupted along inner, upper, and outer margins, frequently fertile at apex. *Croat 8553.*

Occasional, along trails in the forest.

Belize to Peru, Brazil, and French Guiana; Trinidad. In Panama, known from tropical moist forest on the Atlantic slope of the Canal Zone and in San Blas, and from premontane wet forest in Panamá (Lago Cerro Azul).

See Fig. 13.

Adiantum lucidum (Cav.) Sw., Syn. Fil. 121. 1806

Terrestrial, to 70 cm tall; rhizome moderately short-creeping with slender spreading scales. Leaves usually few, 1-pinnate or rarely 2-pinnate; petiole and rachis dark brown or black, persistently pubescent-scaly (at least on rachis); leaflets asymmetrical, usually 5–10 cm long, ± narrowly triangular, acuminate at apex, markedly inequilateral at base, glabrous or sparsely scaly below; sterile leaflets with margins unevenly and coarsely serrate but the proximal third of lower margin as well as the proximal margin entire; terminal leaflet ± ovate. Sori very long and continuous on upper and lower margins (except near apex). *Croat 7731.*

Abundant in the forest.

Distinguished by its long pointed leaflets bearing sori along most of both margins. Tryon (1964) reported the species to be 2-pinnate in Peru, a condition that is rare in Panama.

Panama to Peru and the Guianas; Trinidad and Tobago. In Panama, known from tropical moist forest on both slopes of the Canal Zone and in Panamá and Darién, from premontane moist forest in the Canal Zone (Ancón Hill), and from tropical wet forest in Colón.

See Fig. 14.

Adiantum lunulatum Burm., Fl. Ind. 235. 1768

Terrestrial, to 55 cm tall; rhizome erect, with a few dark, lanceolate-linear scales. Leaves 1-pinnate; petiole and rachis dark reddish-brown, shiny; petiolules slender, 0.3–2.5 cm long; leaflets lunate to reniform, lobed on semicircular distal edge, truncate to obtuse on lower edge, to 4 cm long and 1.8 cm wide, glabrous. Sori interrupted along lobes on distal edge. *Shattuck 1058.*

Rare, in the forest.

This species has been confused with the name *Adiantum philippense* L., which should probably be considered a *nomen dubium.*

Mexico to Colombia and Venezuela; West Indies. In Panama, known from tropical moist forest on both slopes of the Canal Zone and in Veraguas; known also from premontane moist forest in Panamá (Panamá City) and from premontane wet forest in Chiriquí, Coclé, and Panamá.

Adiantum obliquum Willd., Sp. Pl. 5:429. 1810

Terrestrial, to 60 cm tall. Leaves mostly 2-pinnate, a few 1-pinnate; petiole atropurpuraceous, sparsely to moderately scaly at least when young, the threadlike, curly scales persisting on rachis; leaflets asymmetrical, mostly 3–6.5 cm long, seldom more than 1.5 cm wide, narrowly tapered, the apex acute to acuminate, the lower edge nearly straight, the proximal edge nearly paralleling the rachis, the underside not glaucous, the sterile margins unevenly and finely biserrate. Sori interrupted along upper and distal margins with the apex usually sterile. *Croat 7815.*

Occasional, along forest trails and no doubt also in other areas of the forest.

Often confused with *A. petiolatum,* but differing in having the leaflets more narrowly triangular and irregularly serrate and in having the apex of the fertile leaflets free of sori and tapered to a sharp point. The leaflets of *A. petiolatum* are glaucous beneath, with the inner edge frequently cordate.

Throughout the West Indies and Central America, as well as from Colombia to Bolivia, Brazil, and the Guianas. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Darién and from premontane wet forest in Panamá (Chimán).

Fig. 12. *Adiantum fructuosum*

Fig. 13. *Adiantum humile*

Fig. 14. *Adiantum lucidum*

Fig. 15. *Adiantum petiolatum*

Fig. 16. *Anetium citrifolium*

Fig. 17. *Asplenium delitescens*

Adiantum petiolatum Desv., Ges. Naturf. Freunde Berl. Mag. 5:326. 1811

Terrestrial, to 40 cm tall; rhizome with spreading scales, the petiole bases closely spaced. Leaves 1- or 2-pinnate; petioles dark, glabrate; leaflets asymmetrical, obscurely triangular to oblong, rounded to bluntly acuminate at apex, mostly 2–5 cm long, 1–3.5 cm wide, the proximal edge frequently semicordate and overlapping the rachis at base, usually glaucous and glabrous beneath, the sterile margins evenly and finely serrate. Sori interrupted along upper, lower, and sometimes proximal margins, frequently extending to very near the apex. *Croat 6948.*

Common on trails in the forest and at the edge of clearings.

See the discussion of *A. obliquum* for a comparison of the two species.

Mexico to Peru, Bolivia, and Brazil; West Indies. In Panama, known from tropical moist forest in the Canal Zone (BCI and the Pacific slope), Herrera, Panamá, and Darién and from tropical dry forest in Panamá (Taboga Island).

See Fig. 15.

Adiantum pulverulentum L., Sp. Pl. 1096. 1753

Terrestrial, to 1 m tall. Leaves 2-pinnate; petiole and rachis dark reddish-brown, densely pubescent-scaly, the scales fine and curly; leaflets asymmetrical, 1.5–3 cm long, usually of about equal width throughout but gradually curved upward to the sharply toothed, ± acute apex, the lower edge entire and usually straight, the proximal edge ± paralleling rachis, glabrate to scaly beneath, the sterile leaflets and apex of the fertile leaflets coarsely serrate. Sorus 1 (rarely 2), long, on upper margin, with occasionally a shorter one on outer margin. *Croat 4340.*

Occasional, in the forest.

Distinguished by the long sorus on the upper edge of each leaflet.

Mexico to Colombia, Bolivia, Brazil, and the Guianas; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién, from premontane wet forest in Colón and Panamá, and from tropical wet forest in Colón.

Adiantum seemannii Hook., Species filicum 2(5):81A. 1851

Terrestrial, usually to about 50 cm tall; rhizome short-creeping, densely scaly. Leaves 1- or 2-pinnate; petiole, rachis, and petiolules blackish and shiny; leaflets ovate, acuminate at apex, oblique and obtuse to truncate or cordate at base, to 9 cm long and 7 cm wide, glabrous and glaucous beneath, the sterile margins coarsely and unevenly serrate; petiolules slender, 2–7 cm long. Sori interrupted along margin. *Aviles 79.*

Uncommon to rare, in the forest.

Not confused with any other species on the island. Distinguished by its large, ovate, long-petiolate leaflets.

Mexico to Colombia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién, from premontane moist forest in Panamá (Panamá City), and from premontane wet forest in Chiriquí.

ANANTHACORUS Und. & Max.

Ananthacorus angustifolius (Sw.) Und. & Max., Contr. U.S. Natl. Herb. 10:487. 1908

Epiphyte; rhizome moderately short with many fine rootlets densely covered with threadlike, reddish-brown scales; rhizome scales linear-lanceolate, attenuate, clathrate, iridescent. Leaves simple, entire, sessile, ± linear, tapering gradually at both ends, mostly 10–30 cm long, 1–1.5 cm wide (the sterile leaves shorter and relatively broader), ± thick, glabrous to minutely scaly. Sori exindusiate, in continuous or irregularly interrupted lines very near margins. *Croat 4367.*

Occasional, in the forest, usually on smaller trunks and branches moderately near the ground.

Throughout much of tropical America. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Veraguas, and Darién, from premontane wet forest in Chiriquí and Panamá, and from tropical wet forest in Panamá.

ANETIUM (Kunze) Splitg.

Anetium citrifolium (L.) Splitg., Tijdschr. Natuurl. Gesch. Physiol. 7:395. 1840

Epiphyte with a creeping, scaly rhizome; rhizome scales broadly ovate-attenuate, clathrate, iridescent with short-ciliate margins; petioles well spaced with many fine rootlets densely covered with threadlike scales. Leaves simple, entire, glabrous, sessile or nearly so, oblanceolate to obtuse, abruptly acuminate at apex (round on juveniles), gradually tapered to base, usually less than 15 cm long and 4 cm wide, thick, the midrib indistinct except at base, the veins anastomosing. Sporangia scattered chiefly on veins, forming a reticulum. *Croat 11703.*

Infrequent, in the forest, usually on tree trunks very near the ground; often on stilt roots of *Scheelea zonensis* (19. Palmae). Tryon (1964) reported seeing leaves to 100 cm long.

Throughout tropical America. In Panama, known from tropical moist forest on both slopes in the Canal Zone and from tropical wet forest in Veraguas (Atlantic slope) and Colón (Portobelo).

See Fig. 16.

ASPLENIUM L.

The genus occurs in epiphytic habitats similar to those of *Polypodium.* It can be distinguished by its elongate indusiate sori along major veins on the underside of leaves. Most species have oblique leaflets.

KEY TO THE SPECIES OF ASPLENIUM

Leaves simple ..... *A. serratum* L.
Leaves 1-pinnate:
  Leaflets usually more than 6 cm long:
    Plants epiphytic; terminal leaflet similar to lateral leaflets, not pinnatifid ..... *A. falcinellum* Max.
    Plants terrestrial or epipatric (on rocks); terminal leaflet unlike lateral leaflets, pinnatifid .....
    ..... *A. delitescens* (Max.) A. R. Smith
  Leaflets mostly less than 6 cm long:
    Stipe and lower rachis dark purplish, shiny; proximal half of lower edge of leaflet frequently entire ..... *A. laetum* Sw.
    Stipe and lower rachis not dark purplish and shiny; proximal half of lower edge of leaflet usually toothed:
      Veins mostly 1- or 2-forked; blades not very thin .....
      ..... *A. auritum* Sw. var. *auriculatum* (Hook.f.) Mort. & Lell.
      Veins nearly all simple; blades thin ..... *A. pteropus* Kaulf.

Asplenium auritum Sw. var. **auriculatum** (Hook.f.) Mort. & Lell., Mem. New York Bot. Gard. 15:19. 1966

Epiphyte, to 35 cm tall. Leaves 1-pinnate, glabrous; leaflets oblong, reduced above and tapered to a narrowly rounded apex, usually with a small auricle on upper side near base, to 3 cm long, less than 1 cm wide, the margins finely and ± irregularly serrate or the proximal one-fourth of the lower edge entire, the veins mostly 1- or 2-forked. Sori several, oblong, 2–5 mm long, along upper edge of lateral veins, sometimes also on auricle, sharply oblique to midrib; indusium ± lunate, thin. *Croat 11293.*

Uncommon, on trees (seen mostly near the ground) or on rocks, within the forest.

Throughout much of tropical America. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién, from premontane wet forest in Chiriquí, Coclé, and Panamá, from tropical wet forest in Colón, Chiriquí, and Darién, and from lower montane wet and lower montane rain forests in Chiriquí.

Asplenium delitescens (Max.) A. R. Smith, Amer. Fern J. 66:120. 1976

Diplazium delitescens Max.

Terrestrial, to 35(43) cm tall; rhizome short-creeping, with minute, dark, fibrous scales, the petiole bases closely spaced. Leaves few, 1-pinnate; petioles 4.5–20 cm long, with a few scales similar to rhizome scales near base; lateral leaflets mostly narrowly lanceolate, gradually long-acuminate, inequilateral at base with the lower proximal edge acute and the upper proximal edge obtuse to truncate and nearly paralleling rachis, 3–12 cm long, 1–2 cm wide, irregularly serrate, sometimes with a small auricle on upper side; veins 3- or 4-forked; terminal leaflet pinnatifid. Sori linear along upper branch of lateral veins, slightly curved, nearer midrib than margin, usually on distal side of veins, much less frequently on both sides; indusia thin, broad, ending abruptly. *Croat 8643.*

Occasional, in the forest, especially older forest.

Its terrestrial habitat, nonclathrate rhizome scales, and pinnatifid terminal leaflet (unlike the lateral ones) distinguish it from *Asplenium falcinellum,* which has a similar leaflet shape. *A. falcinellum,* an epiphyte, has clathrate rhizome scales and a conform terminal leaflet.

Belize to Panama. In Panama, known from tropical moist forest in the Canal Zone (Pacific slope), Panamá, and Darién and from premontane moist forest in Panamá.

See Fig. 17.

Asplenium falcinellum Max., Contr. U.S. Natl. Herb. 13:14. 1909

Epiphyte, to 40 cm long, at least sometimes pendent; rhizome scales clathrate. Leaves 1-pinnate, few; petioles mostly 8–10 cm long, ± glabrous; leaflets in 7–12 pairs, narrowly lanceolate, gradually long-acuminate, equally or inequilaterally acute at base (the lower side often more acute than the upper), 6–11 cm long, 9–20 mm wide, entire or irregularly and inconspicuously crenate, the terminal leaflets much like the lateral ones. Sori linear, subequal, on distal side of lateral veins. *Croat 12562.*

Infrequent, along trails in the old forest.

See the discussion of *Asplenium delitescens* for a comparison of the two species.

Guatemala to Panama; near sea level to reportedly 1,200 m. In Panama, known from tropical moist forest in the Canal Zone (on and adjacent to BCI), from premontane wet forest in Veraguas, and from tropical wet forest in Colón (Santa Rita Ridge) and Panamá.

Asplenium laetum Sw., Syn. 79:271. 1806

Epiphyte, usually 25–50 cm tall. Leaves 1-pinnate; petiole and base of rachis atropurpureous and shiny; blades reduced toward apex and tapered to a slender tip; leaflets ± oblong, very unequal at base, the lower edge straight to curved, entire, the proximal margin nearly paralleling rachis, the upper and distal margins serrate, the upper margin infrequently auriculate, 2–6 cm long, 8–15 mm wide, the veins simple or 1-forked. Sori several, linear-oblong, on upper side of lateral veins oblique to midrib, mostly on distal half of leaflets; indusium thin. *Croat 8475.*

Occasional, on rocks in stream beds of larger ravines; locally abundant.

Mexico to Paraguay and Venezuela; the Antilles. In Panama, known from tropical moist forest in the Canal Zone (BCI), Bocas del Toro, and Panamá and from tropical wet forest in Colón.

Asplenium pteropus Kaulf., Enum. Fil. 170. 1824

Epiphyte, to 20 cm tall. Leaves 1-pinnate; petiole and rachis with a narrow strip of foliaceous tissue on either side; leaflets oblong-elliptic, acute at apex, unequal at base with a slight auricle on upper side, 1.5–2.5 cm long, ca 8 mm wide, thin, deeply and ± evenly serrate, the veins nearly all simple. Sori several, oblong, on distal side of lateral veins oblique to midrib, usually in all but basal and apical fourth of leaflets.

Reported by Standley, but no specimens were cited and none has been seen from the island. The species has been seen in Frijoles (*Killip 12151*) and could very easily be overlooked.

Easily distinguished by the thin, deeply serrate leaflets with free veins and by the narrowly margined petiole and rachis.

Guatemala south to Venezuela, Brazil, and Bolivia. In Panama, known from lower montane wet forest (usually above 1,000 m) in Chiriquí and Darién (Cerro Pirre); known also from tropical moist forest on BCI and in San Blas and from premontane wet forest in Panamá (Cerro Campana).

Asplenium serratum L., Sp. Pl. 1079. 1753

Epiphyte, to 70 cm tall; rhizome densely scaly, the scales reddish-brown, threadlike. Leaves simple; petioles to 3 cm long, canaliculate; blades oblanceolate, acute at apex, tapered at base, to 70 cm long and 9 cm wide, glabrous except for scales on lower midrib, the scales ± lanceolate, peltate, brown, the midrib raised above, the veins mostly free or branched once. Sori many, linear along distal edge of lateral veins oblique to midrib, of irregular lengths, mostly in midsection of leaf; indusium slender, thin. *Croat 9443.*

Uncommon, on tree trunks in the forest, near the ground or moderately high on the trunks.

Easily distinguished by its simple blade with slender, oblique sori and by its epiphytic habit.

Mexico to Bolivia; the Antilles. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién, from premontane wet forest in Colón and Panamá, and from tropical wet forest in Colón, San Blas, Coclé, and Panamá.

BLECHNUM L.

Blechnum occidentale L., Sp. Pl. ed. 2, 1524. 1763

Terrestrial, 10–100 cm tall; rhizome densely covered with reddish-brown fibrous scales, the lowest part of stipe with lanceolate-linear scales to ca 1 cm long, the scales basifixed with a small auricle. Leaves 1-pinnate, slightly dimorphic; petiole and rachis glabrate or granular-scaly, also sometimes with a few larger lanceolate-linear scales, the petiole 1–35 cm long; leaflets sessile, stiff, confluent, very tapered at apex; sterile leaflets lanceolate-elliptic, acuminate, truncate to subcordate at base, to 7 cm long and 2 cm wide, crenulate to usually entire, not articulate; fertile leaflets similar except longer (to 15 cm long) and narrower (to 1.5 cm wide), curved upward and often very weakly auriculate on lower edge near rachis. Sori continuous along either side of the midrib, usually from or near base to near apex, sometimes along the rachis as well and rarely ± perpendicular to the midrib on the auricle; indusium thin, brown, directed toward the midrib. *Croat 6981.*

Locally abundant on steep exposed banks in the Laboratory Clearing and on eroded shores on the north and east sides of the island.

Widespread in New World tropics and subtropics. In Panama, widespread and ecologically variable; known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, Veraguas, Los Santos, Herrera, Panamá, and Darién, from premontane moist forest in the Canal Zone, from premontane wet forest in Chiriquí, Coclé, and Panamá, from tropical dry forest in Coclé, from tropical wet forest on the Atlantic slope in Veraguas, and from lower montane wet and lower montane rain forests in Chiriquí.

Blechnum serrulatum L. C. Rich., Actes Soc. Hist. Nat. Paris 1:114. 1792

Similar to *B. occidentale,* but having the leaflets serrulate usually throughout (at least near apex), articulate at base, at least the sterile leaflets usually much narrower in relation to their width, seldom more than 1.8 cm wide. *Starry 263.*

Rare or possibly no longer present on BCI; collected once in 1931.

Mexico to Venezuela. In Panama, known only from tropical moist forest in the vicinity of BCI.

BOLBITIS Schott

Bolbitis cladorrhizans (Spreng.) Ching in Christensen, Ind. Suppl. 3:47. 1934

Leptochilus cladorrhizans (Spreng.) Max.

Terrestrial, to 1 m tall; rhizome stout, erect to short-creeping with thin brown lanceolate-linear scales. Leaves 1-pinnate, dimorphic; petiole and rachis with scattered, thin, lanceolate scales, ridged, light brown; sterile leaflets

KEY TO THE SPECIES OF BLECHNUM

Leaflets crenulate to entire, not articulate; plants growing on ± exposed clay banks, locally abundant ..... *B. occidentale* L.

Leaflets serrulate at least near apex, articulate; plants growing in moist areas, rare, if present, on BCI ..... *B. serrulatum* L. C. Rich.

Fig. 18. *Bolbitis cladorrhizans*

Fig. 19. *Bolbitis nicotianifolia*

Fig. 20. *Ctenitis protensa* var. *funestra*

KEY TO THE SPECIES OF BOLBITIS

Plants terrestrial, to 1 m tall; leaflets of sterile leaves usually more than 4 cm wide (to 8 cm) ..... *B. cladorrhizans* (Spreng.) Ching
Plants creeping, epiphytic; leaflets of sterile leaves less than 3 cm wide ..... *B. nicotianifolia* (Sw.) Ching

in 5–7 pairs, ± oblong, long-acuminate, acute to obtuse or rounded and often inequilateral at base, 10–25 cm long and 2–8 cm wide, usually undulate to shallowly lobed and crenate-serrate, confluent toward apex, the veins anastomosing, with scales on midrib beneath like those on petiole; fertile leaflets narrower, oblong to strap-shaped, entire to moderately lobed, 2–20 cm long, 0.5–2.5 cm wide. Sporangia densely covering entire lower surface except midrib. *Croat 5827.*

Common in the forest, usually in creeks or on steep slopes, sometimes growing on stones in rocky stream beds. Seen in fertile condition mostly in the dry season and early in the rainy season.

Nicaragua to Colombia and Venezuela. In Panama, known from tropical moist forest in the Canal Zone and Bocas del Toro, from premontane wet forest in Chiriquí, Coclé, and Darién, and from tropical wet forest in Chiriquí.

See Fig. 18.

Bolbitis nicotianifolia (Sw.) Ching in Christensen, Ind. Suppl. 3:49. 1934

Leptochilus nicotianifolius (Sw.) Christensen

Creeping epiphyte; rhizome closely appressed to trees; scales dark brown, lanceolate-linear, the rhizome scales dense, some deciduous, the petiole scales sparse, mostly near the base. Leaves at first simple, becoming 1-pinnate, ca 1 m long; petioles shorter than blades; sterile leaflets in 1–5 pairs, oblong-elliptic to oblong-oblanceolate, narrowly acuminate, rounded to acute and decurrent at base, 15–40 cm long, 2.5–10 cm wide, entire to irregularly sinuate, the ultimate veins not uniform, the major veins arcuate, parallel to midrib; fertile leaves similar to sterile ones except much reduced, the leaflets 4.5–20 cm long, 0.8–3 cm wide. Sori continuous on underside of blade. *J. H. Faull s.n., Croat 14576.*

Apparently rare.

Honduras south to Colombia, Ecuador, Peru, and the Guianas; West Indies. In Panama, known from tropical moist forest in the Canal Zone and Panamá, from premontane wet forest in Veraguas, and from tropical wet forest in Colón (Río Guanche).

See Fig. 19.

CTENITIS Christensen

Ctenitis protensa (Afz.) Copel. var. **funestra** (Kunze) Proct., Rhodora 63:34. 1961

Epiphyte; rhizome moderately short, the petiole bases closely spaced, covered with light reddish-brown, dense, conspicuous, lanceolate-linear scales, the scales tapered to a threadlike apex, those on petiole similar but shorter. Leaves 1-pinnate-pinnatifid to 2-pinnate, to 25 cm long, tapered to a confluent apex; petioles short; leaflets ± ovate, rounded to acute at apex, merely toothed to deeply pinnatifid (increasingly more deeply dissected toward base), the lobes entire near apex, becoming increasingly toothed toward base, the lowermost lobe at least appearing to be free, itself deeply toothed or even lobed; upper surface and rachis with sessile or stalked glands. Sori minute, rounded, borne on veins below the sinuses, lacking indusium. *Croat 12664.*

Apparently rare, low on tree trunks in the forest.

Panama to Peru, Bolivia, and Brazil; West Indies. In Panama, known from tropical moist forest in the Canal Zone and Panamá and from tropical wet forest in Darién.

See Fig. 20.

Ctenitis sloanei (Poepp.) Mort., Amer. Fern J. 59:66. 1969

Dryopteris ampla (H. & B. ex Willd.) Kunze

Terrestrial, moderately tall. Leaves 2-pinnate-pinnatifid or 3-pinnate; petiole and rachis with deciduous, lanceolate scales especially at nodes; rachis and midrib of leaflets moderately scaly below, densely pubescent above with jointed trichomes; pinnae oblong-lanceolate in outline, ca 40 cm long, tapered to an acuminate apex; secondary pinnae to 10 cm long; leaflets oblong, ca 1.5 cm long, toothed or lobed nearly to middle, blunt at apex, with a few trichomes scattered on lateral veins. Sporangia in round clusters on lateral veins of lobes, in 1 or 2 ± irregular rows along midrib of leaflets. *Wilson 157.*

Collected once on Orchid Island; not seen recently.

Guatemala to Peru and Bolivia; West Indies. In Panama, known from tropical moist forest on BCI and in Panamá, from premontane wet forest in Coclé and Chiriquí, and from tropical wet forest in Colón.

KEY TO THE SPECIES OF CTENITIS

Plants epiphytic, small; leaves 1-pinnate-pinnatifid to barely 2-pinnate-pinnatifid ..... *C. protensa* (Afz.) Copel. var. *funestra* (Kunze) Proct.
Plants terrestrial, moderately tall; leaves 2- or 3-pinnate-pinnatifid ..... *C. sloanei* (Poepp.) Mort.

Fig. 21. *Cyclopeltis semicordata*

Fig. 22. *Dicranoglossum panamense*

Fig. 23. *Dictyoxiphium panamense*

CYCLOPELTIS J. Sm.

Cyclopeltis semicordata (Sw.) J. Sm., Bot. Mag. 72, comp. 36. 1846

Terrestrial, to 1.5 m tall; rhizomes stout, erect, with long, thin, reddish-brown, lanceolate-linear scales, the scales becoming less dense along petiole, rachis, and sometimes midrib of leaflets. Leaves 1-pinnate; petioles much shorter than rachis, ridged; rachis densely short-pubescent; leaflets oblong-linear, acuminate, inequilateral at base with the upper proximal edge usually truncate and the lower proximal edge cordate-auriculate and overlapping rachis, 3–15 cm long, 1–2.2 cm wide, entire or minutely and sharply serrate near apex. Sori round, scattered in 2 or 3 irregular rows on each side of midrib below. *Croat 4287.*

Common in the forest.

Guatemala to Peru, Bolivia, and Brazil; West Indies. In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, Veraguas, Los Santos, Panamá, and Darién, but known also from premontane wet forest in Chiriquí and Panamá and from tropical wet forest in Colón.

See Fig. 21.

DENNSTAEDTIA Bernh.

Dennstaedtia cicutaria (Sw.) Moore, Ind. Fil. 97. 1857

D. rubiginosa (Kaulf.) Moore

Terrestrial, 1–4 m tall; rhizome stout with dense, threadlike, reddish-brown scales. Leaves 3- or 4-pinnate-pinnatifid, finely lacy in appearance; petioles dark brown, somewhat grooved, glabrate to short-pubescent especially in grooves; rachis more densely pubescent; leaflets sparsely pubescent on both surfaces, the veins especially pubescent, the trichomes short and stiff to longer and multicellular; leaflets mostly to 2.5 cm long, pinnatifid, the lobes toothed. Sori borne in sinus between lobes of leaflets; mature indusium saucer- or cup-shaped. *Croat 6406.*

Apparently rare on BCI; collected once on sandbar in Fuertes Cove.

Mexico to Venezuela, Bolivia, and southern Brazil. In Panama, known only from tropical moist forest on BCI and in Panamá and Darién, but probably more widespread than present collections indicate.

DICRANOGLOSSUM J. Sm.

Dicranoglossum panamense (Christensen) Gómez, Brenesia 8:46. 1976

Eschatogramme panamensis Christensen

Epiphyte, usually 10–40 cm tall; rhizome short-creeping, densely scaly near petiole bases, the scales ± triangular. Leaves simple, consisting of several long, irregular lobes; petioles very short; lobes tapered to acuminate apex, to 1 cm wide, each with a midrib branched from center vein and no other conspicuous venation, moderately scaly especially on underside with small, brown, peltate scales, the scales usually narrowly tapered on one end. Sporangia in continuous lines along margins, especially on distal parts of lobes. *Croat 6612.*

Common in the forest.

Reported by Standley as *Eschatogramme furcata* (L.) Trev., which is from the West Indies and Colombia but not known from Panama.

Honduras to Ecuador and Peru; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién, from premontane wet forest in Panamá, and from tropical wet forest in Colón, San Blas, and Panamá.

See Fig. 22.

DICTYOXIPHIUM Hook.

Dictyoxiphium panamense Hook., Gen. Fil. t. 62. 1840

Terrestrial, to 90 cm tall; rhizome erect with reddish-brown, lanceolate scales, and with many fibrous rootlets. Leaves simple, dimorphic; petioles very short or to 2 cm; sterile blades narrowly oblong, ± entire, narrowly acute to acuminate at apex, gradually tapered and decurrent at base, 25–60 cm long, 4–6 cm wide, glabrous except for a few long lanceolate scales at base of midrib on underside; fertile blades much longer and narrower, tapered at both ends, 40–90 cm long, 1.5–3 cm wide. Sporangia in a continuous line along margins, usually beginning well above base and extending to apex. *Croat 6771.*

Common in some areas of the forest.

Mexico to Colombia (Department of Chocó). In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Veraguas, Panamá, and Darién, from premontane wet forest in the Canal Zone and Panamá, and from tropical wet forest in Panamá.

See Fig. 23.

DIPLAZIUM Sw.

Diplazium grandifolium Sw., J. Bot. (Schrader) 1800(2):62. 1801

Terrestrial, to ca 1 m tall; rhizome stout, creeping, with dark scales, the petiole bases closely spaced. Leaves 1-pinnate; petioles dark, to 45 cm long, with dark, deciduous, lanceolate scales near base and short pubescence throughout; leaflets oblong-lanceolate, acuminate at apex, obtuse to truncate or rounded and usually inequilateral at base, to 17 cm long and 4.5 cm wide, reduced and confluent at apex, irregularly toothed, mostly glabrous except for short pubescence on upper surface of canaliculate midrib; veins 1–4-forked. Sori of irregular lengths, on 1 or both sides along lateral veins about halfway between midrib and margin; indusium thin, narrow. *Croat 8329.*

Common in the forest.

Costa Rica to Colombia. In Panama, known from tropical moist forest in the Canal Zone and Panamá, from premontane wet forest in Chiriquí and Panamá, and from tropical wet forest in Colón and Panamá.

See Fig. 24.

Fig. 24. *Diplazium grandifolium*

Fig. 25. *Elaphoglossum herminieri*

Fig. 26. *Elaphoglossum sporadolepis*

DRYOPTERIS Adans.

Dryopteris sordida Max., Contr. U.S. Natl. Herb. 24:60. 1922

Terrestrial, to ca 80 cm tall. Leaves 1-pinnate-pinnatifid; petioles dark brown, dull to shiny, somewhat shorter than blades; leaflets sessile, to 15 cm long and 3.5 cm wide, longest at base of leaf, oblong-lanceolate, acuminate at apex, unequal at base, the upper proximal edge obtuse, the lower proximal edge decurrent, glabrous or nearly so, lobed about halfway to midrib, the lobes bluntly toothed near their apex; basal pair of veinlets on each pair of adjacent lobes meeting sinus at or above its base. Sori round, borne on the veins in 2 rows, 1 on either side of the midrib of the lobes. *W. Knight s.n., Kenoyer 34 (US).*

Not seen in recent years on the island.

This species is similar in appearance to species of *Thelypteris* Sect. *Cyclosorus.*

Known only from Mexico, Guatemala, and Panama. In Panama, known only from tropical moist forest on BCI.

ELAPHOGLOSSUM Schott

Elaphoglossum hayesii (Mett.) Max., Proc. Biol. Soc. Wash. 46:105. 1933

Small epiphyte; rhizomes scaly. Leaves dimorphic, simple; sterile blades linear-oblanceolate, rounded at apex, less than 6 cm long and 1 cm wide, densely and conspicuously scaly, the scales long, lanceolate-linear, light reddish-brown, inconspicuously toothed along their margins; fertile blades spatulate, shorter than sterile leaves. Sporangia covering underside of leaves except for the narrowed base. *Shattuck 593.*

The species was collected once and has not been seen in recent years. Because of its minute size and epiphytic habit, probably high in trees, it could easily be overlooked.

Nicaragua, Costa Rica, and Panama. In Panama, known only from tropical moist forest on BCI and in Panamá.

Elaphoglossum herminieri (Bory & Fée) Moore, Ind. Fil. 16. 1857

Epiphyte, to 1 m long, usually pendent; rhizome with dense, ± linear, thin, light-brown scales to 4.5 cm long and 3 mm broad. Leaves simple and entire, very rarely forked; sterile leaves sessile or with very short petiole, the blades strap-shaped, tapered to blunt apex, very gradually long-tapered to base, 1.5–3.5 cm wide, entire, sparsely and inconspicuously scaly, the scales light brown, peltate-stellate to branched; fertile leaves reduced. Sporangia densely covering underside of leaves. *Croat 7933.*

Rare, in the forest, growing high in trees. Not seen in fertile condition on BCI.

Guatemala to Ecuador, Venezuela, and the Guianas; West Indies. In Panama, known only from tropical moist forest in the Canal Zone (vicinity of BCI) and from tropical wet forest in Colón.

See Fig. 25.

Elaphoglossum sporadolepis (Kunze) Moore, Ind. Fil. 367. 1857

Epiphyte, 20–40 cm tall; rhizome short-creeping, with dense, reddish-brown, lanceolate-linear scales. Leaves simple, dimorphic; sterile leaves nearly sessile or with a slender petiole to 10 cm long, the blades ± linear, tapered to acuminate apex, long-tapered and decurrent at base, 0.8–2.5 cm wide, entire, sparsely and inconspicuously scaly beneath with minute peltate-stellate scales; fertile leaves narrower, with sessile or minutely stalked glands above. Sporangia densely covering underside of leaves. *Croat 10941.*

Common in the forest, usually high in trees. Collected in fertile condition on BCI only in June. Elsewhere in Panama, fertile collections have also been made in September.

Panama and Venezuela. In Panama, known only from tropical moist forest in the Canal Zone (vicinity of BCI).

See Fig. 26.

HEMIDICTYUM Presl

Hemidictyum marginatum (L.) Presl, Tent. Pterid. 111. 1836

Terrestrial, to 2 m tall. Leaves 1-pinnate, glabrous; petiole and rachis canaliculate to ridged; leaflets sessile, oblong, abruptly long-acuminate, inequilateral at base with the upper side ± cuneate and paralleling rachis and the lower side ± truncate, 8–36 cm long, 6–8.5 cm wide, thin, entire, the midvein submarginal, the lateral veins very close, anastomosing in distal third of blade. Sporangia in continuous lines of irregular lengths on distal edge of lateral veins about midway between midrib and margin; indusium thin, very narrow. *Kenoyer 38.*

KEY TO THE SPECIES OF ELAPHOGLOSSUM

Leaves densely and conspicuously scaly, the scales lanceolate-linear, very long ..... *E. hayesii* (Mett.) Max.

Leaves with minute and inconspicuous scales, especially on underside, to almost glabrate:

- Leaf scales stellate to irregularly branched, the branches longer than the width of the united part of the scale ..... *E. herminieri* (Bory & Fée) Moore
- Leaf scales subentire to stellate, the branches, if present, much shorter than the united part of the scale ..... *E. sporadolepis* (Kunze) Moore

Rare, occurring in ravines; not seen in recent years.

Mexico to Peru and Brazil. In Panama, known from tropical moist forest on BCI and in Chiriquí and Darién, as well as from premontane wet forest in Coclé (El Valle) and premontane rain forest in Darién (summit of Cerro Pirre).

LOMARIOPSIS Fée

Lomariopsis vestita Fourn., Bull. Soc. Bot. France 19:250. 1872

Stenochlaena vestita (Fourn.) Und.

Climbing epiphyte; rhizome stout, closely appressed, with dense, long, light-brown, lanceolate-linear scales. Leaves 1-pinnate, to 55 cm long, dimorphic; petiole and lower rachis with scales like those on rhizome; rachis narrowly winged throughout; sterile leaflets usually more than 10 pairs, oblong-lanceolate, usually acute to acuminate at apex, obtuse to truncate at base, 4–8 cm long, 1–2 cm wide, crenate-serrate throughout, glabrous except for sparse, short, gland-tipped trichomes on midrib below, reduced but not confluent at both ends; fertile leaflets linear, mostly 6–8 cm long, ca 2 mm wide. Sporangia densely covering lower surface. *Croat 5316.*

Common in the forest. Fertile during the rainy season (May to September).

Mexico to Panama. In Panama, known from tropical moist forest on BCI and in Bocas del Toro, Veraguas, and Darién, from premontane wet forest in Veraguas, from tropical wet forest in Colón and Panamá, and from lower montane wet forest in Chiriquí.

MAXONIA Christensen

Maxonia apiifolia (Sw.) Christensen, Smithsonian Misc. Collect. 66(9):3. 1916

Hemiepiphytic, closely appressed climber, usually growing from 2–4 m high on tree trunks; rhizome of terrestrial juvenile plants slender, long-creeping, densely scaly, the scales dark reddish-brown, linear-lanceolate, entire, extending only slightly onto petiole bases; rhizome of climbing leaves usually much stouter, 1.5–4.5 cm diam, densely covered with very slender, curly, light reddish-brown scales 1–2 cm or more long, the rootlets long and slender on the side nearest tree, these covered with short, stiff, threadlike scales. Leaves of juvenile plant similar to adult but smaller, to 1 m long; lowermost epiphytic leaves to 50 cm long; adult leaves dimorphic, 3-pinnate-pinnatifid to 4-pinnate; sterile blades to ca 1.5 m long, the petioles ± glabrous except for sparsely scaly base, deeply channeled on upper side, this channel extending throughout upper surface of rachis, pinnular rachis, and tertiary rachis, the canaliculate part densely pubescent except on petiole; pinnae triangular, acuminate; secondary divisions to ca 10 cm long, acuminate and sharply serrate at apex, increasingly more deeply lobed toward base, glabrous except for minute puberulence on tertiary rachis and lower part of midrib of leaflets, the lobes ± oblique, sharply serrate toward apex, the lowermost lobes narrowly obovate, free, or with a minute strip of chlorophyllous tissue along the pinnular rachis. Fertile leaves smaller than sterile leaves, wholly or only partially fertile (if partial, the basal parts fertile); petioles to 25 cm long; blades triangular, 60–80 cm long, borne above sterile leaves; lowermost pinnae to 25 cm long, the leaflets with small, ± rounded lobes each with a prominent free-ending veinlet and with a single sorus on lower surface. Sori round, 1–1.5 mm diam, the indusium round, markedly undulate, attached on one side with an inconspicuous sinus at point of attachment. *Croat 9535.*

Occasional, on trees, especially in deep ravines. All fertile plants were collected from August to October.

This species is distinguished from *Polybotrya villosula* by its three- or four-pinnate leaves and small leaflets (1–3 cm).

Guatemala, Honduras, and Panama; Jamaica and Cuba. In Panama, known only from tropical moist forest on BCI and from premontane wet forest in Panamá (Cerro Campana).

NEPHROLEPIS Schott

Nephrolepis biserrata (Sw.) Schott, Gen. Fil. no. 3. 1834

Epiphyte; rhizome and lower part of petiole with small, thin, lanceolate-linear scales, these affixed subbasally (sometimes moderately scaly throughout petiole and rachis). Leaves 1-pinnate; leaflets lanceolate-linear, long-acuminate on larger leaves, acute to acuminate on smaller ones, obtuse on lower side at base, slightly auriculate on upper side, mostly 7–15 cm long, 1.5–2 cm wide, fibrillose-squamulose and also hirtellous beneath, the margins finely crenate-serrate, the lower leaflets only slightly reduced. Sori round, along margin; indusium orbicular with a very narrow sinus, the sporangia projecting on all sides. *Croat 13106.*

KEY TO THE SPECIES OF NEPHROLEPIS

Indusium ± orbicular, the open side of sorus directed ± toward margin; sporangia projecting on all sides; leaflets commonly acute to acuminate at apex; leaves ± erect ..... *N. biserrata* (Sw.) Schott

Indusium reniform, the open side of sorus directed toward apex; sporangia projecting on open side; leaflets commonly rounded to blunt at apex; leaves usually long-pendent ..... *N. pendula* (Raddi) J. Sm.

Locally common, especially on tree stumps and floating logs in deep shady coves in the vicinity of Fuertes Cove.

New and Old World tropics. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Panamá and from tropical wet forest in Colón.

See fig. on p. 12.

Nephrolepis pendula (Raddi) J. Sm., J. Bot. (Hooker) 4:197. 1842

Epiphyte, often forming a large mass; rhizome with dense reddish-brown, threadlike scales and also with fewer, thin, lanceolate-linear, irregular scales, the scales affixed subbasally (rarely on petiole). Leaves 1-pinnate, broadly arching and ultimately pendent, essentially glabrous; petioles very short or to ca 30 cm long, the rachis usually 0.7–3 m long; leaflets lanceolate-linear, commonly rounded to acute at apex, rounded to subcordate at base, with upper side slightly auriculate at base, 2–5 cm long, 0.5–1 cm wide, ± glabrous, minutely crenulate. Sori discrete along margin; indusium ± thick, reniform to lunate, directed midway between apex and outer margin. *Croat 5045.*

Abundant in the forest from near the ground to the lower branches of even the largest trees. Common in old leaf bases of *Scheelea zonensis* (19. Palmae) and on dead trees at the margin of the lake. In the dead-tree habitat it generally occurs with a variety of other species, most frequently *Sobralia suaveolens* (35. Orchidaceae), *Polypodium phyllitidis,* and *P. crassifolium.*

Tryon (1964) considered this species to be inseparable from *N. cordifolia* (L.) Presl, which has erect leaves. The plant never approaches that appearance on BCI, however, but rather is always pendent.

Widespread in New and Old World tropics. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién, from premontane wet forest in Chiriquí and Panamá, and from lower montane rain forest in Chiriquí (Cerro Horqueta).

See figs. on pp. 14 and 23.

PITYROGRAMMA Link

Pityrogramma calomelanos (L.) Link, Handb. Gewächse 3:20. 1833

Terrestrial, to 1.3 m tall; rhizome scales linear-lanceolate. Leaves 2-pinnate-pinnatifid (sometimes in part 3-pinnate); petiole and rachis reddish-brown and shiny; pinnae to 20 cm long, tapering to a long, slender, connivant apex, sometimes narrowly decurrent on rachis to next pinna; larger leaflets ± irregularly toothed to pinnatifid, white-waxy beneath, mostly 5–25 mm long. Sporangia dispersed over lower surface. *Croat 6921.*

Locally common in open areas, especially on steep, exposed banks.

Distinguished by the white underside of the leaves.

Most tropical areas of the New World. In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Veraguas, Los Santos, Panamá, and Darién; known also from premontane moist forest in Panamá (Panamá City), from premontane wet forest in Colón, Chiriquí, and Panamá, and from tropical wet forest in Chiriquí and Panamá.

See Fig. 27.

POLYBOTRYA H. & B.

Polybotrya villosula H. Christ, Bull. Herb. Boissier, sér. 2, 6:168. 1906

Hemiepiphytic, closely appressed climber growing 2–4 m high on tree trunks; rhizome of terrestrial juvenile plants slender, long-creeping, densely scaly, the scales thick, linear-lanceolate, narrowly acute at apex, dark reddish-brown, 4–8 mm long, not closely imbricated, the surface of the rhizome frequently exposed; rhizome of adult plant stout, 1–3 cm diam, always hemiepiphytic and closely appressed, very densely scaly, the scales ± linear, long-tapered, mostly 1–2 cm long, light reddish-brown, closely imbricated (the rhizome surface not visible). Juvenile leaves much like the adults but usually only 1-pinnate-pinnatifid to 2-pinnate; adult leaves much larger, to ca 1.5 m long, 2-pinnate to 2-pinnate-pinnatifid, ± triangular; petioles about as long as rachis, scaly at base, usually moderately to densely short-pubescent and deeply channeled on upper surface, both channeling and pubescence continuing onto rachis and pinnular rachis, the pubescence of canaliculate part of pinnular rachis and midrib or the leaflets often reddish-brown; pinnae narrowly triangular, the longest pair usually second from base, to 56 cm long, gradually tapered to a slender crenulate apex; leaflets glabrate on upper surface, glabrate below except on midrib or densely short-pilose throughout, ± oblong, rounded to acuminate and crenulate at apex, inequilateral at base, to 12 cm long, becoming confluent toward apex of pinnae, the upper margin of leaflets more prominently toothed or lobed. Fertile leaves smaller, entirely fertile; blades triangular, to 1.2 m long, borne above sterile leaves, 2-pinnate; pinnae triangular at base of leaf, much reduced, linear and simple near apex; leaflets linear, to ca 10 cm long near base of pinnae, ca 2–3 mm wide, glabrous above except for canaliculate midrib. Sori in a broad band along margins of leaflets at maturity appearing to cover entire surface of leaflet. *Croat 10804.*

Common in the forest along Shannon Trail and elsewhere, usually in deep ravines. Plants are usually fertile only during the early rainy season (June and July).

This species has been separated from *P. caudata* Kunze on the grounds of its more dense pubescence. Pubescence is extremely variable, however, even within populations, and further characters are needed to separate the two species.

Belize to Peru, Bolivia, Brazil, and the Guianas; Trinidad. In Panama, known from tropical moist forest in the Canal Zone and Veraguas, from premontane wet forest in Colón and Panamá, and from tropical wet forest in Chiriquí and Panamá.

See Figs. 28 and 29.

Fig. 27. *Pityrogramma calomelanos*

Fig. 28. *Polybotrya villosula*

Fig. 29. *Polybotrya villosula*

POLYPODIUM L.

The genus can be distinguished principally by its epiphytic habit and usually simple, entire, or pinnatifid leaflets with a few rows of discrete, small, round, exindusiate sori. The dominant epiphytic ferns on the island.

Polypodium ciliatum Willd., Sp. Pl. 5:144. 1810

Small, closely appressed epiphyte; rhizome slender, creeping, densely covered with small, thin, lanceolate-linear, peltate scales attenuate to a threadlike apex. Leaves simple, dimorphic, ± evenly spaced on rhizome; petiole very short or to 5 mm long; sterile blades elliptic to lanceolate or rounded, blunt to acute at apex and base, 1–4 cm long, 1–1.5 cm wide, sparsely to densely covered with peltate scales, the scales fimbriate at base and abruptly attenuate to apex; fertile blades oblong-linear, 1–4 cm long and 2–3 mm wide. Sori round, in 2 rows, 1 on each side of midrib, nearly covering blade. *Croat 6618.*

Occasional, in the forest, usually on smaller branches of trees; also occurring on tree branches along the margin of the lake.

Juvenile or aberrant collections of this species may resemble *P. tectum* Kaulf. *Bailey 513* was considered *P. tectum* by Standley.

Costa Rica to Peru, Bolivia, and Amazonian Brazil. In Panama, known only from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién.

Polypodium costaricense H. Christ, Bull. Herb. Boissier 4:660. 1896

Epiphyte; rhizome long-creeping, densely and conspicuously scaly, the scales lanceolate, long-acuminate, reddish-brown, affixed subbasally. Leaves simple, very deeply pinnatifid; petioles 1–8(12) cm long; blades narrowly oblong-lanceolate, tapered to apex, truncate at base, 22–56 cm long and 5–8(13) cm wide, sparsely short-pubescent but especially on midrib below; lobes 4–5(9) mm broad, acute to narrowly rounded at apex, reduced toward apex, less so toward base. Sori round, in 2 rows, 1 on either side of midrib of lobes. *Croat 10365, Kenoyer 19.*

Apparently rare on the island; more common above 500 m elevation elsewhere.

Costa Rica and Panama. In Panama, known from tropical moist forest in the Canal Zone (Pacific slope) and Darién, from premontane wet forest in Chiriquí and Coclé (El Valle), and from tropical wet forest in Panamá.

Polypodium costatum Kunze, Linnaea 9:38. 1834

Epiphyte; rhizome short, the petiole bases very close together. Leaves simple, stiff, brittle, glabrous; petioles 2–6 cm long; blades oblong-oblanceolate, long-acuminate, gradually tapered at base, 15–25 cm long, 2.5–4 cm wide, the leafy tissue ending well above the base. Sori round, scattered on lower surface. *Croat 10991, 17384.*

KEY TO THE SPECIES OF POLYPODIUM

Leaves simple, not deeply lobed:
- Sori in 2 rows, 1 on each side of midrib:
  - Leaves dimorphic, fertile leaf much narrower ..... *P. ciliatum* Willd.
  - Leaves monomorphic:
    - Leaves long-acuminate, more than 10 cm long, prominently scaly below; lateral veins not obvious ..... *P. percussum* Cav.
    - Leaves acute to blunt at apex, less than 8 cm long, not prominently scaly below; lateral veins obvious ..... *P. lycopodioides* L.
- Sori in more than 2 rows:
  - Sori arranged in distinct rows parallel to lateral veins:
    - Sori in a single row between lateral veins; leaf blades thick ..... *P. crassifolium* L.
    - Sori in 2 rows between lateral veins; leaf blades ± thin ..... *P. phyllitidis* L.
  - Sori not in distinct rows:
    - Blades with leafy tissue extending to or almost to base of petiole, membranaceous ..... *P. occultum* H. Christ
    - Blades with leafy tissue ending well above base, stiff, not membranaceous ..... *P. costatum* Kunze

Leaves simple and deeply lobed *or* leaves compound:
- Leaves 1-pinnate ..... *P. triseriale* Sw.
- Leaves simple and deeply lobed:
  - Lobes of blades usually more than 7 mm wide; rhizome scales ± round ... *P. maritimum* Hieron.
  - Lobes of blades mostly less than 7 mm wide; rhizome scales ± lanceolate with a caudate-acuminate apex:
    - Blades mostly less than 25 cm long:
      - Blades densely scaly below ..... *P. polypodioides* (L.) Watt
      - Blades lacking scales below ..... *P. hygrometricum* Splitg.
    - Blades mostly more than 25 cm long:
      - Blades densely pubescent near margin on upper surface ..... *P. pectinatum* L.
      - Blades sparsely pubescent to glabrate near margin on upper surface ..... *P. costaricense* H. Christ

Apparently rare, possibly more abundant and occurring high in trees.

This species can perhaps be confused with *P. crassifolium,* which has a round apex on its leaves.

Panama and the West Indies. In Panama, known from tropical moist forest on both slopes in the Canal Zone and from premontane wet forest in Panamá.

See Fig. 30.

Polypodium crassifolium L., Sp. Pl. 1083. 1753

Epiphyte; rhizome with many fine rootlets, each densely covered with dark, reddish-brown, threadlike scales. Leaves simple, coriaceous, glabrous; blades oblong, round to truncate or often mucronate at apex, tapered at base, the leafy tissue decurrent almost to base of petiole, 13–85 cm long, 3–5 cm wide, covered with a waxlike film when dry. Sori round, large, in single rows between lateral veins in distal third of blade. *Croat 5126.*

Abundant in the forest on larger branches or in the crotches of trees; also frequently found on tree stumps at the margin of the lake. Probably the most common fern on the island.

Mexico to Ecuador, Peru, Brazil, and the Guianas; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Veraguas, Panamá, and Darién, as well as from premontane wet forest in Bocas del Toro, Veraguas, Coclé, and Panamá and from tropical wet forest in Colón (Guásimo).

See Fig. 31 and fig. on p. 14.

Polypodium hygrometricum Splitg., Tijdschr. Natuurl. Gesch. Physiol. 7:409. 1840

P. truncatulum Ros.

Epiphyte; rhizome long-creeping with small, narrowly triangular, reddish-brown scales. Leaves simple, deeply pinnatifid (nearly to midrib), moderately pubescent throughout with silvery, acicular trichomes; petioles and underside of midribs reddish-brown; blades ± irregularly oblong-elliptic, tapered at both ends, more so at apex, 10–30(50) cm long, 1.5–4(9) cm wide, the lobes 3–5 mm wide, often with basal lobes on mature leaves half or more as long as the longest lobe. Sori round, in 2 rows along margins of lobes. *Croat 6312.*

Uncommon, on tree trunks or rocks, usually near the ground.

Costa Rica to Colombia and Venezuela. In Panama, known only from tropical moist forest on BCI.

Polypodium lycopodioides L., Sp. Pl. 1082. 1753

Small creeping epiphyte; rhizome completely covered with reddish-brown, peltate, lanceolate scales tapered to a threadlike end. Leaves simple, glabrous, nearly sessile; blades elliptic to oblong, round to acute at apex, acute to obtuse at base, 2–8 cm long, 1–2 cm wide; lateral veins dark, prominent, branched many times near margin. Sori round, in 2 rows, 1 on each side of midrib, midway between midrib and margin. *Croat 10160.*

Uncommon, on trees in the forest and along the shore.

Mexico to Peru, Bolivia, and Brazil; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Panamá, and Darién and from tropical wet forest in Colón and Coclé.

Polypodium maritimum Hieron., Bot. Jahrb. Syst. 34:527. 1904

Epiphyte; rhizome stout, long-creeping, with appressed, round, peltate scales having irregular margins. Leaves simple, deeply pinnatifid, glabrous; petioles 10–25 cm long; blades triangular, acuminate at apex, truncate at base, 15–60 cm long, 7–15 cm wide, the lobes 10–15 mm broad, obtuse at apex; veins areolate. Sori round, in 2 rows, in areoles along midrib of lobes. *Croat 10363.*

Collected in the Laboratory Clearing. Possibly introduced.

Costa Rica to Colombia, Ecuador, and Venezuela. In Panama, known from tropical moist forest on BCI and in Bocas del Toro, from premontane wet forest in Coclé, and from tropical wet forest in Panamá.

Polypodium occultum H. Christ, Bull. Herb. Boissier, sér. 2, 5:7. 1905

Epiphyte; rhizome moderately long, with short, lanceolate, reddish-brown, peltate scales tapered to a long acicular apex, the petiole bases closely spaced. Leaves simple, membranaceous; blades narrowly oblanceolate, acuminate, narrowly tapered and decurrent at base, 7–40 cm long, 1.5–4 cm wide, bearing fine erect trichomes usually on both surfaces, the margins minutely irregular. Sori round, scattered over lower surface. *Croat 6281.*

Occasional, in the forest, on mossy faces of tree trunks, frequently associated with *Scheelea zonensis* (19. Palmae).

Costa Rica and Panama. In Panama, known from tropical moist forest in the Canal Zone and Darién and from premontane wet forest in Colón.

Polypodium pectinatum L., Sp. Pl. 1085. 1753

Epiphyte; rhizome long-creeping with linear-triangular, dark reddish-brown scales tapered to an acicular apex. Leaves simple, deeply pinnatifid, with short trichomes throughout; petioles 1–10 cm long; petiole and midrib usually reddish-brown; blades oblong, tapered to a narrow apex, tapered also to base, usually 30–60 cm long, 4–10 cm wide, the lobes 3–8 mm wide, broadest at base, the basal lobes of mature leaves much reduced, less than half as long as longest lobes on blade. Sori round, small, in 2 rows, 1 on either side of midrib of lobes. *Croat 6604.*

Abundant in the forest, usually high in trees on the upper side of larger limbs. Sometimes found on rocky banks along the shore.

Costa Rica to Ecuador, Peru, and the Guianas; West Indies. In Panama, known from tropical moist forest in the Canal Zone (Pacific slope) and Panamá and from premontane wet forest in Coclé (El Valle).

See Fig. 32.

Polypodium percussum Cav., Descr. Pl. 243. 1801

Epiphyte; rhizome creeping, with elongate internodes; rhizome scales peltate, lanceolate or round, reddish-brown; petiole bases well spaced on rhizome. Leaves simple, sparsely covered with round or lanceolate, reddish-brown scales, especially beneath; petioles mostly 1–4 cm long; blades oblong-lanceolate, long-acuminate, tapered to a narrowly acute base, 10–22 cm long, 1.5–3 cm wide, moderately thick, sometimes curled inward and lengthwise during the dry season. Sori round, large, in 2 rows, 1 on each side of midrib of leaf. *Croat 5494.*

Frequent in the forest and on trees along the shore. Sometimes forming dense mats on the upper side of larger tree branches.

Guatemala to Peru, Bolivia, and Brazil. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, Veraguas, Los Santos, Panamá, and Darién, from premontane moist forest in the Canal Zone, from premontane wet forest in Bocas del Toro, Veraguas, Coclé, and Panamá, from tropical wet forest in the Canal Zone, Colón, Chiriquí, and Panamá, from lower montane wet forest in Chiriquí, and from premontane rain forest in Darién (Cerro Pirre).

See Fig. 33.

Polypodium phyllitidis L., Sp. Pl. 1083. 1753

Large epiphyte; rhizome stout, moderately long, with many fine rootlets each densely covered with dark reddish-brown, threadlike scales. Leaves simple, large, glabrate; blades oblong-lanceolate, acuminate, tapered to base and narrowly decurrent nearly to base of petiole, 45–100 cm long, 8–12 cm wide, the midrib prominently raised on both surfaces. Sori round, small, in rows along both sides of each lateral vein. *Croat 16532.*

Common in the forest, especially in the crotches of tree trunks close to the ground, but also occurring on smaller limbs and more or less flat surfaces. Less frequent on dead trees at the margin of the lake in full sunlight.

Mexico to Peru, Bolivia, Paraguay, and Brazil; West Indies. In Panama, known from tropical moist forest on the Pacific slope in the Canal Zone, Veraguas, Panamá, and Darién, from premontane wet forest in Panamá, and from tropical wet forest in Chiriquí and Coclé.

See Fig. 34 and fig. on p. 23.

Polypodium polypodioides (L.) Watt, Canad. Naturalist Geol. II, 13:158. 1867

Small epiphyte with creeping rhizome; rhizome scales linear-lanceolate, the margins ciliate; petiole bases well spaced. Leaves simple, deeply pinnatifid, divided nearly to midrib; petioles mostly 2–5 cm long; petioles and underside of blades with dense, lanceolate to round, peltate, reddish-brown scales, their margins scarious and lacerate; blades oblong, thick, narrowest at apex, truncate at base, 3–8 cm long, 1–2.5 cm wide, the lobes ca 2 mm wide, the midrib densely scaly on upper surface. Sori round, in a row along margins of lobes, nearly contiguous. *Croat 5547.*

Infrequent, in the forest, usually growing on larger limbs of trees.

Southern United States to Peru and Argentina. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Panamá, and Darién, from tropical dry forest in Panamá (Taboga Island), from premontane moist forest in Panamá (Panamá City), from premontane wet forest in Chiriquí, Coclé, and Panamá, from tropical wet forest in Chiriquí and Panamá, and from lower montane moist, wet, and rain forests in Chiriquí.

Polypodium triseriale Sw., J. Bot. (Schrader) 1800(2):26. 1801

Epiphyte; rhizome stout, short-creeping, with many fine, densely scaly rootlets, the rhizome scales ovate-acuminate, dull brown, often caudate-acuminate at apex. Leaves 1-pinnate, glabrous; petioles 8–25 cm long; leaflets strap-shaped, acute to acuminate at apex, obtuse at base, 8–37 cm long, 1.2–3.5 cm wide, the margins entire to minutely sinuate, the veins areolate. Sori round, in 2 or 3 rows beside midrib in areoles. *Croat 8608, Foster 1932.*

Rare, in the forest, apparently growing high in trees. Leaf size is variable.

Standley reported *Shattuck 382,* which is this species, as *P. brasiliense* Poir. It has not been determined whether *P. brasiliense* is a synonym of this species.

North America and Mexico to Peru, Bolivia, and Brazil; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Veraguas, and Darién, from premontane wet forest in Chiriquí, Coclé, and Panamá, and from tropical wet forest in Colón.

PTERIS L.

Recognized by its long, marginal, indusiate sori and its regular, rather oblique pinnae.

Pteris altissima Poir. in Lam., Encycl. Méth. Bot. 5:722. 1804

P. kunzeana J. Agardh

Terrestrial, 0.5–2.5 m tall; rhizome erect to creeping with scales narrowly triangular, thick and dark with a thin, flaky margin. Leaves 2-pinnate, rarely almost 3-pinnate at base, moderately pinnatifid; petioles about as long as blades, light brown, shiny; leaflets oblong-lanceolate, tapered to a narrowly triangular, acuminate, sharply serrate apex, lobed to the middle or beyond, glabrous or minutely appressed-pubescent, especially below, not drying shiny; main midrib awned at middle of each lobe; lobes to ca 1 cm broad, to 1.5 cm on juveniles; sterile margins entire to sharply serrate, sometimes with a broad sinus between terminal lobes; veins areolate with 2 or more areolae along the main midrib between the midribs of lateral lobes. Sori elongate, borne along margin of lobes, including sinus, except near apex of lobes; indusium narrow. *Croat 11285.*

Fig. 30. *Polypodium costatum*

Fig. 31. *Polypodium crassifolium*

Fig. 33. *Polypodium percussum*

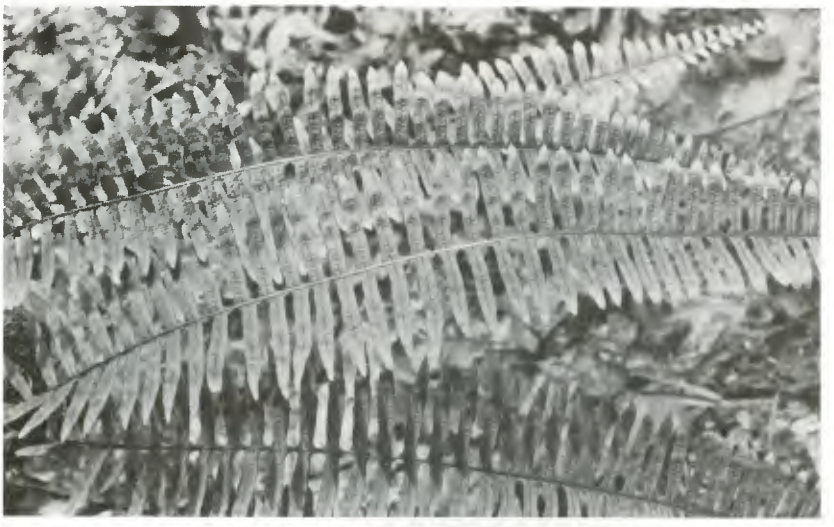


Fig. 32.
Polypodium pectinatum

Fig. 34.
Polypodium phyllitidis

KEY TO THE SPECIES OF PTERIS

Leaves 1-pinnate, entire; veins anastomosing in distal half of their length ..... *P. grandifolia* L.
Leaves 2-pinnate at least at base, pinnatifid; veins free or areolate near midrib:
  Veins free from one another ..... *P. pungens* Willd.
  Veins areolate (i.e., joining together to form areolae):
    Areole single, along the main midrib between midribs of lobes ..... *P. propinqua* J. Agardh
    Areoles 2 or 3, along the main midrib between midribs of lobes ..... *P. altissima* Poir.

Apparently rare, in ravines.

Mexico to Brazil and Bolivia; West Indies. In Panama, known from tropical moist forest on the Pacific slope in the Canal Zone, Chiriquí, Veraguas, and Panamá, from premontane wet forest in Chiriquí, Coclé, and Panamá, from tropical wet forest in Chiriquí and Panamá, and from lower montane moist and wet forests in Chiriquí.

Pteris grandifolia L., Sp. Pl. 1073. 1753

Terrestrial, 1–5 m tall; rhizome stout, to 1.5 cm diam, long-creeping; rhizome scales dense, appressed, light reddish-brown, thin, ± entire, extending onto base of petiole. Leaves 1-pinnate; petioles very stout, about as long as blades, deeply canaliculate; rachis light-colored; leaflets simple, oblong-linear, acuminate, obtuse to acute at base, entire and minutely undulate and hyaline on margin, glabrate to minutely arachnoid-pubescent beneath; veins anastomosing in apical half. Sori borne along much of the margins; indusium narrow. *Kenoyer 50, Shattuck 1169.*

Collected twice on BCI; not seen in recent years. Possibly still present in ravines, although its large size would make it difficult to overlook.

The plant is similar to *Saccoloma elegans,* which has a darker stem and veins seldom branching more than once.

Mexico to Peru; West Indies. In Panama, known only from tropical moist forest on the Atlantic slope of the Canal Zone.

Pteris propinqua J. Agardh, Rec. Spec. Gen. Pterid. 65. 1839

Terrestrial, to 1.5 m tall; otherwise similar to *P. altissima,* except the leaflets having a single areole along the main midrib between midribs of lateral lobes, the blades usually more glossy, at least when dry, the leaf shape not as variable. *Croat 4319.*

Occasional, in the forest. Seen fertile only during the latter part of the rainy season.

The species is doubtfully distinct from *P. altissima*; the areole character separating the two tends to break down.

Mexico to Bolivia and Brazil; Jamaica. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Darién and from tropical wet forest in Colón.

See Fig. 35.

Pteris pungens Willd., Sp. Pl. 5:387. 1810

Terrestrial, 0.3–1(2) m tall; rhizome ± erect, stout, scaly, the scales linear, reddish-brown, with irregular margins. Leaves 2-pinnate at least at base, pinnatifid; petioles scaly at base, about as long as blades, sometimes reddish and armed with minute, blunt spines; leaflets oblong-lanceolate, gradually tapered to a long, narrow, crenate-serrate apex, lobed nearly to main midrib, glabrous; main midrib with two raised margins on upper surface, the margins prominently awned near midrib of each lobe; sterile margins entire to serrate; veins free. Sori borne along margin of lobes; indusium narrow. *Kenoyer 28.*

Not seen on the island in recent years; possibly no longer present.

Mexico to the Guianas and Bolivia; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién and from premontane wet forest in Panamá (near Lago Cerro Azul) and Colón (Santa Rita Ridge).

SACCOLOMA Kaulf.

Saccoloma elegans Kaulf., Berlin. Jahrb. Pharm. 1820:51. 1820

Terrestrial, to 1.5 m tall; rhizome stout, erect to decumbent in age, with thick, shiny, dark-brown scales. Leaves 1-pinnate; petioles slightly prickly to touch near base, often scaly; petiole and rachis dark brown or purplish, shiny; leaflets lanceolate-oblong, gradually long-acuminate, obtuse to acute and often unequal at base, 15–30 cm long, 2–4 cm wide; sterile margins crenulate to serrulate; lateral veins frequently 1-forked above base occasionally in distal half of blades. Sori very numerous along margin, contiguous or nearly so, from near base often to very near apex; indusium thin, hemispherical and glabrous. *Croat 8575.*

Infrequent, usually on stream banks in the forest.

Mexico to Bolivia and Brazil; West Indies. In Panama, known from tropical moist forest in the Canal Zone (both slopes), Panamá, and Darién and from premontane wet forest in Chiriquí and Panamá.

See Fig. 36.

TECTARIA Cav.

Tectaria euryloba (H. Christ) Max., Amer. Fern J. 17:6. 1927

Terrestrial, to 90 cm tall; rhizome stout, creeping. Juvenile leaves often nearly entire; adult leaves simple, with a large apical lobe and 2 or 3 pairs of smaller lateral lobes; petioles to 40 cm long with lanceolate-linear scales nearly 1 cm long, most dense near base; blades ovate in outline,

Fig. 35. *Pteris propinqua*

Fig. 36. *Saccoloma elegans*

KEY TO THE SPECIES OF TECTARIA

Leaves simple ..... *T. euryloba* (H. Christ) Max.
Leaves compound ..... *T. incisa* Cav.

long-acuminate at apex, cordate at base, to 50 cm long and 35 cm wide, glabrous above, the veins on underside bearing sparse scales similar to those on petiole and appressed trichomes, the smaller veins reticulate; lobes ± oblong-elliptic, long-acuminate, 4.5–8 cm wide, the terminal lobe about twice as wide as lateral lobes (to 15 cm wide). Sori round, small, scattered ± all over lower surface. *Croat 6488.*

Occasional, on stream banks in the forest.

Guatemala to Colombia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Darién and from tropical wet forest in Chiriquí and Panamá.

See Fig. 37.

Tectaria incisa Cav., Descr. Pl. 249. 1802

T. martinicensis (Spreng.) Copel.

Terrestrial, to 90 cm tall; rhizome stout, creeping, the petiole bases very close together. Leaves 1-pinnate; petioles slender, to 45 cm long, densely scaly, the scales fine, short; leaflets ± lanceolate-elliptic, acuminate, variable and often inequilateral at base, mostly 20–30 cm long and 5–10 cm wide, entire to undulate or irregularly lobed, glabrous or septate-pilose or hirsute on both surfaces, the basal pair of leaflets with a large, basiscopic lobe; smaller veins reticulate. Sori round, usually in irregular rows alongside each major lateral vein; indusium round-peltate, pubescent. *Croat 12299.*

Abundant throughout the forest and at the margins of clearings. The species is probably the most abundant terrestrial fern of the island.

BCI material includes both var. *pilosa* (Fée) Mort., which is pubescent, and var. *incisa,* which is less pubescent and evidently less common.

Costa Rica to Colombia at low elevations. In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, San Blas, Chiriquí, Veraguas, Los Santos, Panamá, and Darién, but also from premontane wet forest in Coclé and Panamá, from tropical wet forest in Chiriquí and Panamá, and from lower montane wet forest in Chiriquí.

See Fig. 38.

THELYPTERIS Schmidel

Thelypteris can be distinguished by its terrestrial habit, once-pinnate leaves, and usually toothed to pinnatifid leaflets. Sori are usually round, discrete, and in rows and are sometimes furnished with a peltate indusium.

Thelypteris balbisii (Spreng.) Ching, Bull. Fan Mem. Inst. Biol. 10:250. 1941

T. sprengelii (Kaulf.) O. Kuntze

Terrestrial, to ca 1 m tall; rhizome erect, the scales broad or narrow, pubescent, the rootlets numerous, fine. Leaves 1-pinnate-pinnatifid; petioles glabrous or short-pubescent, very short or to 25 cm long; rachis sparsely pubescent and also with sessile glands; leaflets sessile, the largest to

KEY TO THE SPECIES OF THELYPTERIS

Leaves 1-pinnate, the leaflets not pinnatifid (not deeply lobed):
  Sori linear (several times longer than broad) ..... *T. serrata* (Cav.) Alston
  Sori round ..... *T. poiteana* (Bory) Proct.
Leaves 1-pinnate-pinnatifid *or* leaves more than 1-pinnate:
  Leaves 2-pinnate-pinnatifid ..... *T. torresiana* (Gaud.) Alston
  Leaves 1-pinnate-pinnatifid:
    Basal veins of adjacent segments not joining below the sinus and not with an excurrent vein running to the sinus (in *T. extensa,* the basal veins touching and running side-by-side to the sinus, but not joining):
      Basal veins of adjacent segments meeting margin well above base of sinus; lobes less than 3 mm wide ..... *T. balbisii* (Spreng.) Ching
      Basal veins of adjacent segments touching at or below sinus; lobes (at least those near base of leaflets) more than 3 mm long ..... *T. extensa* (Blume) Mort.
    Basal veins of adjacent segments meeting below the sinus with an excurrent vein extending to the sinus:
      Leaflets mostly more than 3 cm wide ..... *T. nicaraguensis* (Fourn.) Mort.
      Leaflets less than 3 cm wide:
        Leaflets nearly glabrous; the lobes ± triangular; plants aquatic ... *T. totta* (Thunb.) Schelpe
        Leaflets densely pubescent; the lobes scarcely triangular, nearly as broad at the apex as at the base; plants not aquatic ..... *T. dentata* (Forssk.) E. St. John

Fig. 37. *Tectaria euryloba*

Fig. 38. *Tectaria incisa*

Fig. 39. *Thelypteris dentata*

Fig. 40.
Thelypteris nicaraguensis

12(19) cm long and 1.7(2.5) cm wide, abruptly reduced at base and gradually reduced toward apex, dissected to near midrib, sparsely short-pubescent on upper surface, sometimes bearing much longer, ± jointed trichomes on underside chiefly on costule and scattered, orange, shiny, sessile glands on whole surface; lobes 2–3 mm wide, sparsely short-ciliolate. Sori round, moderately close in 2 rows, 1 on either side of midrib of lobes; indusium usually with orange glands on margin. *Croat 6691.*

Apparently rare; collected once on Orchid Island in a forest ravine.

Mexico to Panama; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Darién, from premontane wet forest in Coclé, and from lower montane wet forest in Chiriquí (Bambito).

Thelypteris dentata (Forssk.) E. St. John, Amer. Fern J. 26:44. 1936

Dryopteris dentata (Forssk.) Christensen

Terrestrial, 55–130 cm tall; rhizome short-creeping. Petioles darkened and often purplish, 15–45 cm long, scaly at base, the scales linear-lanceolate, with dark-brown trichomes on margin; rachis pubescent; leaves 1-pinnate, 40–92 cm long (not including petiole), 14–34 cm wide, tapering evenly toward pinnatifid apex; largest leaflets 7–17 cm long, 1.1–2.7 cm wide, lobed one-half to three-fourths of the way to the base, the lowermost pairs of leaflets ± reduced and auricled at the base, the basal pair of veinlets from adjacent segments broadly united below the sinus with an excurrent vein to the sinus; pubescence of mostly short trichomes less than 0.2 mm long with scattered longer ones. Sori in 2 rows, 1 along each side of midvein of each segment; indusium pubescent. *Croat 6957, 12412.*

Frequent in open places on forest trails and at the edges of clearings; occasional on exposed shore banks.

The species is often confused with *Thelypteris quadrangularis* (Fée) Schelpe var. *quadrangularis.* Determinations of BCI specimens were made by A. R. Smith, who revised *Thelypteris* Sect. *Cyclosorus.*

Probably native to the Old World, but introduced into the United States, West Indies, and Central America. In Panama, known only from tropical moist forest in the Canal Zone.

See Fig. 39.

Thelypteris extensa (Blume) Mort., Amer. Fern J. 49:113. 1959

Terrestrial; rhizome moderately stout, long to short-creeping, scaly at apex, the scales linear-attenuate. Leaves 1-pinnate-pinnatifid; petioles usually short-pubescent, to 80 cm long, dark and scaly at base, light brown above; blades to 80 cm long; rachis and lower costae short-pubescent and with minute, gland-tipped trichomes; leaflets sessile or short-stalked, to 30 cm long and 2.7 cm wide, the longest usually at the base, dissected two-thirds to three-fourths of the way to midrib, the lower surface short-pubescent and with sulfur-yellow, sessile glands (especially on veins), the upper surface, costule, and margin with longer, stiff trichomes; basal pair of veinlets of each pair of adjacent lobes connivent at the sinus or coming together below the sinus but not actually joining. Sori round, borne on veinlets in a row on either side of the midrib of the lobes; indusium glabrous or sparsely short-pubescent. *Croat 6517.*

Occasional, in forest ravines.

The species is easily distinguished from other *Thelypteris* species on BCI by the sulfur-yellow glands on the lower blade surface.

Native to the Old World: Sri Lanka, southern India, and Burma to southern China, and Malaysia to the Philippines. According to A. R. Smith (1971), it has been introduced and naturalized in Costa Rica, Panama, Colombia, Guyana, and Martinique. In Panama, known only from tropical moist forest in the Canal Zone and San Blas.

Thelypteris nicaraguensis (Fourn.) Mort., Contr. U.S. Natl. Herb. 38:55. 1967

Dryopteris nicaraguensis (Fourn.) Christensen

Terrestrial, 30–100 cm tall; rhizome moderately long-creeping, the petiole bases close together, but only a few leaves borne at any one time. Leaves 1-pinnate-pinnatifid; petioles as long as or much longer than blades; petiole and rachis with moderately dense, short puberulence, the trichomes simple to stalked and minutely tufted at apex; leaflets oblong-elliptic or oblong-lanceolate, pinnatifid, divided one-half to two-thirds of the way to midrib, less so toward apex, ultimately long-acuminate and entire, lobed to near base, the base rounded to cuneate, mostly 10–21 cm long, 2.5–5.5 cm wide, the veins sparsely pubescent on both surfaces, especially below, the trichomes short, stiff, sharply pointed; lobes 5–8 mm wide, curved slightly toward apex of leaflets; 2 or more pairs of connivent veins at the sinus between the lobes. Sori close, round, exindusiate, borne on veins in a row on either side of the midrib of the lobe; sporangia glabrous, interspersed with a few short acicular paraphyses. *Croat 4251.*

Abundant in the forest and at the edges of clearings.

The species is easily confused with *T. tristis* (Kunze) Tryon, which does not occur on BCI.

Guatemala to Panama; usually at less than 300 m altitude. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Panamá, and Darién and from tropical wet forest in Colón.

See Fig. 40.

Thelypteris poiteana (Bory) Proct., Bull. Inst. Jamaica, Sci. Ser. 5:63. 1953

Dryopteris poiteana (Bory) Urban

Terrestrial, to ca 1 m tall; rhizome much like *T. nicaraguensis.* Leaves 1-pinnate; petioles as long as or longer than blades; petiole and especially rachis moderately to densely puberulent, the trichomes mostly stalked-tufted; leaflets sessile, ± oblong, acuminate, rounded to obtuse at base, 11–22 cm long, 3.5–5 cm wide, shallowly lobed throughout except near apex, pubescent on both surfaces (especially underside), the trichomes irregular, sharp and stiff; lower 3 or 4 pairs of veins meniscoid (joining and

forming an excurrent vein that ends before meeting next pair of veins). Sori round, exindusiate, moderately spaced, borne on veins in rows on either side of midrib; sporangia sparsely pubescent. *Croat 6651.*

Common in the forest and at the edges of clearings.

Guatemala to Ecuador below 1,100 m; the Antilles. In Panama, known only from tropical moist forest in the Canal Zone and Bocas del Toro.

Thelypteris serrata (Cav.) Alston, Bull. Misc. Inform. 1932:309. 1932

Terrestrial or aquatic, to 1.3 m tall; rhizome very stout, ± erect, the petiole bases moderately close together, but only a few leaves borne at any one time. Leaves 1-pinnate; petioles as long as or much longer than blades, glabrous to sparsely pubescent, the trichomes simple; rachis more densely pubescent; leaflets narrowly oblong to oblong-lanceolate, acuminate, acute to rounded at base, sessile or with petiole to 1 cm long, mostly (13)20–25(35) cm long and (1.5)3–4 cm wide near middle of blades, only slightly reduced toward base, much decreased upward, the margins uncinate-serrate to entire, glabrate to sparsely pubescent especially on the veins below, the trichomes stiff, straight; veins meniscoid. Sori much longer than broad, curved, exindusiate, the sporangia borne along most opposing pairs of veinlets between the major lateral veins. *Croat 5253.*

Occasional, on eroding banks near the edge of the shore and locally common in floating masses of vegetation along the shores on the south side of the island; elsewhere in the Canal Zone, common on roadbanks.

Widespread, from the United States and Mexico to Argentina and Brazil; West Indies; usually at less than 300 m elevation. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, and Panamá and from premontane wet forest in Veraguas and Panamá.

Thelypteris torresiana (Gaud.) Alston, Lilloa 30:111. 1960

Terrestrial; rhizome stout, ± erect; petiole bases close and few; rhizome and petiole bases with short, stiff, whitish trichomes as well as reddish-brown lanceolate-linear scales to ca 1 cm long, basifixed and often auriculate, at least 1 surface bearing pubescence like that on the rhizome. Leaves 2-pinnate-pinnatifid (at least appearing so); petioles light in color, as long as or shorter than blades; rachis grooved on upper side and with dense pubescence on the medial ridge, the ridge extending in a narrow line onto midrib of pinnae; pinnae lacy, sessile, mostly to 12 cm long, oblong-lanceolate and long-acuminate, the leaflets toothed to deeply pinnatifid, divided to very near the base but at least appearing to be free, the upper surface with stiff acicular trichomes on veins, the lower surface bearing similar but longer, jointed trichomes and minute stalked glands. Sori small with moderately few sporangia, borne in a row on either side of midrib of leaflets; indusium small, thin, sparsely long-ciliate. *Croat 7715.*

Apparently rare; collected once along the steep, moist creek bank near Lutz Trail.

Costa Rica and Panama; Hawaii. In Panama, known only from tropical moist forest on BCI and from premontane wet forest in Panamá.

Thelypteris totta (Thunb.) Schelpe, J. S. African Bot. 29:91. 1963

Dryopteris gongylodes (Schkuhr) O. Kuntze; *Nephrodium terminans* Hook.; *T. interrupta* (Willd.) I. Wats.

Terrestrial or aquatic, to 1.8 m tall; rhizome long-creeping, black, the petiole bases widely spaced (2–9 cm apart). Leaves 1-pinnate; petioles stramineous except dark at base, to 1 m long, glabrous or scaly only near base; blades moderately stiff, 30–80 cm long, 14–60 cm wide, gradually tapered to apex; leaflets sessile or short-stalked, the largest 7–30 cm long, 1–2.2 cm wide, lobed mostly one-third to one-half of the way to midrib, the lobes nearly obtuse to rounded at apex, glabrous or scaly on underside, the scales sparse, stramineous, deltoid, the midrib sparsely short-pubescent, the upper surface often also glandular, the glands sessile; 1 or more pairs of veins connivent before reaching the sinus. Sori indusiate, often confluent when mature, in a row on either side of midrib of lobes (forming V-shaped pattern); indusium glabrous or ciliate. *Croat 13970.*

Occasional, in standing water along the shore or on floating islands of vegetation near the shore on the south side of the island.

Pantropical; in the New World in southern Florida, Central and South America, and the West Indies. In Panama, known from tropical moist forest on BCI and from tropical wet forest in Colón (Miguel de la Borda).

VITTARIA J. Sm.

Vittaria graminifolia Kaulf., Enum. Fil. 192. 1824

Superficially identical to *V. lineata,* but the rhizome scales multiseriate to apex (or with a short, uniseriate tip), the cell walls at margin of scale thinner than those in center; the paraphyses stout, distinctly club-shaped,

KEY TO THE SPECIES OF VITTARIA

Rhizome scales multiseriate to apex (or with short, uniseriate tip), the cell walls at margin of scale thinner than those at center; paraphyses (structures interspersed with spores) stout, distinctly clavate; spores tetrahedral-globose, trilete ..... *V. graminifolia* Kaulf.

Rhizome scales with long, uniseriate, filiform tip with cell walls all the same thickness; paraphyses slender, linear to slightly clavate; spores reniform, monolete ..... *V. lineata* (L.) J. Sm.

reddish-brown or darker, the apical cell enlarged; the spores tetrahedral-globose, trilete. *Croat 4011a.*

Less abundant than *V. lineata,* and doubtfully distinct.

Throughout tropical America. In Panama, known from tropical moist forest on BCI and from premontane wet and lower montane wet forests in Chiriquí.

Vittaria lineata (L.) J. Sm., Mem. Acad. Roy. Sci. (Turin) 5:421. 1793

Pendent epiphyte, 25–75(100) cm long; rhizome with many congested rootlets and scaly, the scales iridescent, lanceolate-linear, 1-costate, with irregular margins and a long uniseriate tip (filiform tip and cell walls all of same thickness), some scales also fine, threadlike, reddish-brown. Leaves simple; petioles scarcely distinguishable from blades; blades linear, 1–2 mm wide, sharp to blunt at apex, glabrous. Sporangia in deep, submarginal grooves, exindusiate; paraphyses slender, linear to slightly club-shaped, tan to light reddish-brown, the apical cells not or not much enlarged; spores reniform, monolete. *Croat 5902.*

Abundant throughout the forest, usually high in trees. Often found with other epiphytic Polypodiaceae.

Throughout tropical America. In Panama, known from tropical moist forest in the Canal Zone, from premontane wet forest in Bocas del Toro and Chiriquí, from tropical wet forest in Colón and Panamá, and from lower montane wet forest in Chiriquí.

11. SALVINIACEAE

Minute, heterosporous, floating aquatics; rhizomes horizontal, freely branched. Leaves straight in vernation, in whorls of 3, of which 2 entire and ± flattened and floating, 1 finely dissected and pendent in water (substituting for a root). Sori borne on the dissected water leaves, subtended by a basifixed indusium; microsporangia numerous, each with 64 microspores, the microspores germinating within the sporangium, the prothallia emerging through its walls as fine tubes, the tubes bearing antheridia apically; megasporangia few, each with a single megaspore, the megaspores producing prothallia bearing archegonia in a manner similar to microsporangia.

Distinguished by their floating aquatic habitat and the two flaplike leaves covered with regularly arranged clusters of trichomes.

Salvinia is often vegetatively dispersed by plants floating away. Any minute part of the stem bearing an axillary bud may produce another plant (Schulthorpe, 1967).

Two genera and 16 species; tropics, subtropics, and warm temperate regions.

SALVINIA Seg.

Salvinia auriculata was reported by Standley (1933), but all material seen has proved to be *S. radula.* It is included in the key, however, because it could easily occur on the island.

Salvinia radula Baker, J. Bot. 24:98. 1886

Very small, floating aquatic, the plants usually less than 4 cm diam; stems short. Stems and fertile leaves bearing slender, jointed trichomes; floating sterile leaves usually flat, usually elliptic to oblong-elliptic or obovate, rounded at apex, subcordate at base, mostly 1–1.5 cm long, the lower surface smooth, with numerous, slender, long, jointed trichomes, the upper surface with ± regular, close rows of short papillae, the rows directed at about a 45° angle from the midrib; papillae bearing usually 4-jointed trichomes (papillae often very reduced and represented only by the trichomes), solitary trichomes sometimes also between the rows. Fertile leaflet much divided, the segments slender, numerous. Sporocarps globular, borne in stalked clusters beneath the leaves, ca 2 mm diam. *Croat 7954.*

Frequent in quiet water at the margin of the lake.

Panama, Colombia, Ecuador, and the Guianas; Cuba. In Panama, known only from tropical moist forest in the Canal Zone and Bocas del Toro.

KEY TO THE SPECIES OF SALVINIA

Floating leaves boat-shaped or conduplicate, usually widest at the broadly cordate base, distinctly broader than long; papillae well developed, 1 mm or more long in center of leaf; leaf tissue usually glabrous between the papillae ..... *S. auriculata* Aubl.

Floating leaves flat, broadly elliptic to oblong-elliptic to obovate, widest at or above the middle; papillae low or sometimes obsolete; leaf tissue often with single trichomes between the rows of papillae ..... *S. radula* Baker

Coniferophyta

12. ARAUCARIACEAE

Dioecious or monoecious trees, evergreen and resinous; branches regularly whorled. Leaves alternate, awl-shaped, compressed, sharp-pointed. Staminate catkins cylindrical, axillary or terminal; staminate flowers with numerous, spirally arranged stamens, the filaments expanded to form a tough anther-scale; sporangia numerous, free, linear, borne on lower surface of scale; pistillate flowers in terminal heads, the carpels numerous, spirally imbricate, terminally thickened with abrupt sharp apex, the ligule ± adnate to carpel, the ovule 1, immersed in ligule; nucellus free; flowering heads becoming large globular woody cones at maturity, disintegrating.

Two genera and 38 species; tropical and subtropical areas of the Southern Hemisphere (with the exception of Africa).

ARAUCARIA Adr. Juss.

Araucaria excelsa R. Br. in Ait., Hort. Kew ed. 2, 5:412. 1813

Tree, becoming 66 m tall, glabrous; branches ± whorled at regular intervals along the stem. Leaves closely spiraled on numerous approximate branchlets along the stem; juvenile leaves subulate, sharp at apex, flattened or 3-sided, 8–15 mm long, ca 1 mm thick; adult leaves densely imbricate, lanceolate to ovate-triangular, the midrib obscure. Staminate catkins 3.5–5 cm long. Fruiting cones ovoid, 10–12.5 cm long. (Description of flowers and cones taken from Bailey, 1949.) *Croat 44758.*

Cultivated in the Laboratory Clearing. The plant is still juvenile.

Native of Norfolk Island; cultivated throughout the world.

Gnetophyta

13. GNETACEAE

Lianas. Leaves opposite, decussate, petiolate; blades simple, entire, glabrous; venation pinnate; stipules lacking. Flowers unisexual (dioecious), actinomorphic, in strobili, axillary or terminal, simple, or 1- or 2-branched, the whorls of the staminate strobili very closely spaced, subtended by a cup- or saucer-shaped collar of bracts, the whorls of the pistillate strobili separated by conspicuous internodes; perianth tubular, angulate; stamen 1; microsporangia 2, 1-celled; ovule 1, having 2 integuments. Seeds oblong, drupelike.

Though a gymnosperm, the genus *Gnetum* appears in almost every respect like a dicot. It is not, however, to be confused with any other genus.

One genus, with 30 species; humid tropics.

GNETUM L.

Gnetum leyboldii Tul. var. **woodsonianum** Markg., Ann. Missouri Bot. Gard. 52:385. 1965

Dioecious liana, glabrous, highly ramified, contorted, widely spreading (usually in a single large tree), to more than 30 m in canopy; trunk 15–20 cm diam near ground, coarse, unfissured, the nodes enlarged. Leaves opposite, decussate; petioles 5–12 mm long, canaliculate above; blades narrowly to broadly ovate, acute to short-acuminate, acute to rounded at base, 9–15 cm long, 4–10 cm wide, ± thick, the midrib usually ± arched, the margin weakly revolute. Staminate inflorescences axillary and terminal, 1- or 2-branched, the main axis of 1–4 tiers, each 1–4 cm long and terminated by 2 small, opposite, acute, connate bracts subtending a dense cluster of moniliform trichomes, a whorl of 2–9 simple strobili, and the axis of the next higher tier; side branches of 1 or 2 tiers identical to those of the main axis; staminate strobili greenish-brown, 10–18 mm long and 3 mm wide, their stalks slender, 5–10 mm long; staminate flowers numerous, in 6 or 7 whorls, 1–2.5 mm apart (uppermost whorl of a few, usually sterile, pistillate flowers, interspersed in a dense mat of white moniliform trichomes 1.5–1.8 mm long); each whorl of staminate flowers on the strobilus subtended by a collar of circular bracts, these at first cup-shaped, becoming saucer-shaped; staminate perianth obconic, brownish, angulate, 0.8 mm long and 0.3 mm wide; stamen solitary, 1.2 mm long, with 2 unilocular microsporangia. Pistillate inflorescences smaller and more reduced than staminate; strobili simple or 1-branched, the main axis of 3–5 tiers, each terminated by 2 opposite, acute, connate bracts subtending the axis of the next higher tier and a whorl of 5 pistillate flowers embedded in a dense cluster of moniliform trichomes; pistillate flowers brownish-yellow, subglobose, 0.5 mm wide and high, ovule 1 (most soon abort). Fruiting internodes 5–30 mm long, ca 2 mm wide, the nodes swollen; mature seeds oblong, 4.5–5 cm long and ca 2 cm wide, rounded on ends (apex apiculate on drying); external envelope red-orange becoming violet-purple, smooth, leathery, 2 mm thick; inner envelope brown, thin, faintly veined. *Croat 7958.*

Infrequent, in the forest. The species appears to flower twice per season, principally from February to April and at least sometimes again in August or September. The fruits from the dry-season flowering develop to mature size by July or August, whereas the wet-season flowers produce fruits in the early dry season. Foster (pers. comm.) reports that the plants flowering during August and September are not the same individuals as those that flowered in the dry season. However, there are indications that individuals may flower twice per year, since I have observed plants in April with both flowers and fruits. Because it is unlikely that the fruits persisted on the plant all year, they were probably the result of a second flowering. Foster also observed an individual, seen bearing fruits in July and August 1971, with mature-sized green fruits in January 1973. This indicates that if individual plants flower only once a year, i.e., in dry or wet season, they are not necessarily restricted to that single period.

Fruits are probably mammal dispersed. Oppenheimer (1968) reported that white-faced monkeys probably feed on the fruits.

The typical variety of *Gnetum leyboldii* is restricted to the Amazon basin, principally in Brazil, Colombia, and Ecuador. The variety *woodsonianum* extends from Coclé in Panama to northern Colombia. In Panama, it is known principally from tropical moist forest in the Canal Zone, Coclé, and Darién, but also from Cerro Pirre in Darién, which ranges from tropical wet forest to premontane rain and lower montane rain forests.

See Figs. 41 and 42.

Fig. 41. *Gnetum leyboldii* var. *woodsonianum*

Fig. 42. *Gnetum leyboldii* var. *woodsonianum*

ANTHOPHYTA
Monocotyledoneae

KEY TO THE MONOCOTYLEDONEAE

- Plants aquatic:
  - Leaf blades narrow, at least 3 times longer than wide, strap-shaped, filiform or grasslike:
    - Leaf blades usually ± succulent (at least at base) and basal; flowers ± large and showy, the petals ca 1 cm or more long, white:
      - Leaves strap-shaped, of ± equal width throughout, obvious petiolar portion lacking; flowers bisexual, having a prominent perianth tube more than 15 cm long; perianth lobes more than 4 cm long ..... 28. AMARYLLIDACEAE (*Crinum erubescens* Ait.)
      - Leaves lanceolate to elliptic, the petiole obvious; flowers unisexual, lacking a perianth tube; petals less than 2 cm long ..... 15. ALISMATACEAE (*Sagittaria lancifolia* L.)
    - Leaf blades not succulent, usually cauline; flowers minute, greenish, usually individually inconspicuous:
      - Plants completely submersed; leaves in distinct whorls of 3, less than 4 cm long and 2 mm wide, serrate; flowers unisexual in minute, axillary inflorescences ..... 16. HYDROCHARITACEAE (*Hydrilla verticillata* (L.f.) Royle)
      - Plants at least partly held above the surface of the water; leaves not in distinct whorls of 3, more than 4 cm long and 2 mm wide; flowers either bisexual or not, in minute axillary clusters:
        - Flowers unisexual, very densely arranged into solid cylindrical inflorescences, the staminate part of the spike separated from the pistillate part by a short sterile section (commonly known as Cattail) ..... 14. TYPHACEAE (*Typha domingensis* Pers.)
        - Flowers usually bisexual, usually arranged in panicles or ± loose spikes, not in dense cylindrical spikes:
          - Stems usually terete with hollow internodes, never trigonous; leaves 2-ranked, with usually open sheaths; florets enveloped by 2 opposing scales; anthers versatile ..... 17. GRAMINEAE (in part)
          - Stems usually 3-sided, solid throughout; leaves 3-ranked, usually with closed sheaths; florets subtended by a simple or saccate scale; anthers basifixed ..... 18. CYPERACEAE (in part)
  - Leaf blades broad, less than 3 times longer than broad, never grasslike:
    - Plants free-floating on surface of water:
      - Leaves more than 20 cm long, prominently petiolate; flowers showy, blue, more than 3.5 cm long ..... 24. PONTEDERIACEAE (*Eichhornia*)
      - Leaves less than 12 cm long, sessile; flowers inconspicuous, greenish, minute, enclosed within a spathe ..... 21. ARACEAE (*Pistia stratiotes* L.)
    - Plants not free-floating, rooted in soil:
      - Leaf blades lobed at base:
        - Plants erect, 1.5–3 m tall; stems spiny; blades with pinnate venation, veins not all closely parallel; flowers unisexual, individually small and inconspicuous ..... 21. ARACEAE (*Montrichardia arborescens* (L.) Schott)
        - Plants sprawling over water; stems unarmed; blades with all veins closely parallel; flowers bisexual, showy, blue ..... 24. PONTEDERIACEAE (*Pontederia rotundifolia* L.f.)

Leaf blades not cordate at base:
Plants floating on surface of water; blades ± rounded or oval, less than 7 cm long . . . . . 16. HYDROCHARITACEAE (*Limnobium stoloniferum* (G. Meyer) Griseb.)
Plants erect, to more than 1 m tall; blades lanceolate to elliptic, more than 15 cm long . . . . . 15. ALISMATACEAE (*Sagittaria lancifolia* L.)

• Plants not aquatic:
Plants lacking chlorophyll (minute terrestrial saprophytes) . . . . . 34. BURMANNIACEAE (*Thismia panamensis* (Standl.) Jonk.)
Plants with chlorophyll:
Leaves like those of banana plant (large or small but not palmlike), i.e., the lateral veins closely parallel, fine and all ± equal, very much less conspicuous than and not parallel to the midrib; leaf surface thin, not at all coriaceous:
Petiole canaliculate on upper side near its apex, lacking a callus (swollen or discolored area); bracts boat-shaped and elongate, usually more than 6 cm long, directed at a broad angle to the main axis of inflorescence, congested and distichous or widely spaced and spirally arranged; inflorescence always unbranched, sometimes pendent; flowers appearing ± actinomorphic; stamens 5 or 6 . . . . . 31. MUSACEAE
Petiole terete near its apex, often with a callus; bracts of the inflorescence not elongate or if so less than 5 cm long, usually congested and usually spirally arranged with the spike ± terete (distichous in *Calathea insignis*) *or* the inflorescence compound; inflorescence never pendent; flowers usually asymmetrical; fertile stamen 1, the remainder transformed into petaloid stamens often more conspicuous than the inner perianth . . . . . 33. MARANTACEAE
Leaves not as above (either not at all banana-like or, if banana-like, with the veins all strictly parallel):
Plants palmlike, the leaves often pinnately or palmately lobed or compound; blade surface usually plicate between major veins:
Perianth segments 4, many, or none; ovules many; inflorescences simple, enclosed in several spathes; staminodia filamentous, usually conspicuous; fruit a fleshy syncarp (fruits united; shaped like a large screw in *Cyclanthus*); seeds minute, numerous; plants mostly acaulescent or nearly so . . . . . 20. CYCLANTHACEAE (in part)
Perianth segments 6 in 2 whorls; ovules 1–7; inflorescences usually compound (simple in *Geonoma cuneata* and *G. procumbens*), apparently enclosed in a single, often woody spathe; staminodia inconspicuous or lacking; fruits usually free from one another; seeds usually 1 per fruit (to 3), usually large; plants usually with a trunk (often very short in *G. procumbens*) . . . . . 19. PALMAE
Plants not palmlike; blades simple or if lobed the blade surface not plicate between major veins:
◆ Plants herbaceous vines:
Plants epiphytic:
Flowers minute, usually actinomorphic, congested into a dense spike (spadix) subtended by one or more spathes or spathe scars; fruit a berry or a syncarp of connate berries:
Spathes 3, deciduous, leaving scars . . . . . 20. CYCLANTHACEAE (*Ludovia integrifolia* (Woods.) Harl.)
Spathes 1, often persistent, sometimes enveloping spadix after anthesis . . . . . 21. ARACEAE (in part)
Flowers not very minute, usually zygomorphic, not congested into a spike subtended by a spathe (in bracteate racemes or panicles); fruit a 3-valved capsule . . . . . 35. ORCHIDACEAE (in part)
Plants not epiphytic:
Blades having all veins closely parallel; reticulate venation absent; flowers bisexual, more than 3 cm diam, blue, showy; plants growing along bodies of water . . . . . 24. PONTEDERIACEAE (*Pontederia rotundifolia* L.f.)
Blades having 3 or more lateral veins paralleling midrib; reticulate venation conspicuous; flowers unisexual (plants dioecious), less than 1 cm diam, greenish; plants usually not growing along bodies of water:
Ovary superior; flowers in umbelliform clusters, the inflorescences usually not long and slender; leaves usually lacking glands; fruit a 1–3-seeded berry . . . . . 26. SMILACACEAE
Ovary inferior; flowers in long spikes, racemes, or narrow, elongate panicles; leaves often with plate-shaped glands; fruit a winged capsule . . . . . 29. DIOSCOREACEAE (*Dioscorea*)
◆ Plants not herbaceous vines:

Plants grasslike or with grasslike leaves conspicuously sheathed at the base, the sheath either closed around the stem or bearing a ligule within at the apex, or both; plants never with equitant leaves (completely folded along midrib):
Flowers individually conspicuous, usually white to blue, not subtended by distichous or imbricate scales; leaves lacking ligules (minute flap of tissue extending above apex of sheath next to stem); fruits bearing 3 or more seeds ..... 23. COMMELINACEAE (in part)
Flowers individually inconspicuous, usually not colorful, subtended by distichous or imbricate scales; leaves having ligules; fruits bearing 1 seed:
Stems usually terete with hollow internodes, never 3-sided; leaves 2-ranked, with usually open sheaths; florets enveloped by 2 opposing scales; anthers versatile ..... 17. GRAMINEAE (in part)
Stems usually trigonous, solid throughout; leaves 3-ranked, with usually closed sheaths; florets subtended by a simple or saccate scale; anthers basifixed ..... 18. CYPERACEAE (in part)
Plants not grasslike, usually lacking a closed sheath; plants with or without equitant leaves:
■ Plants epiphytic:
Flowers minute, individually inconspicuous, congested on a spadix subtended by a spathe; fruits usually fleshy ..... 21. ARACEAE (in part)
Flowers usually moderately large and showy, not congested into a condensed spike subtended by a spathe; fruits generally capsular:
Leaf blades never plicate or folded, usually closely imbricated at base to form a watertight reservoir; flowers with all petals ± equal; stamens and style not fused together; each fruit a several-seeded berry or a capsule with many conspicuously comose seeds (tufts of silky trichomes on seed) ..... 22. BROMELIACEAE
Leaf blades usually plicate or folded along the midrib, never closely imbricated to form a watertight reservoir; flowers with 1 petal modified into a lip; stamens and style fused into a column; pollen in pollinia (modified saccate structures); each fruit a capsule with very numerous, minute, inconspicuous, naked seeds ..... 35. ORCHIDACEAE (in part)
■ Plants not epiphytic:
Flowers usually zygomorphic, with a single prominent lip, the lip usually variously shaped and colored and usually larger than the sepals and petals:
Plants rarely to 1 m tall and if so the leaf blades plicate; leaves often basal; stamens and style fused into a column; lip of flower consisting of a modified petal; pollen contained in pollinia; capsules with very numerous, inconspicuous, naked seeds ..... 35. ORCHIDACEAE (in part)
Plants usually more than 1 m tall or if less the leaf blades not plicate; leaves either distichous or spirally arranged, never basal; stamens and style not fused into a single structure; lip of flower consisting of modified stamens; pollen in a normal anther borne on a petaloid filament; capsules with moderately large arillate seeds (more than 2 mm long) .... 32. ZINGIBERACEAE
Flowers usually actinomorphic or lacking a single prominent lip (1 petal reduced in *Commelina*):
Plants caulescent (with a definite stem):
Shrubs with ± woody stem, ca 2 m or more tall; leaves without a closed sheath ..... 25. LILIACEAE (*Cordyline fruticosa* (L.) Goepp.)
Herbs usually less than 1 m tall; leaves with a closed sheath ..... 23. COMMELINACEAE
Plants acaulescent (the leaves arising from root or rhizome):
Flowers numerous, less than 1 cm long, in a broad panicle, white; fruits red berries less than 1 cm long; plants common ..... 27. HAEMODORACEAE (*Xiphidium caeruleum* Aubl.)
Flowers 1 to several (rarely up to 15), more than 3 cm long, arising from a bracteate scape or laterally from a leaflike peduncle; fruits capsules:
Leaves ensiform (folded along midrib), more than 50 cm long; flowers yellowish with purple markings; seeds red, arillate ..... 30. IRIDACEAE (*Neomarica gracilis* (Herb.) Sprague)
Leaves not folded, less than 50 cm long; flowers white or red-orange; seeds pale green or shiny and black, not arillate ..... 28. AMARYLLIDACEAE (except *Crinum*)

14. TYPHACEAE

Rhizomatous perennial herbs. Leaves arising from rhizome, having a petiolar sheath; blades simple, linear, entire; venation parallel; stipules absent. Flowers unisexual (monoecious), actinomorphic, in a dense spadix, the staminate flowers borne toward the apex, the pistillate flowers toward the base, each flower subtended by a bractlike spathe; perianth represented by bristles; stamens about 2; filaments basally united; anthers 2-celled, basifixed, dehiscing longitudinally; ovary superior, 1-locular and 1-carpellate; ovule 1, pendulous; style simple, filiform. Fruit a nutlet with a persistent style; seeds with mealy endosperm.

Flowers are wind pollinated (Schulthorpe, 1967). The perianth has bristles that may aid in catching pollen grains.

One genus, with about 15 species; widely distributed.

TYPHA L.

Typha domingensis Pers., Synops. Pl. 2:532. 1807

T. angustifolia L.

Cattail

Large, monoecious, semiaquatic herb 1–3 m tall; rhizomes long, fleshy. Leaves equitant; blades sword-shaped, acute at apex, ensheathing stem at base, more than 1 m long, 3–10 mm wide. Inflorescences cylindrical, elongate, 1–2.5 cm diam, 50–120 cm long; flowers in dense spikes, the staminate flowers above the pistillate, separated by 3–10 cm of naked peduncle; perianth reduced to bristles; pistillate flowers usually having filiform bractlets with dilated tips; ovary stipitate, 1- or 2-celled. Mature inflorescences becoming fluffy with loosening comose nutlets; mature nutlets ca 1 mm long, attached to a slender stipe ca 5 mm long. *Croat 4671.*

Rare, along the shore. Fertile in the dry season.

This linear-leaved aquatic is confused with no other plant.

The persistent perianth bristles assure wide dispersal in the wind.

Widely distributed in tropics and subtropics throughout the world. In Panama, in marshy areas; known from tropical moist forest in the Canal Zone and Bocas del Toro and from premontane dry forest in Los Santos.

15. ALISMATACEAE

Herbs. Leaves basal, petiolate, simple, with small scales in axils; blades entire, glabrous; venation parallel, converging. Flowers unisexual (in ours), actinomorphic, in axillary whorls; sepals 3, free, imbricate; petals 3, free, imbricate, white; stamens many (in ours), free; anthers 2-celled, extrorse or dehiscing by lateral slits; pistils many; ovaries superior, unilocular; ovules solitary, basal, anatropous or amphitropous; styles and stigmas continuous, acicular. Fruits achenes, the mature ovules lacking endosperm.

Thirteen genera and about 90 species; widely distributed.

SAGITTARIA L.

Sagittaria lancifolia L., Syst. Nat. ed. 10, 1270. 1759

Glabrous, monoecious, aquatic herb, usually 1–1.5 m tall. Leaves basal; petioles fleshy, vaginate in lower third, becoming terete above, usually longer than blades; blades lanceolate to elliptic, gradually tapered to both ends, mostly 25–40 cm long, 4.5–10 cm wide. Inflorescences held above leaves, usually branched; flowers in whorls of 3 at each node, those at the lower nodes usually pistillate, those at the upper nodes staminate; bracts 3 at each node, lanceolate, 5–20 mm long; pedicels 1–3 cm long, ascending; sepals 3, ovate, to 1 cm long; petals 3, obovate, white, to 1.3 cm long, spreading at anthesis; stamens many; filaments free, pubescent in lower half. Fruit a cluster of numerous achenes, the clusters depressed-globose, ca 1 cm wide; achenes ± flattened, oblique, beaked at apex, to 2.5 mm long. *Croat 8446.*

Uncommon, but locally abundant in marshes. Flowers and fruits November to July, principally March to July.

Seeds are probably dispersed by small shorebirds, though many are no doubt spilled locally.

Throughout tropical and subtropical regions of the New World. In Panama, known from marshy areas of tropical moist forest in the Canal Zone, Bocas del Toro, and Darién and from premontane moist forest in the Canal Zone and Panamá.

16. HYDROCHARITACEAE

Submerged, glabrous, aquatic herbs. Leaves whorled (*Hydrilla*) or basal (*Limnobium*); blades simple, entire or serrulate; stipules lacking. Flowers unisexual (dioecious in ours), actinomorphic, the pistillate flowers solitary, the staminate flowers solitary or in umbels arising from axillary spathes; sepals 3, free, imbricate; petals 3, free, imbricate; stamens 3 (*Hydrilla*) or 6–12 (*Limnobium*), free, alternate with the petals; anthers 4-celled, basifixed, dehiscing longitudinally; ovary inferior, 1-locular, 3- or 6-9-carpellate; placentation parietal; ovules many, ana-

KEY TO THE SPECIES OF HYDROCHARITACEAE

Leaves sessile, in whorls of 3–8 along stem; blades 1–2 mm wide and at most 4 cm long, serrulate ..... *Hydrilla verticillata* (L.f.) Royle

Leaves basal with terete petioles 7–15 cm long; blades ± oval, 4–6 cm long, entire ..... *Limnobium stoloniferum* (G. Meyer) Griseb.

tropous; styles as many as carpels. Fruits berrylike, bearing 2-6 seeds, the seeds lacking endosperm.

Pistillate flowers come to the surface of the water by the elongating pedicel, and the perianth opens. Sexual parts remain dry as the flower floats on the surface. Staminate flowers break loose from the plant and float to the surface; when the flower opens, the spring-loaded stamens discharge pollen into the air (Ernst-Schwarzenbach, 1945). The pollen must contact the pistillate flowers directly as it falls, because floating pollen cannot reach the stigma of the pistillate flower.

Any part of the plant of *Hydrilla verticillata* is capable of regenerating a new plant (Schulthorpe, 1967). Vegetative reproduction is probably important in the dispersal of this genus, as it is in similar aquatics such as *Elodea* (van der Pijl, 1968).

Fourteen genera and about 100 species; mostly the warmer regions of the world.

HYDRILLA L. C. Rich.

Hydrilla verticillata (L.f.) Royle, Ill. Bot. Himal. 376. 1839

Dioecious, perennial, submerged, freshwater herb; main axis erect, rooting basally, the roots unbranched; stems slender, weak, branched. Leaves sessile, linear to elliptic to obovate, acute at apex, 1–2(4) cm long, 1–2 mm wide, serrulate, translucent, green, having only a midvein; lower leaves alternate or in whorls of 3, the middle and upper leaves in whorls of 3–8, densely clustered and rosette-like at apex of stems; inflorescences axillary, 1-flowered, sessile or subsessile; spathes of 2 connate bracts; staminate spathes solitary, subsessile, globose, in leaf axils, 1.2–1.5 mm long, tearing open when the flower is released; pedicels 1–2 mm long; sepals and petals 3, white, sometimes tinged with red; sepals 1.5–3 mm long and 1 mm wide; petals 2–3 mm long and 0.5 mm wide; stamens 3, having slender, short filaments, the anthers linear. Pistillate spathes ca 5 mm long, sepals 3, white, sometimes with red dots, 1.5–3 mm long and 0.7 mm wide; petals 3, white, 1.5–3 mm long, 0.3–0.5 mm wide, the long hypanthium 1.5–10 cm long; ovary 3–4 mm long; styles 3, 0.8–1 mm long. Fruits elongate, constricted between pairs of seeds, 4–7 mm long, basally surrounded by remnants of the spathe and apically bearing remnants of the hypanthium (1.5–3 cm long); seeds 2–6, in a row, cylindrical, oblong, apiculate on one side, 2–3 mm long, smooth, dark brown. *Croat 7909.*

Extremely abundant around the edges of Gatun Lake. Seasonality not determined.

The habit of *Hydrilla* is much like that of *Elodea,* which has not been found on the island. There is no single known vegetative character that may distinguish the two genera with certainty.

Widely distributed in the Old World: from southern and eastern Europe, Africa, Asia, and Australia. In Panama, known from tropical moist forest in the Canal Zone; these collections are the first from the Americas.

LIMNOBIUM L. C. Rich.

Limnobium stoloniferum (G. Meyer) Griseb., Fl. Brit. W. Ind. 506. 1862

Dioecious, floating or loosely rooted, aquatic herb, stoloniferous. Leaves basal, floating on surface of water and rosulate; petioles terete, fleshy, 7–15 cm long (shorter on juveniles); blades oblong-oval to rounded-oval, 4–6 cm long, 3–3.5 cm wide, obtuse to rounded at apex, acute to truncate at base, entire, spongy-reticulate on lower surface. Flowers unisexual; staminate spathes pedunculate with 2 or 3 long-pedicellate flowers; sepals 3, lanceolate, spreading; petals 3; stamens 6–12; filaments subulate, shorter than the linear anthers. Pistillate spathes of 2 bracts, bearing a short-pedicellate flower; ovary 6–9-carpellate; stigmas as many as carpels, 2-parted. Fruits baccate, many-seeded. *Shattuck 401.*

Rare, around the margin of the lake. Collected once by Shattuck but recently seen also by Dressler (pers. comm.). Seasonality not determined.

Shattuck 401 was reported by Standley (1933) as *Hydrocleys nymphoides.* The species was apparently overlooked by C. den Hartog in the *Flora of Panama* treatment (1973).

Guatemala, Panama, South America; West Indies; doubtless also in other parts of Central America. In Panama, known only from Gatun Lake.

17. GRAMINEAE (POACEAE)

Annual or perennial herbs, rarely woody and shrub- or vinelike (bamboos), sometimes aquatic, rarely armed (*Guadua*); stems terete, often arising from stolons or rhizomes. Leaves alternate, 2-ranked, petiolate; petioles sheathing, ligulate; blades simple, entire; venation parallel. Flowers bisexual or unisexual (monoecious or in *Gynerium* dioecious), more or less zygomorphic, in usually terminal panicles, racemes, or spikes; flowers compounded in the highly modified spikelets consisting generally of 2 bracts, the glumes subtending a rachilla, the rachilla bearing 1 to many sessile flowers, each flower generally subtended by usually 2 bracts, the lemma, and the palea; perianth reduced to 2 or sometimes 3 inconspicuous lodicules; stamens 3 or sometimes 6, free; anthers 2-celled, dehiscing longitudinally; ovary 1, 1-locular, 3-carpellate; ovule 1, usually anatropous; styles 2 or rarely 3, simple; stigmas generally plumose. Fruit a caryopsis (in *Sporobolus* the pericarp free from the seed and subachenial); seeds having starchy endosperm.

Flowers are principally wind pollinated (Faegri & van der Pijl, 1966), though some forest grasses such as *Olyra* and *Lithachne* are visited and perhaps pollinated by insects (Soderstrom & Calderon, 1971). Both of these genera are monoecious and have plumose stigmas. It is believed that the pistillate flowers may receive pollen accidentally from insects that visit the staminate flowers

KEY TO THE TAXA OF GRAMINEAE

Plants bamboolike or at least with one, often woody main culm (*Chusquea* only slightly woody), the branches much smaller than the main culm, often fasciculate or whorled at nodes:
Main culms more than 1 cm wide, often armed; cultivated at the Laboratory Clearing or rare in the forest ..... *Bambusa*
Main culms less than 1 cm wide, usually much less, unarmed; common in the forest and along the shore:
Blades lacking a prominent tuft of trichomes near the base on lower surface (puberulent throughout below and with longer but not tufted trichomes near base); all veins ± equal; plants usually growing in dense clumps ..... *Rhipidocladum racemiflorum* (Steud.) McClure
Blades densely tufted near the base on lower surface (otherwise only minutely scabridulous); midrib more prominent than other veins; plants growing in small clumps or solitary .... *Chusquea simpliciflora* Munro
Plants herbaceous (woody with subglobose spikelets in *Lasiacis*), the branches when present not much smaller than the main culm:
Inflorescence a solitary spike or a solitary spikelike raceme or panicle:
Inflorescence with conspicuous, threadlike bristles or awns (longer than the spikelet proper):
Spikelets subtended by straight bristles (more than 1 per spikelet except sometimes in *Setaria vulpiseta*):
Inflorescence a true spike; spikelets sessile, enclosed in burs subtended by a ring of retrorsely barbed bristles ..... *Cenchrus brownii* R. & S.
Inflorescence a spikelike panicle; spikelets subtended by a few, antrorsely barbed bristles ..... *Setaria*
Spikelets lacking bristles:
Awns less than 2 cm long, geniculate, then straight to the apex; plants of clearings:
Racemes to 5.5 cm long; spikelets lacking transverse ridges, pubescent throughout; awns less than 8 mm long ..... *Polytrias amaura* (Miq.) O. Kuntze
Racemes usually more than 6 cm long; spikelets with prominent transverse ridges, densely pubescent only near base; awns ca 15 mm long ... *Ischaemum rugosum* Salisb.
Awns 2 cm or more long, often prominently curled at apex; plants growing only within the forest:
Blades linear, more than 30 cm long, usually less than 2.2 cm wide .... *Streptogyne americana* C. E. Hubb.
Blades mostly narrowly lanceolate-elliptic, less than 30 cm long, more than 2.5 cm wide ..... *Streptochaeta*
Inflorescence lacking conspicuous, threadlike awns or bristles (the spikelet sometimes narrowed to a point but this seldom as long as the spikelet proper):
Inflorescences less than 3.5 cm long; spikelets obovate, in pairs; plants creeping, often small; growing in clearings ..... *Paspalum decumbens* Sw.
Inflorescences more than 5 cm long; spikelets not obovate; plants erect:
Inflorescence a spikelike panicle, the branches slender, bearing several pedicellate spikelets; spikelets slender, acuminate, not indurate; plants generally aquatic:
Lemma narrowly acuminate, scabrid on veins .. *Hymenachne amplexicaulis* (Rudge) Nees
Lemma acute to blunt, usually glabrous ..... *Sacciolepis striata* (L.) Nash
Inflorescence racemose; spikelets indurate; plants not aquatic:
Blades less than 20 cm long; spikelets in groups of 4 on a short stipe, the rachis not cylindrical ..... *Anthephora hermaphrodita* (L.) O. Kuntze
Blades more than 20 cm long; spikelets paired on a thick, jointed, cylindrical rachis ..... *Rottboellia exaltata* (L.) L.f.
Inflorescence paniculate or of more than 1 raceme:
• Inflorescence of paired or digitate spikes or racemes or of racemes clustered very near apex; racemes not both densely fuzzy-pubescent and subtended by narrow spathaceous bracts:
Spikelets with conspicuous awns, the awns often geniculate:
Florets on spikes, the spikes several, digitate, not merely closely aggregated at apex; spikelets with 1 fertile floret and a rudiment of several sterile lemmas ..... *Chloris*
Florets on racemes, the racemes paired or several merely closely aggregated at apex but not digitate:
Racemes merely crowded at apex of inflorescence, not paired; spikelet with a prominent, deep, round pit in the glume ..... *Bothriochloa pertusa* (L.) A. Camus
Racemes paired; spikelet without depression in the glume:
Racemes usually less than 3 cm long, pubescent throughout with reddish-brown trichomes; inflorescences many, diffuse on plant; peduncles mostly less than 6 cm long ..... *Hyparrhenia rufa* (Nees) Stapf
Racemes usually more than 3 cm long, nearly glabrous or pubescent with white trichomes; inflorescences few; peduncles mostly more than 6 cm long .... *Ischaemum*

Spikelets without awns:
Spikelets 2 or more at each node of the rachis ..... *Digitaria*
Spikelets solitary at each node of the rachis:
Racemes digitate, 4–7 per inflorescence ..... *Cynodon dactylon* (L.) Pers.
Racemes not digitate, paired or congested near apex:
Spikelets of 3 or more florets each ..... *Eleusine indica* (L.) Gaertn.
Spikelets of 1 floret each:
Spikelets 2 or more times as long as broad, acute at apex; at least some inflorescences with other racemes below the apical pair ..... *Axonopus compressus* (Sw.) Beauv.
Spikelets less than 2 times as long as broad, usually rounded or blunt at apex; most inflorescences with a single pair of racemes:
Spikelets usually less than 2 mm long, with long, fine, white trichomes on margin; plants stoloniferous ..... *Paspalum conjugatum* Bergius
Spikelets usually more than 3 mm long, the margins glabrous; plants rhizomatous ..... *Paspalum notatum* Flugge

• Inflorescence paniculate or racemose with the racemes not clustered near the apex of the peduncle; racemes densely fuzzy-pubescent (the trichomes longer than spikelets) and subtended by narrow spathaceous bracts:
◆ Spikelets conspicuously awned or long-acuminate, appearing awned, or subtended by long bristles and/or the inflorescence conspicuously long-pubescent, having an overall fuzzy appearance:
Leaf blades mostly more than 30 cm long:
Spikelets subtended by long firm bristles ..... *Setaria*
Spikelets not subtended by long firm bristles (sometimes with tufts of silky trichomes):
Blades more than 1 cm wide; plants usually aquatic or growing near water (at least on BCI):
Blades more than 1 m long and 4 cm wide; panicles usually more than 1 m long ..... *Gynerium sagittatum* (Aubl.) Beauv.
Blades usually less than 75 cm long and 3.5 cm wide; panicles usually less than 60 cm long:
Spikelets not indurate, not awned but the lemma long-acuminate; lemma ± glabrous, spreading at maturity to expose long silky trichomes; frequent on shore ..... *Phragmites australis* (Cav.) Trin.
Spikelets indurate, ridged, awned; lemma hispidulous, not spreading at maturity, without long silky trichomes; rare or absent from BCI ..... *Oryza latifolia* Desv.
Blades mostly less than 1 cm wide; plants aquatic or terrestrial:
Spikelets awnless:
Inflorescence branched once, usually much longer than broad, the branches (racemes) floriferous to the base; plants ca 4 m tall; racemes with tufts of trichomes 1 cm or more long at base of spikelets; racemes not arising from persistent sheaths ..... *Saccharum*
Inflorescence branched many times, nearly as broad as long, the branches long, floriferous only at apex; plants usually less than 1.5 m tall; racemes with scattered trichomes usually less than 1 cm long; racemes arising from persistent sheaths ..... *Andropogon bicornis* L.
Spikelets awned:
Racemes not arising from spathes; trichomes at base of spikelets much shorter than spikelets ..... *Bothriochloa intermedia* (R. Br.) A. Camus
Racemes arising from (and often partially enveloped at base by) conspicuous narrow spathes; trichomes at base of spikelets usually much longer than the spikelets:
Racemes scattered in a long loose inflorescence; spathes usually longer than the racemes; ultimate branches glabrous or nearly so just below the spathes ..... *Andropogon virginicus* L.
Racemes aggregated in a dense compound inflorescence; spathes often shorter than the racemes and obscured by them; ultimate branches densely villous just below the spathes ..... *Andropogon glomeratus* (Walt.) B.S.P.
Leaf blades mostly less than 30 cm long:
⊙ Inflorescence less than 6 cm long *or* of few (usually less than 8) widely spaced racemes each less than 4 cm long:
■ Spikelets conspicuously awned, the awns many times longer than spikelets:
Leaf blades mostly less than 5 mm wide, the awns geniculate and twisted ..... *Schizachyrium brevifolium* Kunth
Leaf blades mostly more than 5 mm wide, the awns ± straight ..... *Oplismenus*

■ Spikelets not conspicuously awned (glumes usually long-acuminate):
Inflorescence with silky pubescence much longer than spikelets; fruits not white and shiny ..... *Andropogon leucostachyus* H.B.K.
Inflorescence glabrous or inconspicuously pubescent; fruits white and shiny:
Plants less than 60 cm tall; terminal inflorescence entirely staminate or wanting, the axillary inflorescences each with 1 pistillate spikelet and several staminate spikelets about as long as the pistillate and arising from nearly the same point; fruits truncate at apex, solitary ..... *Lithachne pauciflora* (Sw.) Poir.
Plants 1.5–5 m tall; inflorescences terminal or upper axillary, each branch with a single pistillate spikelet and with several much shorter staminate ones on branches below; fruits acute at apex ..... *Olyra latifolia* L.
⊙ Inflorescence more than 6 cm long, not of widely spaced racemes:
Plants of the forest; inflorescence not conspicuously pubescent to the naked eye, not feathery in appearance:
Petioles very short; blades lacking cross-veins; spikelets on short branches usually less than 3 cm long; glumes very long-acuminate, often 1–2 cm long; fruits white, shiny, indurate ..... *Olyra latifolia* L.
Petioles usually 1–3 cm long; blades with conspicuous cross-veins; spikelets near the ends of slender branches usually more than 6 cm long; glumes merely acuminate; fruits inconspicuous ..... *Orthoclada laxa* (L. C. Rich.) Beauv.
Plants of clearings or lakeshores; inflorescence conspicuously pubescent, ± feathery:
Plants usually 2 m or more tall; racemes 15–30 cm long, not emerging from narrow persistent spathes; spikelets very numerous, not awned, borne in 2 rows on 1 side of a flattened rachis ..... *Paspalum saccharoides* Nees
Plants 1–1.5 m tall; racemes usually less than 10 cm long, emerging from slender, persistent spathes; spikelets few, awned, borne on a slender, terete, broadly sinuate rachis ..... *Schizachyrium microstachyum* (Desv.) Roseng., Arr. & Izag.
◆ Spikelets neither conspicuously awned nor long-acuminate so as to appear awned; inflorescence not conspicuously long-pubescent and therefore not having an overall fuzzy appearance:
▲ Inflorescence with primary lateral branches strictly racemose or with slender, ± uniform, raceme-like panicles (the inflorescence thus at least appearing 1-pinnate):
Uppermost primary lateral branches of inflorescence paired or digitate (arising from same point at apex of inflorescence):
Spikelets solitary at each node of rachis ..... *Axonopus compressus* (Sw.) Beauv.
Spikelets paired at each node of rachis ..... *Digitaria*
Uppermost primary lateral branches not digitate:
Spikelets with 3 or 4 florets; lemmas conspicuously flattened, imbricate, ciliate on inner margin, sometimes awned ..... *Leptochloa virgata* (L.) Beauv.
Spikelets with 1 floret, convex on at least 1 side; lemmas not ciliate or awned:
Spikelets ± ellipsoid (broadest at or near middle) to obovoid, mostly obtuse to rounded at apex (acute at apex in *Paspalum repens*), convex on one side, flattened on the other (*Brachiaria mutica* may appear convex/flat but is not) ..... *Paspalum*
Spikelets ± ovoid, acute at apex, convex on both sides:
Leaf blades ovate-lanceolate, less than 5 cm long; spikelets with 2 or more light, pinpoint-size glands on the sterile lemma ..... *Panicum pulchellum* Raddi
Leaf blades ± linear, mostly more than 5 cm long; spikelets lacking crateriform glands:
Rachis or pedicel with hispid trichomes ca 1 mm long:
Spikelet less than 1.5 mm long; primary lateral branches strictly racemose, the rachis with hispid pubescence among spikelets ..... *Panicum pilosum* Sw.
Spikelets more than 2 mm long; primary lateral branches appearing racemose but spikelets borne on very short secondary branches, these with sparse, long, stiff trichomes ..... *Brachiaria mutica* (Forssk.) Stapf
Rachis and pedicel lacking long-hispid pubescence:
Rachis with wing broader than width of spikelets ... *Paspalum repens* Bergius
Rachis wingless or wing narrower than width of spikelets:
Spikelets less than 1.5 mm long, usually 2 or more at each node of rachis, ± spreading from slender rachis ..... *Panicum milleflorum* Hitchc. & Chase
Spikelets more than 2 mm long, solitary at each node of rachis, closely fitted into winged sinuous rachis ..... *Paspalidium geminatum* Stapf

▲ Inflorescence with branches compounded 2 or more times, diffuse, open, lacking distinctly racemose branches:
Blades distinctly long-petiolate above sheath, with prominent cross-veins when dry:
Spikelets green, uniform (all bisexual), borne near apex of very slender branches; blades mostly less than 17 cm long; fruits enclosed, not emerging, essentially glabrous ..... *Orthoclada laxa* (L. C. Rich.) Beauv.
Spikelets brown, unisexual (staminate and much larger pistillate spikelets paired at nodes); blades more than 15 cm long; fruits densely pubescent at apex, emerging ..... *Pharus*
Blades lacking petiole above sheath, lacking cross-veins:
Plants with stout culms, erect, usually more than 1.5 m tall, usually unbranched:
Blades cordate-clasping at base ..... *Lasiacis procerrima* (Hack.) Hitchc.
Blades not cordate-clasping at base:
Fruits not at all transversely rugose; ligule glabrous or only shallowly fringed at apex, the cilia scarcely longer than the ligule itself; plants aquatic:
Blades less than 40 cm long and 3 cm wide; spikelets obovate to subglobose, more than 2 mm wide ..... *Panicum mertensii* Roth
Blades to 1 m long and 6 cm wide; spikelets oblong-elliptic, less than 1 mm wide ..... *Panicum grande* Hitchc. & Chase
Fruits at least weakly transversely rugose; ligule long ciliate from below the apex, the cilia at least twice as long as the ligule itself; plants usually in clearings:
Blades plicate, more than 3 cm wide ..... *Setaria paniculifera* (Steud.) Fourn.
Blades not plicate, less than 3 cm wide ..... *Panicum maximum* Jacq.
Plants mostly less than 1 m tall or vinelike and clambering:
Plants with stout, ± woody culms, clambering; spikelets ± round; second glume and lemmas with a tuft of woolly trichomes at apex ..... *Lasiacis*
Plants not with stout, ± woody culms, clambering or erect; spikelets round or not, lacking tufts of trichomes:
Mature spikelets purplish:
Plants aquatic; spikelets strongly hispid-ciliate, lacking glumes ..... *Leersia hexandra* Sw.
Plants not aquatic; spikelets glabrous, not ciliate, having glumes ..... *Panicum fasciculatum* Sw.
Mature spikelets green:
Spikelets with several flowers, more than 6 times as long as wide; lemmas long-ciliate; small, creeping to erect plant ..... *Ichnanthus*
Spikelets with 1 fertile flower, usually less than 3 times as long as wide; lemmas not long-ciliate:
Spikelets more than 3 mm long:
Spikelets having second glume and sterile lemma laterally compressed and keeled at apex; fruits white, with a small, usually green crest at apex; usually found in moist, open areas .... *Acroceras oryzoides* Stapf
Spikelets not laterally compressed and keeled only at apex; fruits white or tan, lacking a crest:
Spikelets glabrous on glumes (i.e., on outside), villous near margin of lemmas; fruits inconspicuous, lacking scars or wings near base ..... *Homolepis aturensis* (H.B.K.) Chase
Spikelets having glumes minutely scabrid on keel, often throughout, the lemmas glabrous; fruits exposed at maturity, tan, bearing scars or narrow wings near base (a continuation from the rachilla or secondary axis of the inflorescence) ..... *Ichnanthus*
Spikelets less than 2 mm long:
★ Plants inhabiting marshes, floating islands, ditches, wet thickets, or sandbars at the margin of the lake:
Leaf blades less than 5 cm long; spikelets obovate, blunt at apex; glumes frequently pubescent; fruits plano-convex, densely pubescent ..... *Isachne polygonoides* (Lam.) Doell
Leaf blades mostly more than 5 cm long; spikelets ellipsoid to narrowly ovoid, acute at apex; glumes glabrous; fruits glabrous:
Spikelets borne on long, slender stalks, 5 mm or more long ..... *Panicum trichanthum* Nees
Spikelets borne on short stalks, seldom more than 1–2 mm long ..... *Panicum polygonatum* Schult.

★ Plants not inhabiting marshes or other wet areas, usually in clearings:
Leaf blades linear, usually 15 cm or more long, very narrow . . . . . *Sporobolus indicus* (L.) R. Br.
Leaf blades less than 12 cm long:
Spikelets ca 1 mm long on pedicels 3 mm or more long; blades narrowly ovoid, less than 7 cm long, to 1.5 cm wide . . . . . *Panicum trichoides* Sw.
Spikelets 1.5–2 mm long on pedicels less than 1.5 mm long; blades linear-lanceolate, to 12 cm long and 12 mm wide . . . . . *Panicum polygonatum* Schult.

to feed on pollen. *Paspalum virgatum* is probably pollinated by small noctuid moths, which visit plants in the evening apparently for the sticky, sweet fluid present at the time of flowering (Karr, 1976). In Costa Rica, *Panicum fasciculatum* and *P. laxum* Sw. are heavily visited by the bees *Trigona, Augochloropsis* (Halictidae), and *Caenaugochlora* (Halictidae) (R. Heithaus, pers. comm.).

It could be expected that other species that occur deep in the forest, where wind currents are poor in the dry season, are also insect pollinated. On the other hand *Pharus,* which may occur in dense forest, is believed to be wind pollinated (G. Davidse, pers. comm.). Fewer than 15 grass species are restricted to the forest, of which only the bamboos (including *Rhipidocladum* and *Chusquea*), which rarely flower, and *Pharus, Streptochaeta,* and *Streptogyne* usually occur in dense, unopened forest. The remainder, including *Lithachne, Orthoclada, Olyra, Ichnanthus,* and *Panicum pulchellum,* are generally found in open areas or along trails, where wind pollination may be effective. Except for *Lithachne,* which may be insect pollinated, the species of open areas flower principally in the dry season, when winds are greatest.

Most species occur in clearings. The flowers of *Lasiacis* open between 7:30 and 9:30 A.M., but insect visitors have never been seen (G. Davidse, pers. comm.) so the flowers are apparently wind pollinated.

Grasses are far more diverse in diaspore strategy than in their pollinating agents. Wind plays a principal role (van der Pijl, 1968), especially for those taxa with plumed spikelets or feathery inflorescences such as *Andropogon, Schizachyrium, Gynerium, Saccharum, Paspalum saccharoides, Bothriochloa,* and *Phragmites.* In addition to these, many other species have small disarticulating spikelets or inflorescence parts that are probably also in part wind dispersed.

Small birds disperse the seeds of many species, particularly those with larger or more attractive spikelets, including *Oryza* and most of the panicoid grasses, as well as species with attractive fruits such as *Lithachne, Olyra,* and especially *Lasiacis.* Investigations by Davidse and Morton (1973) showed that many fruit-eating birds eat the spikelets of *Lasiacis* in great numbers. The glumes contain relatively large amounts of oil, which provides nourishment for the birds, and the caryopsis passes through the bird unharmed. Birds no doubt eat the fruits of a wide variety of grass species, but in general it is uncertain what percentage of the seeds pass through the gizzard unharmed. Ridley (1930) suggested that some seeds may be picked up by birds from the ground as they look for grit for their gizzard. Enders (1935) reported that iguanas eat *Brachiaria mutica* and *Panicum grande.* Elsewhere many grasses are dispersed by herbivores, which swallow the seeds while grazing and regurgitate or pass them unharmed (Ridley, 1930). *Eleusine indica* and *Cynodon dactylon,* both grasses of clearings, have their seeds carried by ants (Ridley, 1930; Wheeler, 1910).

A number of grasses are adapted for epizoochorous dispersal by appendages on the spikelets. These include *Cenchrus, Pharus, Streptochaeta,* and *Streptogyne,* and probably *Paspalum conjugatum, Oplismenus, Leersia, Oryza, Chloris, Orthoclada,* and most species with feathery, disarticulating inflorescences. The awn or awnlike structure of *Oplismenus, Oryza,* and *Chloris* probably serves as much in ensuring disarticulation of the spikelet as in dispersal. Plants of many other species also have prominently geniculate and twisted awns, such as *Hyparrhenia, Ischaemum, Polytrias, Schizachyrium,* and *Bothriochloa.* These probably function in part in epizoochorous dispersal and perhaps also for implantation, such as in the well-known case of *Stipa.*

Those taxa that are restricted to aquatic habitats along the shore probably rely in part on dispersal by water currents. These include *Hymenachne, Isachne, Leersia, Oryza, Brachiaria, Panicum grande, P. mertensii, P. milleflorum, P. polygonatum, P. trichanthum, Paspalidium geminatum, Paspalum repens,* and *Phragmites.*

Unlike most forest species, such as trees with seeds that germinate soon after falling, grasses have seeds that may remain dormant for considerable periods (Corner, 1964).

Some 620–700 genera and 10,000 species; distributed worldwide.

ACROCERAS Stapf

Acroceras oryzoides Stapf in Prain, Fl. Trop. Africa 9:622. 1920
Panicum zizanoides H.B.K.

Perennial, mostly 0.5–1.5 (2) m tall, decumbent-spreading, rooting at lower nodes. Sheaths shorter than the internodes, glabrous or hispid near apex; blades mostly 5–15 cm long, 1–2 (3) cm wide, acuminate, cordate-clasping at the base, the margin white and scabrid sometimes with submarginal hispid trichomes. Inflorescence a sparsely branched panicle, mostly terminal, 10–20 cm long; spikelets paired, narrowly acuminate at apex, rather widely spaced, appressed, 5–6 mm long, glabrous, each pair unequally short-pedicellate; pedicels flattened, scabrid;

first glume keeled, two-thirds as long as spikelet; second glume and sterile lemma equal, laterally compressed and keeled at the apex. Fruits 4–5 mm long, white and shiny, the apex having a green crest. *Croat 7066.*

Common in moist clearings, forming dense stands near the dock and in some areas along the shore.

Most easily distinguished by the crest at the apex of the fruit. The sharply pointed spikelets might function in epizoochorous dispersal.

Mexico to Paraguay; West Indies. Known from tropical moist forest throughout Panama and also occasionally from premontane wet forest in Bocas del Toro (Río Guarumo).

ANDROPOGON L.

Andropogon bicornis L., Sp. Pl. 1046. 1753
Rabo de chibo, Rabo de venado

Coarse perennial, 1–1.5(2.5) m tall, erect, often growing in large stands of clumps of 4–6 plants each; culms glabrous. At least upper sheaths shorter than the internodes, glabrous, weakly keeled toward apex; blades often 25–60 cm or more long, to 7 mm wide, scabridulous throughout above and on margins and midrib below. Panicle branches numerous, very compound, forming a dense, corymbose, feathery inflorescence; racemes paired, 2–3 cm long, often partly enclosed in narrow inconspicuous spathes; rachis and sterile pedicel conspicuously pilose; spikelets paired, one sessile and perfect, the other pedicellate, staminate, and soon falling; sessile spikelet 2.5–3 mm long, glabrous, awnless; racemes disarticulating below each fertile spikelet. Fruits narrowly oblong, dispersing with the pedicel of the staminate flower. *Croat 14918.*

Common in clearings, often the dominant plant in small navigational-sign clearings along the canal; also commonly encountered in marshes. Seems to flower principally in the rainy season.

Perhaps most easily confused with *Schizachyrium microstachyum,* but that species has flexuous rachises and glabrous blades.

Central Mexico to Panama and south to Venezuela, the Guianas, Bolivia, Paraguay, and eastern Brazil; West Indies. Throughout Panama in tropical moist forest; known also from premontane wet forest in Chiriquí and Coclé and from tropical wet forest in Colón.

Andropogon glomeratus (Walt.) B.S.P., Prel. Cat. N.Y. 67. 1888

Densely tufted, erect perennial, 1–1.5 m high; culms glabrous, to 1 cm thick at modes. Sheaths keeled, often hirsute near apex; blades 30–70 cm or more long, to 1 cm broad, minutely scabridulous on both sides and margin, often with longer trichomes near base. Panicles aggregated, sometimes nearly half the length of the culm; racemes paired, spathes often shorter than racemes and obscured by them; rachis and sterile pedicel villous, the ultimate branches densely villous just below the spathes; spikelets paired, one sessile and perfect, the other pedicellate and staminate (soon falling); sessile spikelet 3–4 mm long with a straight awn 1–1.5 cm long. Fruits narrowly oblong, brown, ca 1.5 mm long. *Woodworth & Vestal 541.*

Occasional, on steep shore banks and in marshes and floating islands. Inflorescences are seen throughout the rainy season into the early dry season.

Similar in habit and appearance to *A. bicornis,* but easily confused with *A. virginicus,* to which it is more closely related.

Southeastern United States and Mexico to Panama and northern South America; West Indies. Probably in tropical moist forest throughout Panama (known from the Canal Zone, Panamá, and San Blas); known also in premontane wet forest areas in Chiriquí.

Andropogon leucostachyus H.B.K., Nov. Gen. & Sp. 1:187. 1816

Small tufted perennial, 25–70 cm tall; culms glabrous. Sheaths narrow, compressed; ligules 1–2 mm long, truncate, minutely erose; blades 5–15 cm long (except on new shoots), 1–3 mm wide, scaberulous. Flowering branches few, sparingly branched, long and slender; racemes paired (sometimes in 3s); peduncles long and slender; spathes long and slender but inconspicuous; rachis and sterile pedicel slender, densely silky-pubescent, the trichomes ca 1 cm long, sessile; spikelets ca 3 mm long, glabrous, awnless; pedicellate spikelets lacking. Fruits narrowly oblong, tan, 2 mm long. *Croat 6916.*

Occasional, in the Laboratory Clearing. Probably flowers and fruits much of the year, but mostly in the early dry and early rainy seasons. It has not been seen in flower in the late rainy season.

KEY TO THE SPECIES OF ANDROPOGON

Spikelets awned:
- Racemes scattered in a long loose inflorescence; spathes usually longer than the racemes; ultimate branches glabrous just below the spathes ..... *A. virginicus* L.
- Racemes aggregated in a dense compound inflorescence; spathes often shorter than the racemes and obscured by them; ultimate branches densely villous just below the spathes ..... *A. glomeratus* (Walt.) B.S.P.

Spikelets not awned:
- Plants usually more than 1 m tall; blades much more than 15 cm long; spathes aggregate in a usually dense inflorescence ..... *A. bicornis* L.
- Plants usually less than 70 cm tall; blades usually less than 15 cm long; spathes not aggregated (the flowering branches few and sparingly branched) ..... *A. leucostachyus* H.B.K.

Mexico to Argentina; West Indies. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone and Panamá, from premontane wet forest in Colón (Santa Rita Ridge), Chiriquí (Boquete), and Panamá (Cerro Campana), and from lower montane moist forest in Chiriquí (lava flows between Volcán and Cerro Punta).

Andropogon virginicus L., Sp. Pl. 1046. 1753

Densely tufted, erect perennial, 80–150 cm tall; mostly glabrous. Lower leaves in basal cluster; sheaths flattened, keeled, glabrous or hirsute, much shorter than the internodes; blades 15–30 cm or more long (basal leaves longest), to 4 mm wide, the margins obscurely scabridulous. Inflorescences loose and elongate, the flowering branches from the middle to upper nodes; racemes paired, slender, spreading, often partly enclosed in a slender spathe, the spathe exceeding the raceme; rachis flexuous, the ultimate branches glabrous just below the spathes; spikelets paired, one sessile and perfect, 3–4 mm long, the other pedicellate and staminate (soon falling); awn straight, 1–1.5 cm long; first glume acuminate. Fruits narrowly oblong, tan, ca 1 mm long. *Ebinger 590.*

Collected once near the shore in the Drayton House Clearing. Apparently less abundant in Panama than *A. glomeratus.* Seasonal behavior unknown, probably flowers during the rainy season.

Eastern United States and Mexico to Panama; West Indies; Hawaii. In Panama, known from tropical moist forest in the Canal Zone and Panamá (doubtless elsewhere) and from premontane wet forest in Panamá (slopes of Cerro Campana).

ANTHEPHORA Schreb.

Anthephora hermaphrodita (L.) O. Kuntze, Rev. Gen. Pl. 2:759. 1891

Erect annual, to 50 cm high; culms rooting at lower nodes. Leaf sheaths prominently veined, puberulent and papillose-hirsute near apex; blades 5–20 cm long, 3–8 mm wide, puberulent and papillose-hirsute on both surfaces. Racemes 5–10 cm long; spikelets in groups of 4, the first glumes united at the base and forming a false involucre around the rest of the spikelets, the groups short-pedicellate; first glume 5–7 mm long, scabrid on the margins, indurate. Fruits lanceolate, acuminate, tan, ca 3.5 mm long. *Shattuck 418.*

Collected once along the shore; not seen in recent years. Flowers and fruits chiefly in the rainy season.

The spikelets disarticulate from the rachis in groups of four. This unit has no obvious means of dispersal, but since the caryopsis is well protected by the indurate glumes, the spikelets may be bird dispersed.

Throughout tropical America. In Panama, from tropical moist forest in the Canal Zone (both slopes), Colón, and Panamá and from tropical dry forest in Panamá (Taboga Island).

AXONOPUS Beauv.

Axonopus compressus (Sw.) Beauv., Ess. Agrost. 12. 1812
Carpetgrass

Perennial, 20–60 cm tall; stoloniferous, often in dense stands; culms ± erect, flattened, pubescent at nodes. Sheaths flattened, glabrous throughout except at collar and sometimes ciliate on the margins; blades 5–15 cm long, 6–12 mm wide, glabrous below, glabrous to sparsely long-pubescent above, the margins scabrid, usually ciliate at least near base. Inflorescences terminal or upper axillary, with 2–5 racemes 3–10 cm long, the upper 2 conjugate, the others a short distance below; spikelets mostly 2–2.5 mm long, 2 or more times longer than broad, acute at apex, alternate on a triangular, narrowly winged rachis, glabrous or sparsely pubescent; first glume lacking; second glume and sterile lemma acute, exceeding fruit. Fruits to 2 mm long, oblong-elliptic, blunt at apex, whitish, minutely roughened. *Croat 16573.*

Common to locally abundant in the Laboratory Clearing. Flowers all year, especially in the rainy season.

Similar to *Digitaria horizontalis,* but having a single spikelet per node of the inflorescence.

Throughout warmer regions of New and Old Worlds. In Panama, widespread in tropical moist forest; known also in premontane dry forest in Coclé (Aguadulce), tropical dry forest in Panamá (Taboga Island), and lower montane wet forest in Chiriquí (Volcán).

BAMBUSA Schreb.

Bambusa amplexifolia (Presl) Schult.f., Syst. Veg. 7(2):1348. 1830

Bamboo growing in isolated clumps of as many as 10 culms each; culms to ca 8 cm diam and 10 m long, erect to arching, often leaning on other vegetation; culm sheaths triangular when flattened, acute at apex, ca 25 cm long, densely ferruginous-pubescent on outer surface; branches glabrous, long and spreading, heavily armed at nodes with spines mostly 8–25 mm long. Leaves mostly on outer parts of branches, mostly 1–1.5 cm apart on the stem; leaves on juvenile culms 2.5–4.5 cm apart, the blades to 24 cm long and 4.5 cm wide, the sheaths 4–8 cm long; mature sheaths ca 2.5 cm long, glabrous except usually ciliate along one or both margins, the truncate apex with a stout branched trichome on either side 7–13 mm long; petioles 0.5–2 m long; blades oblong-lanceolate, narrowly acute to acuminate at apex, rounded at base, 3–15 cm long, 10–25 mm wide, glabrous, the margins sparsely and inconspicuously scabrid. Inflorescences not seen. *Croat 10101.*

Rare; known only from near the beginning of Armour Trail and along the stream near Chapman Trail 900. Forming small stands in the forest.

Mexico to Colombia and Venezuela. Range in Panama unknown.

KEY TO THE SPECIES OF BAMBUSA

Plants unarmed; main culms usually less than 2 cm wide; leaf blades short-pubescent on lower surface, ± pruinose ..... *B. glaucescens* Munro
Plants armed with spines at least at some nodes; main culms usually more than 6 cm diam; leaf blades glabrous, not at all pruinose:
Plants ca 20 m tall, in large congested clumps, with a dense tangle of many stout, heavily armed, leafless branches at base; culms 11–12 cm diam; culm sheaths broad, wrinkled along upper margins ..... *B. arundinacea* Retz.
Plants 5–10 m (or more) tall, usually solitary or few, lacking a dense tangle of spiny branches at base; culms 1–8 cm (or more) diam; culm sheaths ± continuous with the blade, triangular when flattened ..... *B. amplexifolia* (Presl) Schult.f.

Bambusa arundinacea Retz., Obs. Bot. 5:24. 1789.

Erect bamboo to 20(25) m tall; culms olive-green, shiny, 11–12 cm diam, erect to broadly arching, densely rooting at lower nodes, occurring in congested clumps of ca 4 m or more in diameter; internodes mostly 10–25 cm long near the base, the basal ones thick-walled (to ca 1 cm thick); nodes with a conspicuous leaf-sheath scar and with many stout branches to 3 cm diam, soon becoming slender, usually 1- or 2-branched, wide-spreading, forming a tangled mass to 5 m high, heavily armed at the nodes, the spines to 1.5 cm long; branch apices also spine-like; sheath blades broadly triangular, appressed (reflexed at upper nodes); branches on main culm to 2 m or more long, their axes flexuose, the nodes with a prominent ring-like sheath scar and often with stout spines, the spines often weakly curved, with short internodes; the lower 1.5 cm of the base of each branch encircled by several short sheathlike bracts, the smaller leafy branches with leaves clustered mostly toward their apices. Sheaths glabrous except often short-pubescent along upper margin, truncate to auriculate at apex, often bearing a few, thick, usually deciduous trichomes; leaf blades linear-lanceolate, acuminate, (2.5)7–15(20) cm long, (5)8–18(25) mm wide, glabrous or with a few long trichomes near base on upper surface, glabrous or puberulent on lower surface. Inflorescences not seen. *Croat 17038.*

Cultivated in the Laboratory Clearing northwest of the dining hall.

Native to India; introduced occasionally in other tropical areas of the world.

Bambusa glaucescens (Willd.) Sieb. ex Munro, Trans. Linn. Soc. London 26:89. 1868

Slender, clumped bamboo, to 5 m tall; culms very numerous, closely aggregated, 1–2 cm diam, erect when young, leaning in age, appressed-pubescent below internodes, pruinose when young (including sheath); the reduced leaves of the main axis tightly appressed to culms, brown, acuminate at apex, mostly 18–26 cm long (including sheath), appressed-pubescent outside above ligules; ligules ca 2 mm high, the margins irregular; branches clustered at the nodes, of various lengths, to 2 m long, these in turn branched, the branchlets to ca 1 m long. Leaves linear, acuminate, acute to rounded at base, mostly 3–18 cm long and 6–16 mm wide, pruinose and short-pubescent below, ± glabrous above, the margins scabrid, the midrib weak, the sheaths turning brown in age, bristled on the upper margin. Inflorescences not seen. *Croat 16563.*

Cultivated at the Laboratory Clearing near ZMA House and the bridge to the animal cages.

Native to Asia, probably China; cultivated throughout the tropics.

BOTHRIOCHLOA O. Kuntze

Bothriochloa intermedia (R. Br.) A. Camus, Ann. Soc. Linn. Lyon n. sér. 76(1930):164. 1931

Perennial, mostly 1–1.5 m tall, erect, usually unbranched; culms glabrous, striate. Leaves glabrous except for scabrid margins; sheaths ± as long as internodes; blades 25–55 cm long, 3–10 mm wide. Panicles terminal, 6–20 cm long, held above the leaves, the primary axis glabrous, the branches usually 1- or 2-branched, bearded at their base; racemes mostly 1.5–4 cm long; rachis and sterile pedicel villous; spikelets in pairs, one sessile, perfect, ca 3 mm long, the other pedicellate, sterile, ca 2.5 mm long; sessile spikelet bearing a tuft of trichomes at the base and a pubescent, reddish-brown, geniculate awn 8–13 mm long; glumes brown to purplish, the glume of the sessile spikelet pubescent toward the base. Fruits not seen. *Croat 6973, 16523.*

Frequent in the Laboratory Clearing. Probably in flower or fruit much of the year.

This species, var. *intermedia,* is introduced on BCI.

India to Australia and Africa; introduced into most tropical areas. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and San Blas.

KEY TO THE SPECIES OF BOTHRIOCHLOA

Spikelets awned, bearing a prominent pinhole-like pit in the glume ..... *B. pertusa* (L.) A. Camus
Spikelets awnless, not with a hole in the glume ..... *B. intermedia* (R. Br.) A. Camus

Bothriochloa pertusa (L.) A. Camus, Ann. Soc. Linn. Lyon n. sér. 76(1930):164. 1931

Small annual, to 50 cm tall, usually growing as isolated individuals, usually unbranched, the base sometimes decumbent; culms glabrous, with nodes bearded. Sheaths glabrous or ciliate on margin, shorter than internodes; blades 1.5–10 cm long, to 3 mm wide, conspicuously pubescent on upper and lower surfaces, the trichome bases enlarged. Racemes usually 5 or 6 clustered near apex, 3–6 cm long, held well above leaves; rachis and sterile pedicel prominently long-villous; spikelets in pairs, one sessile and perfect, the other pedicellate and sterile; sessile spikelet awned, 3.5–4 mm long, the glume with a prominent small, round, deep pit above the middle; awns brown, generally twice-geniculate, to ca 2 cm long; pedicellate spikelet awnless, about as long as sessile one. Fruits not seen. *Croat 9206.*

Occasional, in open areas in the Laboratory Clearing during the dry season.

Bothriochloa bladhii (Retz.) S. T. Blake, native to India and Africa, has a pit in the glume similar to that in *B. pertusa,* but it has not been collected on the island.

Panama; West Indies. In Panama, known from tropical moist forest in the Canal Zone and Panamá and from premontane dry forest in Coclé (Río Hato).

BRACHIARIA Griseb.

Brachiaria mutica (Forssk.) Stapf in Prain, Fl. Trop. Africa 9:526. 1919

Panicum barbinode Trin.; *P. purpurascens* Raddi

Stoloniferous perennial, to 2(6) m long; culms erect or decumbent, rooting and often geniculate at lower nodes, densely villous at nodes. Sheaths mostly longer than the internodes, stiffly papillose-pubescent; blades mostly 15–25 cm long, to 1.5 cm wide, glabrous with finely scabrous margins. Panicles 10–20 cm long, the branches many, raceme-like, mostly 3–5 cm long, densely pubescent at the base, angulate, scabrid; branchlets and pedicels both scabrid and with sparse, long, stiff trichomes; spikelets 2.7–3 mm long, glabrous, often tinged with purple; first glume approximately one-third as long as spikelet; second glume and sterile lemma covering fruit. Fruits pale, longitudinally striate, minutely transversely rugose. *Croat 8679.*

Infrequent but locally common on open, swampy edges of the lake near the dock. Apparently flowers from late in the rainy season to the middle of the dry season (September to March).

This species was reported incorrectly by Standley as *Eriochloa punctata* (L.) Desv. ex Ham.

Throughout tropical and subtropical America. In Panama, from tropical moist forest in the Canal Zone and in premontane moist forest in Panamá (Perlas Islands).

See Fig. 43.

CENCHRUS L.

Cenchrus brownii R. & S., Syst. Veg. 2:258. 1817

C. viridis Spreng.

Pega-pega, Cadillo

Erect or decumbent-spreading annual, less than 1 m tall, rooting at lower nodes. Sheaths longer than internodes, flattened, glabrous; blades 10–30 cm long, 5–8(12) mm wide, glabrous or scabrid on upper surface and on margins with longer trichomes at least near the base. Spikes to 10 cm long; spikelets sessile, ca 4 mm long, enclosed in burs, usually 3 in each bur, the burs dense, ca 4 mm wide, subtended by a ring of retrorsely barbed bristles. Fruits not seen. *Shattuck 391.*

Common in open areas in the Canal Zone; perhaps once common also on BCI but possibly no longer occurring there. Flowers throughout the rainy season and into the early dry season.

Southern United States through Central America to Bolivia and Brazil; West Indies; Australia and South Pacific Islands. In Panama, from tropical moist forest all along the Pacific slope and in Bocas del Toro, and from premontane wet forest in Panamá (Perlas Islands).

CHLORIS Sw.

Chloris radiata (L.) Sw., Prodr. Veg. Ind. Occ. 26. 1788

Perennial, to 60 cm tall; culms ± erect, rooting at lower nodes. Sheaths flattened, keeled, longer than the internodes, scabrid to glabrous; blades 4–12 cm long, to ca 5 mm wide, scabrid on upper and lower surfaces. Inflorescences terminal, of subdigitate or closely clustered spikes 4–8 cm long; spikelets to ca 3 mm long, with 1 fertile floret and several reduced sterile lemmas in a club-shaped rudiment; glumes scarious with a stout, scabrid keel; fertile floret 2.5–3 mm long, glabrous except at base and apex below awn, the awn 5–10 mm long, antrorsely scabrid; rudiment minute, almost hidden by fertile floret, its awn 4–6 mm long. Fruits oblong, ca 1 mm long. *Standley 41125.*

Collected once by Standley; not seen recently on the island, but to be expected in clearings. Probably flowers throughout the year.

Throughout most tropical regions of the Hemisphere. From tropical moist forest throughout Panama and from tropical dry forest in Panamá (Taboga Island).

KEY TO THE SPECIES OF CHLORIS

Fertile lemma bearing short, inconspicuous tufts of trichomes, these much shorter than lemma; rudiment slender, acute at apex, often obscured by fertile lemma ..... *C. radiata* (L.) Sw.

Fertile lemma tufted near apex, the trichomes nearly as long as the lemma; rudiment truncate at apex, not hidden in fertile lemma ..... *C. virgata* Sw.

Chloris virgata Sw., Fl. Ind. Occ. 203. 1797

Annual, 10–100 cm tall; culms ± erect or decumbent at base. Sheaths flattened, keeled, mostly longer than the internodes, glabrous; blades 4–25 cm long, 3–7 mm wide, mostly glabrous to scaberulous, the margins scabrid. Inflorescences terminal, of several digitate spikes 3–9 cm long; spikelets 3–3.5 mm long, with 1 fertile floret and a rudiment of several sterile lemmas, disarticulating below the fertile lemma; glumes scabrous on the keel, unequal, the second glume with a short awn; fertile floret 3–3.5 mm long, bearded on margins below awn, the awn on the lemma scabrid, to 1 cm long; rudiment stout, 2–2.5 mm long, with an awn 3–7 mm long. Fruits not seen. *Kenoyer 119.*

Collected once by Kenoyer; not seen recently but to be expected in clearings. Apparently flowering principally in the dry season.

A native of Africa, now introduced throughout warmer regions of the world. In Panama, known from tropical moist forest in the Canal Zone.

CHUSQUEA Kunth

Chusquea simpliciflora Munro, Trans. Linn. Soc. London 26:54. 1868

Carricillo

Slender, arching or clambering, vinelike plant, to 25 m long; culms solitary or few in a clump, mostly less than 5 (8) mm diam, glabrous; branches few to many, 7–30 cm long on sterile plants, the nodes usually ciliate. Sheaths ciliate, the lowermost without blades; blades lanceolate, mostly 5–9 cm long, 8–15 mm broad, nearly glabrous except for long, somewhat tufted trichomes at base on lower surface, the margins and midrib on upper surface scabrous, the lower surface with prominent midrib and usually 3 lateral veins. Fertile shoots rare, 2–8 cm long, their leaves much reduced; panicles very small, of 1–4 spikelets, the spikelets 7–9 mm long; glumes minute; sterile lemmas acuminate; fertile lemmas acute. Fruits not seen. *Shattuck 717, Croat 4358.*

Abundant in the forest, often very abundant locally on the shore. *Shattuck 717* was collected in flower early in the dry season. Elsewhere flowers have been seen in October. Plants probably flower only at intervals of several years.

Might be confused with either *Rhipidocladum racemiflorum* or *Lasiacis divaricata* (L.) Hitchc.; the latter species is not known from BCI.

Guatemala to Panama. In Panama, known from tropical moist forest in the Canal Zone and its vicinity.

See Fig. 44.

CYNODON L. C. Rich.

Cynodon dactylon (L.) Pers., Synops. Pl. 1:85. 1805

Bermuda grass

Stoloniferous, widely creeping perennial; rhizomatous; culms slender, 10–40 cm tall, glabrous. Sheaths longer than the internodes, glabrous or sparsely pilose at the apex; blades 2–20 cm long (often less than 5 cm long), 2–4 mm wide, glabrous to scabrous, especially on margins. Inflorescences terminal with several digitate spikes 2–7 cm long, ca 1 mm wide; rachilla prolonged beyond the spikelets; spikelets 1-flowered, 2–3 mm long; glumes nearly equal. Fruits not seen. *Ebinger 246.*

Infrequent in the Laboratory Clearing near the Animal House. Flowering throughout the year.

Under certain environmental conditions the species produces hydrocyanic acid (Blohm, 1962). The toxin affects the nervous and circulatory system of animals by eliminating the normal digestive tract flora, which is necessary for synthesis of the vitamin B complex.

Throughout warmer regions of the world. Probably throughout tropical moist regions of Panama.

DIGITARIA Haller

Digitaria ciliaris (Retz.) Koel., Descr. Gram. 27. 1802

D. adscendens Henr.; *D. sanguinalis* sensu auct. non (L.) Scop.

Annual; culms decumbent or geniculate-spreading to erect, often rooting at lower nodes, glabrous. Sheaths glabrous to papillose-hirsute (especially at apex); ligules membranaceous, truncate; blades mostly 4–10 cm long and 4–10 mm wide, minutely scabrous and also sparsely pilose; racemes 2 to several, digitate or in up to 3 whorls; rachis ca 1 mm wide, narrowly winged, its margin scabrous; spikelets paried on rachis, one nearly sessile, the other pedicellate, ca 3 mm long, the first glume minute, the second glume one-half to three-fourths as long as fruit; sterile lemma longer than fruit, prominently veined, the margins often villous. Fruits lanceolate, pale brown, ca 3.5 mm long, bearing several rows of long villous trichomes. *Shattuck 356a.*

Rare weed in clearings; collected once by Shattuck. Flowers throughout the year, principally during rainy season.

Distinguished from *Axonopus compressus,* with which it may be confused, by having two spikelets per node.

KEY TO THE SPECIES OF DIGITARIA

Spikelets ca 3 mm long; rachis ca 1 mm wide ..... *D. ciliaris* (Retz.) Koel.
Spikelets ca 2 mm long or less; rachis less than 0.7 mm wide:
  Leaves ± glabrous; spikelets ca 1.3 mm long, lacking scattered, long, white trichomes along rachis; second glume equaling fruit ..... *D. violascens* Link
  Leaves conspicuously pubescent; spikelets ca 2 mm long with scattered, long, white trichomes along rachis; second glume about half as long as fruit ..... *D. horizontalis* Willd.

Fig. 43. *Brachiaria mutica*

Fig. 44. *Chusquea simpliciflora*

Fig. 45. *Gynerium sagittatum*

This species was treated by Standley (1933) and the *Flora of Panama* as *D. sanguinalis* (L.) Scop. However, *D. sanguinalis* is restricted to temperate regions, whereas this species inhabits tropical and subtropical regions.

Throughout tropics and subtropics of the world, ecologically variable. In Panama, known from most tropical moist forest regions and from premontane wet forest in Chiriquí (Boquete), from tropical wet forest in Colón (Miguel de la Borda), and from premontane dry forest in Coclé (Santa Clara Beach).

Digitaria horizontalis Willd., Enum. Pl. 92. 1809
Crabgrass

Similar in habit, size, and most other aspects to *D. ciliaris*, except the margins of the leaves lighter in color, scabrous, usually densely pilose; the racemes digitate or more commonly closely grouped on axis; the rachis to 0.5 mm wide, winged, the margins scabrid, but also sometimes bearing a few scattered long trichomes; the spikelets 2 mm long, the first glume minute or lacking, the second glume about half as long as fruit, the sterile lemma glabrous or nearly so. Fruits dark brown, shiny, ca 1.3 mm long. *Croat 8563.*

Frequent weed of clearings. Probably flowers throughout the year, especially in the rainy season.

Most easily distinguished from *D. ciliaris* by its smaller spikelets with a glabrous lemma.

Common in tropical and subtropical regions. In Panama, ecologically variable; from tropical moist forests in Bocas del Toro, Panamá, Darién, and the Canal Zone (doubtless elsewhere), from tropical dry forest in Panamá (Taboga Island), from premontane wet forest in Panamá, and from lower montane wet forest in Chiriquí (Volcán).

Digitaria violascens Link, Hort. Berol. 1:229. 1827

Small perennial, ca 35 cm tall; culms slender, glabrous. Sheaths longer than the internodes, glabrous; blades mostly 8–15 cm long, ca 4 mm wide, glabrous or nearly so. Inflorescences of several, digitate racemes 6–10 cm long; rachis winged, scabrid on margins; spikelets 2 or 3 per node, appressed, ca 1.3 mm long; pedicels short, of variable lengths; first glume absent; second glume and sterile lemma equaling fruit, minutely pubescent at least near margin. Fruits dark brown, shiny, minutely striate. *Croat 16572.*

Collected once in the Laboratory Clearing. That specimen had fruits in early August.

Wide but scattered distribution in the New World; Panama through northern South America; West Indies; occasionally East Asia, from where it may have been introduced. In Panama, from tropical moist forest on BCI and in Colón.

ELEUSINE Gaertn.

Eleusine indica (L.) Gaertn., Fruct. & Sem. Pl. 1:8. 1788
Goosegrass

Annual, growing in spreading clumps, 20–50(70) cm tall, glabrous except for tufts of trichomes at apex of sheaths and at base of racemes. Sheaths flattened, pubescent near margin at apex, margins hyaline; ligules membranaceous, ca 1 mm long, erose; blades 7–25 cm long, 3–5(8) mm wide, often conduplicate, sometimes sparsely pilose above, scabrous on margins. Inflorescences of 2 to several spikes, the spikes 5–10 cm long, digitate or with 1 or 2 a short distance below; spikelets solitary at each node, each spikelet of few to several flowers, sessile, 2–5 mm long; glumes shorter than the first floret; glumes and lemmas with a scabrid keel, green near the keel, otherwise very light. Fruits dark brown, finely ridged, enclosed in a loose, thin exocarp. *Croat 10305.*

Occasional, in clearings. Flowers throughout the year, principally in the rainy season.

Southern half of United States south to northern Argentina and Uruguay; West Indies; Galápagos Islands; also in the Old World. In Panama, from tropical moist forest in Bocas del Toro, Colón, San Blas, Coclé, Panamá, Darién, and the Canal Zone and from tropical dry forest in Coclé and Panamá.

GYNERIUM Willd. ex Beauv.

Gynerium sagittatum (Aubl.) Beauv., Ess. Agrost. 138, pl. 24, f. 6. 1812
Uva grass, Wild cane, Cana blanca

Large, dioecious perennial, usually to 3.5 m tall (frequently taller elsewhere); culms glabrous, becoming woody, to 1.5 cm or more diam, frequently branching near the base and sometimes with stout, leafy stolons. Sheaths longer than the internodes, with a long patch of pilose-woolly trichomes on the outside below the blades and also along the margins near the apex; blades to 1 or 2 m long, 4–6 cm wide, forming a fan-shaped summit on a sterile culm. Panicles 1 m or more long, the branches erect to drooping, white turning reddish-brown; pistillate spikelets with glumes very unequal, the first 4–5 mm long, the second 9–12 mm long and scabridulous, the lemma narrow, tapered to a long awn, together with the awn 6–10 mm long, with long spreading-pilose trichomes exceeding the awn; staminate spikelets with glumes ± equal, 2–3 mm long, the lemma glabrous. Fruits narrowly oblong, ca 1 mm long, brown. *Croat 10384.*

Occurring on shore on the steep banks of the north shore and on the few sandy beaches, where large lateral runners may extend considerable distances across the beach front, producing numerous erect branches. Flowers throughout the year, especially in the early rainy season.

Southern Mexico to Paraguay; West Indies. In Panama, known from tropical moist forest in the Canal Zone and vicinity and in Darién.

See Fig. 45.

HOMOLEPIS Chase

Homolepis aturensis (H.B.K.) Chase, Proc. Biol. Soc. Wash. 24:146, f. 12. 1921

Perennial, stoloniferous, ± erect, mostly 20–60 cm tall; culms slender, glabrous. Sheaths mostly shorter than internodes, glabrous but with pubescence on collar and

long-ciliate margins; blades narrowly lanceolate, 4–12 cm long, 1–1.5 cm wide, rounded to subcordate at base, long-pilose above, glabrous to long-pilose below, scabrous and long-ciliate on margins, minutely cross-veined. Panicles 5–10 cm long, narrow, having very slender, few-flowered branches; spikelets ca 7 mm long, acuminate; glumes glabrous, nearly equal, covering sterile lemma and fertile floret, the sterile lemma villous between lateral veins. Fruits indurate, acuminate, white or tan, smooth, shiny. *Croat 5624.*

Common in clearings. Flowers are seen all year, but especially during the rainy season.

Sometimes confused with *Acroceras oryzoides,* but is distinguished by the nearly equal glumes covering the fruit and by the pubescence of the sterile lemma.

Southern Mexico south to Peru, Bolivia, and northern and eastern Brazil. In Panama, ecologically variable; known throughout tropical moist forest and from tropical wet forest in Colón, Panamá, and Bocas del Toro, from premontane rain forest in Panamá (Cerro Jefe), and from lower montane rain forest in Chiriquí (Volcán).

HYMENACHNE Beauv.

Hymenachne amplexicaulis (Rudge) Nees, Agrost. Bras. 276. 1829

Aquatic perennial, mostly 1–2 m tall; culms ± stout, rooting at nodes. Sheaths mostly shorter than internodes, glabrous, sometimes ciliate; blades 15–35 cm long, 1.5–3 cm wide, cordate-clasping at base, glabrous, scabrid on margins and ciliate near the base. Inflorescence a dense, spikelike panicle 8–30(50) cm long, 1–1.5 cm thick; spikelets 3–4 mm long, acuminate; first glume one-fourth to one-half as long as spikelet with scabrous keel; second glume and sterile lemma covering fruit, scabrous on veins, the sterile lemma narrowly acuminate. Fruits oblong-elliptic, ± flattened, dull, light greenish. *Croat 7197.*

Infrequent, usually growing in shallow water at the edge of the lake. Flowers throughout the year, especially in the late rainy and early dry seasons.

The spikelets are probably dispersed in part by water, but the sharply pointed sterile lemma could easily be caught and carried in bird feathers.

Throughout tropics of Western and Eastern hemispheres. In Panama, from tropical moist forest in Coclé, Darién, and the Canal Zone and from tropical dry forest in Coclé (Aguadulce).

HYPARRHENIA N. J. Andersson

Hyparrhenia rufa (Nees) Stapf in Prain, Fl. Trop. Africa 9:304. 1919

Faragua

Erect perennial, 1–2(2.5) m tall; culms glabrous, in large dense clumps. Sheaths glabrous or strigose between veins, especially near margins; blades to ca 35 cm long, 2–8 mm wide, glabrous or scaberulous, usually scabrid on margins. Inflorescences usually open, 20–40 cm or more long, with paired racemes at ends of ultimate branchlets subtended by a narrow spathe; peduncles long, slender, strigose; racemes 2–4 cm long; spikelets 3–4 mm long, densely covered with long reddish-brown trichomes, paired, the pedicellate one awnless; sessile spikelets with geniculate, reddish-brown awn 1.5–2 cm long. Fruits not seen. *Croat 6995.*

Common in the Laboratory Clearing and rarely encountered along exposed areas of the shore. Flowers throughout the year.

This species is the most abundant grass along roadsides in the Canal Zone and one of the most widely used forage grasses in lowland Panama, forming virtually complete stands where grazed and burned.

Veracruz, Mexico, south to Panama, Peru, and Brazil; Cuba, Jamaica; throughout Africa, where it is native. Ecologically wide-ranging throughout Panama.

ICHNANTHUS Beauv.

Ichnanthus brevivaginatus Swall., Phytologia 4:425. 1953

Perennial, ± erect except at decumbent base, rooting at lower nodes, villous especially at nodes. Sheaths much shorter than internodes, prominently ribbed, villous; blades linear-lanceolate to ovate-lanceolate, acuminate, inequilateral and obtuse to rounded at base, 5–10 cm

KEY TO THE SPECIES OF ICHNANTHUS

Leaf blades usually less than 3.5 cm long and 1 cm wide, ± linear-lanceolate to short ovate-lanceolate, pubescent with papillose trichomes. . . . . *I. tenuis* (Presl) Hitchc. & Chase

Leaf blades usually more than 5 cm long and 1 cm wide, long linear-lanceolate to obovate-lanceolate, glabrous or pubescent (if pubescent, the trichomes not papillose except at margin of blade just above sheath):

- Inflorescences with 2 or more branches from terminal node of stem; longest panicle 15–26 cm long and 4–5 cm wide, beginning to branch ca 11 cm from base; axillary nodes of stems producing inflorescences; leaf blades obovate . . . . . *I. pallens* (Sw.) Benth.
- Inflorescences with 1 branch from terminal node of stem (if 2, neither is long); longest panicle 7–12 cm long and 2–4 cm wide, beginning to branch 2.5–5.5 cm from base; axillary nodes of stems usually lacking visible inflorescences; leaf blades linear-lanceolate . . . . . *I. brevivaginatus* Swall.

long, 7–20 mm wide, glabrous or with deciduous stiff trichomes on upper surface. Inflorescences with a few short branches from upper node of stem, the longest panicles 7–12 cm long and 2–4 cm wide, beginning to branch 2.5–5.5 cm from base; axillary nodes of stems usually without visible inflorescences; spikelets 3.5–4 mm long, scabrous on keel of first and second glumes; first glume about two-thirds the length of spikelet, acute to acuminate; second glume much longer than fruit, acuminate to ± aristate; sterile lemma slightly longer than fruit, long-ciliate, blunt. Fruits oblong-elliptic, ca 2 mm long, dull white. *Croat 8351, 12868.*

Rare, along trails in the forest, mostly on the western side of the island.

Belize to Panama. In Panama, known from tropical moist forest in the Canal Zone and Panamá and from premontane wet forest in Chiriquí (San Félix).

Ichnanthus pallens (Sw.) Munro ex Benth., Fl. Hongk. 414. 1861

Perennial, decumbent-spreading, rooting at lower nodes, to 1 m or more long, glabrous or sparsely pilose, the nodes not villous. Sheaths much shorter than internodes, glabrous to pilose or papillose-pilose, especially on margins; ligules thin, ca 1 mm long; blades lanceolate to obovate, acuminate, rounded and ± clasping and asymmetrical at base, 5–12 cm long, mostly 5–15 mm wide, scaberulous, finely cross-veined downward. Inflorescences with 2 or more branches from terminal node of stem, the longest panicle 15–26 cm long and 4–5 cm wide, beginning to branch ca 11 cm from base; axillary nodes of stems producing inflorescences; spikelets 3–3.5 mm long, glabrous or sparsely pilose or hirsute; first glume acuminate, one-half to two-thirds as long as spikelet, scabrous on keel; second glume and sterile lemma acuminate, subequal; sterile lemma long-ciliate. Fruits ca 2 mm long, oblong-elliptic, the scars extending downward into very narrow wings. *Croat 4228, 7893.*

Occasional, along trails and at the edges of clearings on the shore. Plants may become locally abundant in open areas of forest trails, especially on slopes. Flowers principally in the late rainy and early dry seasons. Most fruits are gone by the end of the dry season.

Like *I. tenuis,* the species frequently has proliferated spikelets, which give the plants a very different appearance, often more like that of the genus *Poa.*

Throughout tropical America. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién, from tropical dry forest in Panamá (Taboga Island), and from premontane wet forest in Chiriquí.

Ichnanthus tenuis (Presl) Hitchc. & Chase, Contr. U.S. Natl. Herb. 18:334. 1917

Creeping annual; culms forming large loose mats, rooting at lower nodes, freely branching, usually pubescent. Sheaths usually much shorter than internodes, pilose or papillate-pilose with spreading trichomes; blades ± linear-lanceolate to short ovate-lanceolate, acuminate, 1–3.5(5) cm long, 4–10 mm wide, usually papillate-pilose. Inflorescences of 2 to several spreading racemes, pubescent in axils, the lowermost 1–3 cm long; spikelets 3–4 mm long, appressed, sparsely pilose especially along margins on glumes and sterile lemma; first glume acuminate or attenuate, almost aristate, two-thirds or more as long as spikelet; second glume and sterile lemma ± equal, longer than fruit. Fruits 2–2.5 mm long, oblong-elliptic, the wings reduced to inconspicuous scars. *Ebinger 282.*

Collected once in the small clearing at Fairchild Point. Flowers throughout the year, especially in the early dry season and the middle of the rainy season (November to January and July to September).

Guatemala south to Colombia, Venezuela, the Guianas, and Brazil; Trinidad. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Panamá, from premontane moist forest in the Canal Zone and Panamá, and from premontane wet forest in Chiriquí.

ISACHNE R. Br.

Isachne polygonoides (Lam.) Doell in Mart., Fl. Brasil. 2(2):273. 1877

Annual; decumbent-spreading, rooting at lower nodes; culms slender, glabrous, freely branching. Sheaths much shorter than internodes, papillose-hispid and ciliate, prominently veined; blades lanceolate, 2–5 cm long, 5–10(15) mm wide, rounded to subcordate at base, strigose to papillose-hispid especially below, the margins white and scabrid. Panicles diffuse, 5–10 cm long, nearly as wide, the branches slender, glandular-spotted; spikelets subglobose, 1.5–2 mm long; glumes equal, slightly shorter than spikelet, glabrous to sparsely pubescent above middle; florets 2, one staminate and similar in size and texture to the second glume, the other perfect. Fruits ca 1.3 mm long, white, plano-convex, densely pubescent. *Croat 13242.*

Infrequent, in marshes and floating masses of vegetation along the shore. Probably flowers throughout the year.

Costa Rica to Peru and Brazil; West Indies. In Panama, in swamps and marshes throughout a wide range of life zones; known from tropical moist forest in the Canal Zone, Chiriquí, Veraguas, and Panamá (doubtless elsewhere also), from tropical dry forest in Coclé (Aguadulce), from tropical wet forest in Colón (Portobelo), and from premontane wet forest in Chiriquí.

ISCHAEMUM L.

Ischaemum indicum (Houtt.) Merr., J. Arnold Arbor. 19:320. 1938

Erect, stoloniferous plant, mostly to 50 cm tall; culms slender, glabrous except for long tufts at collar. Sheaths slightly shorter than the internodes, long-ciliate, papillose-

KEY TO THE SPECIES OF ISCHAEMUM

Spikelets pubescent at apex, the glume lacking transverse ridges ..... *I. indicum* (Houtt.) Merr.
Spikelets glabrous except at base, the glume bearing several prominent, transverse ridges ..... *I. rugosum* Salisb.

pubescent; blades 4–12 cm long, ca 5 mm wide, short-pilose throughout, minutely scabrid on margins. Inflorescences of paired racemes 3–7 cm long; rachis and pedicel pilose-ciliate, disarticulating; spikelets paired, to 5.5 mm long, the long-pedicellate spikelet often not fruitful; glumes rounded at base, narrowly acuminate, pilose above middle, scabrid on margins; lemmas hyaline, the fertile lemma with a geniculate, twisted awn, the awn ca 7 mm long. Fruits not seen. *Croat 7003.*

Locally abundant in the Laboratory Clearing north of the dock and along the stairs to the dining hall. Rather seasonal and conspicuous when in flower, otherwise inconspicuous. Flowering mostly in the dry season, abundantly in the early dry season.

The species resembles *Polytrias amaura,* but is distinguished from it by having only a single spike per peduncle.

Mexico to Ecuador and Brazil; West Indies. Introduced in Panama and currently known only from the vicinity of the Canal Zone.

Ischaemum rugosum Salisb., Icon. Stirp. Rar. 1: pl. 1. 1791

Annual; culms ± stout, glabrous except for bearded nodes, freely branching. Sheaths keeled toward apex, glabrous except sometimes near the apex; blades 10–20 cm long, 6–13 mm wide, sparsely pubescent, scabrid on margins. Inflorescences of paired terminal racemes 3–13 cm long, held tightly together when young, often partly enclosed in a sheath; rachis and pedicel thick, long-ciliate; spikelets paired, 3–5 mm long, bearded at base, the pedicellate spikelet often not fruitful; first glume and sessile spikelet strongly transversely ridged, ciliate and acute at apex; lemmas hyaline, the fertile lemma bifid with a long, geniculate, twisted awn to 1.5 cm long between teeth. Fruits ca 1.7 mm long, whitish. *Croat 12941.*

Infrequent in the Laboratory Clearing. Flowering from November to April, principally in the dry season.

Native to the Old World; introduced throughout the tropics. In Panama, from tropical moist forest in the Canal Zone, Bocas del Toro, Coclé, Panamá, and Darién and from tropical dry forest in Los Santos.

LASIACIS (Griseb.) Hitchc.

The genus is related to *Panicum,* but is distinguishable from it by having globose spikelets borne obliquely on pedicels, woolly pubescence at the apex of the spikelet bracts, black coloration of the spikelet, oil production of the glumes and sterile lemma, and very indurate fertile florets. The last three characters are adaptations for bird dispersal of the fruit (Davidse & Morton, 1973).

Lasiacis oaxacensis (Steud.) Hitchc., Proc. Biol. Soc. Wash. 24:145. 1911

Perennial; culms extensively creeping, rooting at nodes, the ultimate parts ± erect, 0.5–2 m tall, branched many times; internodes 2–5 mm thick, mostly herbaceous, solid, rarely partially hollow, glabrous. Sheaths usually glabrous, one or both margins usually ciliate; ligules prominent, 2.5–5 mm long; blades narrowly linear-lanceolate, acuminate, nearly symmetrical at base, (13)17–29 cm long, 1.2–2.4 cm wide, usually scabrous, especially along midrib. Panicles mostly terminal, 16–31 cm long; branches widely spreading, usually naked in lower half to two-thirds; spikelets in pairs or small clusters, mostly 3.8–4.2 mm long; first glume 7–11-veined, about half as long as second glume; second glume and lemmas woolly-pubescent at apex; sterile floret usually bearing a staminate flower; sterile palea as long as fertile floret. Seeds to 3 mm long and 1.6 mm wide. *Croat 7730.*

Common along the margins of larger clearings. Flowers in the latest part of the rainy season and early in the dry season. The fruits develop quickly and may be present during most of the dry season. Davidse and Morton (1973) reported that both *L. oaxacensis* and *L. sorghoidea* are most abundant in the early dry season.

As for *L. sorghoidea,* fruits are dispersed by small birds.

Mexico (Nayarit and Veracruz) south through Central America to Colombia, Venezuela, Ecuador, and Peru; Greater Antilles. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Panamá, also known from premontane wet forest and lower montane wet forest in Chiriquí and from premontane moist forest in Panamá (Juan Diaz).

KEY TO THE SPECIES OF LASIACIS

Plants erect, rarely branched; leaves cordate-clasping at base, frequently more than 3.5 cm wide ..... *L. procerrima* (Hack.) Hitchc.
Plants usually ± clambering, not stiffly erect; leaves not cordate-clasping, always less than 3.5 cm wide:
  Culms hollow, or partially hollow with some pith remnants; ligules inconspicuous, usually less than 1.5 mm long ..... *L. sorghoidea* (Ham.) Hitchc. & Chase var. *sorghoidea*
  Culms solid, pithy; ligules conspicuous, usually more than 2.5 mm long ..... *L. oaxacensis* (Steud.) Hitchc.

Lasiacis procerrima (Hack.) Hitchc., Proc. Biol. Soc. Wash. 24:145. 1911

Coarse, erect, short-lived perennial or annual, 1–2(4) m tall; culms semiwoody at base, to 1 cm thick, usually unbranched, glabrous, rooting at lower nodes. Sheaths shorter than the internodes near base, closely overlapping near apex, glabrous or puberulent and glaucous, often ciliate near apex; ligules usually 0.5–1.5 cm long; blades linear-lanceolate or lanceolate, cordate-clasping at the base, 15–40 cm long, 2–5 cm wide, glabrous above, glabrate below, scabrous on the margins. Inflorescence a large, diffuse panicle to 1 m long, the branches mostly whorled toward the base, ridged, scabrous on ridges; spikelets broadly obovate, ca 3.5 mm long, sessile to short-pedicellate; first glume one-half to one-third as long as spikelet, lanate-pubescent at tip; second glume and sterile lemma slightly shorter than the fruit, similarly pubescent at tip. Fruits indurate, white and shiny. *Croat 6108.*

Uncommon, on the shore and in the Rear Lighthouse Clearing. Flowers and fruits throughout most of the rainy season, with most flowers appearing in June and July, most fruits by September.

Mexico (Sinaloa and Puebla) south throughout Central America to Colombia, Venezuela, Peru, and western Brazil. In Panama, ecologically variable; known from tropical moist forest all along the Atlantic slope and on the Pacific slope in the Canal Zone and Panamá; known also from tropical dry forest in Panamá (Taboga Island) and from premontane moist forest in Chiriquí and Panamá.

Lasiacis sorghoidea (Desv. ex Ham.) Hitchc. & Chase var. **sorghoidea,** Contr. U.S. Natl. Herb. 18:338. 1917
Carricillo, Millo

Perennial; culms caespitose, 1–10 m long, erect at base, arching and leaning on surrounding vegetation; internodes 5–15 mm thick, hollow, glabrous or with pubescence papillose or reduced to a single line, at least the older ones somewhat woody; nodes glabrous. Sheaths pubescent, rarely glabrate, often papillate-pubescent, especially near apex; ligules inconspicuous, usually to 1.5 mm long; blades mostly elliptic to linear-lanceolate, acuminate at apex, often asymmetrical at base, 8–20 cm long, 1–3.5 cm wide, usually puberulent above and velutinous below, the margins scabrid. Panicles terminal, (5)9–25(35) cm long; branches usually scabrous, at first ascending, spreading when fruiting; spikelets obovate to elliptic, green to purple-black at maturity of fruit, mostly 3.5–4 mm long; first glume 7–11-veined, one-third to one-half as long as second glume; second glume and sterile lemma woolly-pubescent at tip; sterile floret with or without a staminate flower; lemma 9–11-veined; palea one-half as long to same length as fertile floret. Seeds 1.8–2.3 mm long. *Croat 8009.*

Locally abundant along the edges of point clearings and along exposed banks at the margin of the lake; less frequent in the larger clearings. Flowers from the late rainy season to the middle of the dry season, but especially in the early dry season. Most fruits mature from middle to late dry season.

The entire spikelet becomes purple-black at maturity. The caryopsis is carried away with the rest of the spikelet by small birds.

Mexico (Oaxaca and Veracruz) through Central and South America to northern Argentina and southern Brazil; West Indies; usually at less than 1,000 m elevation but ranging to 1,800 m. In Panama, known from tropical moist forest in the Canal Zone, San Blas, and Panamá (doubtless elsewhere also), and from premontane wet forest in Chiriquí.

LEERSIA Sw.

Leersia hexandra Sw., Prodr. Veg. Ind. Occ. 21. 1788

Slender, aquatic perennial, to 1 m tall; culms rooting at lower nodes, erect, retrorsely hirsute at nodes. Sheaths shorter than the internodes, keeled, glabrous to sparsely retrorsely hirsute, ciliate, with a small auricle at apex; ligule to 3 mm long, truncate, fused with auricles; blades mostly 15–30 cm long, 5–12 mm wide, scabrid at least on midrib below. Inflorescence a narrow panicle to 20 cm long, the branches scabrous; spikelets 3 mm long, often purplish, inequilateral in side view, lacking glumes; lemma and palea equal in length, the veins scabrid, the margins hispid-ciliate. Fruits not seen. *Croat 12939.*

Frequent in the marshes at the edge of the lake. Flowers sporadically throughout the year, especially in the rainy season.

The prominent hispid-ciliate margins of the fruits seem to be logically designed for epizoochorous dispersal, but the fruit is probably dispersed by water currents to some extent also.

Virginia to Texas in the United States and south to Ecuador, Argentina, and southern Brazil; West Indies; cosmopolitan in Asia and elsewhere. In Panama, from tropical moist forest in the Canal Zone and Panamá and from tropical dry forest in Coclé.

LEPTOCHLOA Beauv.

Leptochloa virgata (L.) Beauv., Ess. Agrost. 71, 161, 166, pl. 15, f. 1. 1812

Perennial; culms mostly erect, usually about 1 m tall, glabrous. Sheaths as long as or longer than the internodes; blades 10–27 cm long, 4–12 mm wide, minutely scabrid, the margins scabrous. Inflorescence a panicle of slender racemes 5–12 cm long; rachis scabrid; spikelets 3- or 4-flowered, 2–3 mm long; glumes keeled, the keel scabrid, the second glume slightly longer than the first; lemmas flattened, imbricate, sparsely pilose on the margin, sometimes awned. Fruits oblong-elliptic, brown, ca 0.8 mm long. *Stattuck 461.*

Collected once by Shattuck at the end of Miller Trail; not seen recently on the island. Flowers throughout the year, especially during the rainy season.

The small, sharply pointed spikelets are possibly dispersed in part by adhering to passing animals and also in part by wind.

Occurring in most tropical and subtropical areas of the

Western Hemisphere; cosmopolitan in eastern Asia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Panamá, and Darién; known also from premontane moist forest in Los Santos and Panamá and from tropical dry forest in Panamá (Taboga Island).

LITHACHNE Beauv.

Lithachne pauciflora (Sw.) Beauv. ex Poir., Dict. Sci. Nat. 27:60. 1823

Monoecious perennial, to 60 cm tall; culms slender, glabrous, constricted at nodes, somewhat geniculate at the lower nodes. Sheaths except the uppermost shorter than the internodes, ± glabrous, sometimes ciliate, the lower ones bladeless; blades asymmetrical, acuminate, ± rounded to acute on one side of base, obtuse on the other, 5–10 cm long, 1.5–2.5 cm wide, glabrous except on and near the scabrid margins. Inflorescence a small panicle either terminal and staminate or axillary with 1 pistillate spikelet and 2 to several staminate ones; staminate spikelets lacking glumes, 4–6 mm long, soon deciduous; pistillate spikelets lacking first glume; second glume and sterile lemma nearly equal, exceeding fruit, long-acuminate, to 1 cm long, prominently veined, the veins scabrid near the apex. Fruits white, shiny, indurate, triangular, truncate at apex, 4–5 mm long. *Croat 6474.*

Common in the forest, mostly along trails, usually in small clumps. Flowering and fruiting throughout the year, especially in the rainy season.

Easily distinguished by the solitary, white, triangular fruits.

Mexico to northern Argentina; West Indies. In Panama, known from tropical moist forest in the Canal Zone and Panamá and from premontane wet forest in Chiriquí (Boquete).

OLYRA L.

Olyra latifolia L., Syst. Nat. ed. 10, 1261. 1759
O. cordifolia H.B.K.
Carricillo

Monoecious perennial, mostly 2–3 m tall and erect to arching, rarely to 5 m long and clambering; culms becoming woody, to 6 mm diam, often mottled with purple, freely branching at upper nodes. Sheaths glabrous to hispid, usually longer than the internodes, the lowermost short and nearly bladeless; blades lance-linear to lance-oblong, inequilateral, acuminate at apex, acute to rounded at base, very short-petiolate, the lower surface usually glabrous, the margins and midrib on upper surface scabrous, the upper surface papillate or papillate-scabridulous. Panicles terminal or upper-axillary, narrow to pyramidal, 5–17 cm long; branches and peduncles closely scabrid and sparsely hispid, the branches with a single pistillate spikelet at the end, the staminate spikelets scattered along branch below it; staminate spikelet reduced to the awned lemma and palea, deciduous, 4–5 mm long excluding awn, the awn 2–3 mm long; pistillate spikelet lacking first glume; second glume and sterile lemma 1–2 (2.5) cm long, long-acuminate, minutely scabridulous, diverging and exposing fruit at maturity, often purplish along margin. Fruits white, shiny, smooth, indurate, acute at apex, 5–6 mm long. *Croat 6634, 11713.*

Frequent in the forest. Plants flower and fruit principally throughout the rainy season, though they are occasionally fertile during the early dry season.

Plants are extremely variable, especially in size of leaves and inflorescences. The larger plants, which may represent tetraploid races, have previously been separated as *O. cordifolia* H.B.K., but the species is now considered polymorphic.

Throughout most tropical areas of the New World; Africa. In Panama, known from tropical moist forest in the Canal Zone, Veraguas, Panamá, and Darién, from premontane wet forest in Colón, Chiriquí, and Panamá, from tropical wet forest in Colón, and from premontane rain forest in Panamá (summit of Cerro Jefe).

OPLISMENUS Beauv.

Oplismenus burmanni (Retz.) Beauv., Ess. Agrost. 54. 1812
Pajita de ratón

Low, creeping annual, often in dense stands; culms slender, ± decumbent with erect branches, bearing fine soft trichomes, rooting at lower nodes, often purplish. Sheaths usually much shorter than the internodes, long-pubescent especially near the margins, the trichomes longer and sparser above; blades lance-elliptic, acuminate, 2–5 cm long, 5–15 mm wide, sparsely long-pubescent, the margins scabrid. Inflorescence a panicle of 3–6 short, widely spaced racemes to 2 cm long; rachis and spikelet densely villous; spikelets dense, 2–3 mm long; glumes nearly equal, long-awned; awns antrorsely scabrous, 10–14 mm long on first glume, 3–8 mm long on second glume; sterile lemma exceeding fruit, usually awnless. Fruits narrowly elliptic, indurate, 1.5–2 mm long. *Croat 6947.*

Common to locally abundant in the forest on trails and sometimes on stream banks; common in clearings. Flowering chiefly at the beginning of the dry season.

Throughout the tropics of Western and Eastern hemi-

KEY TO THE SPECIES OF OPLISMENUS

Awns antrorsely scabrous; pubescence of rachis obscuring surface, the surface variably hispid and puberulent ..... *O. burmanni* (Retz.) Beauv.
Awns smooth; pubescence of rachis not obscuring surface, the surface densely and uniformly scabrid ..... *O. hirtellus* (L.) Beauv.

spheres. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién, from tropical dry forest in Panamá (Taboga Island), from premontane wet forest in Chiriquí, Los Santos, and Panamá, and from lower montane rain forest in Chiriquí.

Oplismenus hirtellus (L.) Beauv., Ess. Agrost. 54. 1812

Freely branching perennial, to 70 cm long; culms decumbent-spreading, rooting at the nodes, glabrous to short-pubescent, the pubescence most dense in slender rows. Sheaths shorter than or ± equal to the internodes, glabrous to hispid, the margins ciliate; blades 3–10.5 cm long, 10–20 mm wide, ± asymmetrical, usually short-pubescent on upper and lower surfaces, the margins scabrid. Inflorescence to 20 cm long, a terminal panicle of 3–7 widely spaced racemes 1.5–4 cm long, the rachis minutely and densely scabrid with pustular hispid trichomes; spikelets 3–4 mm long excluding awns; glumes about equal, two-thirds the length of the sterile lemma, sparsely pubescent, awned; awns glabrous, 5–12 mm long on first glume, 2–4 mm long on second; sterile lemma exceeding fruit, acuminate. Fruits indurate, white, shiny, ca 3 mm long, minutely striate. *Croat 13267.*

Common on trails in the forest and sometimes on rocks in streams. Flowers are most abundant in the early dry season.

Throughout the tropics of the Western Hemisphere. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién, from premontane wet forest in Chiriquí, Panamá, and Darién, and from lower montane wet forest in Chiriquí.

ORTHOCLADA Beauv.

Orthoclada laxa (L. C. Rich.) Beauv., Ess. Agrost. 70, 149, 168. 1812

Perennial, ± erect, 0.5–2 m tall; culms glabrous or nearly so, sometimes geniculate at lower nodes. Sheaths glabrous to short-pubescent, prominently veined; blades 5–20 cm long, 1–3.5 cm wide, the petioles distinct, 2–3 cm long, sparsely hispid above, glabrous to short-pubescent and conspicuously cross-veined below. Panicles diffuse, 15–30 cm long, about as wide, the branches slender, minutely antrorse-pubescent, the spikelets only near ends; spikelets 6–7 mm long, long-pedicellate, glabrous but with scabrous veins and margins of glumes and lemmas; first glume shorter than second, both shorter than sterile lemma; sterile lemma long-acuminate. Fruits indurate, dark brown, ± glabrous, weakly striate, 2.7–4 mm long. *Croat 7840.*

Frequent in the forest. Flowering mostly in the early dry season.

Spikelets disarticulate immediately below the spikelet and are possibly dispersed by attachment of the long-acuminate sterile lemma to passing animals.

Mexico to Peru and Brazil. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Panamá and from tropical wet forest in Colón.

See Fig. 46.

ORYZA L.

Oryza latifolia Desv., Jour. de Bot. (Desv.) 1:77. 1813

Coarse, erect perennial, 1–2 m tall; culms stout. Sheaths longer than the internodes, glabrous, keeled near the apex, the margins scabridulous; blades 15–50 cm long, 1–4 cm wide, sparsely pubescent or scabrous above and below, the margins scabrid. Panicles 25–40 cm long, the branches verticillate, scabrous, with spikelets in upper two-thirds; glumes minute; lemma indurate, 5–6 mm long, stoutly scabrous, minutely striate, awned, the awn 1–2 cm long. *Shattuck 849.*

Collected several times by Shattuck along the shore, but not seen recently. Flowering and fruiting throughout the year.

Belize to Brazil; West Indies; in marshes and along rivers and ditches. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Panamá, and Darién.

PANICUM L.

Panicum fasciculatum Sw., Prodr. Veg. Ind. Occ. 22. 1788

Espigadilla, Granadilla

Erect annual, 15–100 cm tall; culms glabrous to hispid. Sheaths hispid, especially on margins; blades 10–25 cm

KEY TO THE SPECIES OF PANICUM

This key includes some common species often confused with *Panicum.*

Spikelets short-pedicellate along one side of the panicle branches forming spikelike or 1-sided racemes:
- Fruits transversely rugose ..... *Paspalidium geminatum* Stapf
- Fruits smooth, not rugose:
  - Blades lanceolate or ovate-lanceolate ..... *Panicum pulchellum* Raddi
  - Blades linear, often elongate, frequently cordate at base:
    - Spikelets nearly sessile, densely arranged along 1 side of the rachis:
      - Plants usually less than 1 m tall, growing in clearings or on trails; blades less than 20 cm long ..... *Panicum pilosum* Sw.
      - Plants usually more than 1 m tall, growing in marshes or moist areas; blades often more than 20 cm long ..... *Panicum milleflorum* Hitchc. & Chase
    - Spikelets sessile or pedicellate, in part on short branches along the lower side of the rachis; culms with nodes conspicuously bearded ..... *Panicum polygonatum* Schult.

Fig. 47. *Panicum grande*

Fig. 46. *Orthoclada laxa*

Fig. 48. *Panicum grande*

Spikelets in open or contracted panicles but not on 1-sided racemes:
- Fruits transversely rugose:
  - Plants perennial; culms in large coarse clumps, 1–2.5 m tall; spikelets green; cilia of ligule 3–4 mm long ..... *Panicum maximum* Jacq.
  - Plants annual; culms slender, to 1 m tall; spikes brown to reddish; cilia of ligule ca 1 mm long ..... *Panicum fasciculatum* Sw.
- Fruits not rugose:
  - First glume much less than one-fourth as long as the spikelet ..... *Panicum trichanthum* Nees
  - First glume more than one-fourth as long as the spikelet:
    - Blades as much as 1 m long and 6 cm wide ..... *Panicum grande* Hitchc. & Chase
    - Blades much smaller:
      - Fruits crested at apex ..... *Acroceras oryzoides* Stapf
      - Fruits not crested:
        - Panicles 40–60 cm long; branches in verticils ..... *Panicum mertensii* Roth.
        - Panicles not more than 30 cm long; branches not in verticils:
          - Inflorescences widely branched; spikelets ca 1 mm long, borne on pedicels many times longer than spikelets ..... *Panicum trichoides* Sw.
          - Inflorescences not widely branched; spikelets more than 3 mm long, borne on pedicels only a few times longer than spikelets ..... *Ichnanthus pallens* Benth.

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long, 5–20 mm wide, mostly glabrous but with scabrid margins. Panicles mostly 10–15 cm long, rather dense; branches scabrid; spikelets 2.5–3 mm long, dark purplish-brown, glabrous; first glume one-third to one-half as long as spikelet; second glume and sterile lemma exceeding fruit. Fruits white, 1.5–2 mm long, transversely rugose. *Croat 11612.*

Infrequent in both the Laboratory Clearing and the Rear #8 Lighthouse Clearing. Flowering and fruiting throughout the year, especially during the rainy season.

Throughout most tropical areas of the Western Hemisphere. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, Panamá, and Darién and from tropical wet forest in Colón.

Panicum grande Hitchc. & Chase, Contr. U.S. Natl. Herb. 17:529, f. 143. 1915
Guinea grass

Stoloniferous perennial, 1.5–2 m or more tall; culms hollow, decumbent at the base; nodes with a narrow band of short sericeous trichomes. Sheaths mostly longer than the internodes, glabrous or sparsely hispid at the throat; ligules 2–3 mm long, the upper margin irregular and fringed; larger blades (mid-culm) to 1 m long and 6 cm wide, the margins scabrous. Panicles terminal, 30–60 cm long, to 40 cm wide; axis ± ribbed, the ribs scabrid; branches stiffly ascending, naked at base; spikelets oblong-elliptic, narrowly acute at apex, ca 2.5 mm long, glabrous; first glume to three-fourths the length of the spikelet; second glume as long as the spikelet, ribbed. Fruits 1.3–1.8 mm long, pale, smooth, shiny. *Croat 12700.*

Occasional, along the shore, often forming huge stands during the rainy season on silt deposits in Fuertes Cove. Seasonal behavior uncertain. Probably flowering and fruiting in the rainy season.

Distinguished from other *Panicum* by its large leaves.

Nicaragua to Venezuela; Trinidad. In Panama, known from tropical moist forest in the Canal Zone, Colón, Panamá, and Darién.

See Figs. 47 and 48.

Panicum maximum Jacq., Coll. Not. 1:76. 1786
Guinea grass

Tall, erect perennial, 1–2.5 m high; culms stout, glabrous but with bearded nodes. Sheaths mostly shorter than the internodes, papillose-hirsute becoming glabrous; ligules truncate and erose with dense cilia behind the ligule 4–5 times as long as the ligule, 3–4 mm long; blades to 70 cm long and 3 cm wide, glabrous to sparsely hispid with scabrous trichomes. Inflorescence a diffuse terminal panicle 20–45 cm long; branches slender, scabrid; spikelets long-pedicellate, 2.7–3.7 mm long, glabrous; first glume one-fourth to one-third as long as spikelet; second glume and sterile lemma nearly equal to each other and exceeding fruit. Fruits ca 2.7 mm long, greenish-white, transversely rugose. *Croat 6001, 11990.*

Common locally at the Laboratory Clearing along the stairs from the dock and in the Lighthouse Clearing. One of the most abundant roadside and pasture grasses in the isthmus.

Introduced throughout the tropics of the Western Hemisphere; native to Africa. In Panama, known from tropical moist forest in the Canal Zone, Veraguas, Los Santos, Herrera, Panamá, and Darién, from tropical dry forest in Panamá, and from premontane dry forest in Coclé.

Panicum mertensii Roth in R. & S., Syst. Veg. 2:458. 1817
P. megiston Schult.

Stout, erect perennial, 1–2 m tall; culms glabrous. Sheaths shorter than the internodes, sparsely papillose-pilose; ligules irregular and ciliate at apex, lacking long trichomes behind the ligule; blades 15–40 cm long, 15–30 mm wide, glabrous but with scabrid margins. Inflorescence a terminal panicle 40–60 cm long, the main axis ± stout, the branches slender, whorled at intervals; spikelets obovate to subglobose, pedicellate, 2.7–3.3 mm long, glabrous; first glume about one-fourth as long as spikelet; second glume and sterile lemma covering fruit. Fruits

greenish-white, ca 3 mm long, smooth, obovate. *Croat 11804.*

Infrequent, but locally abundant in quiet marshes. Flowers and fruits in the rainy season, mostly in the early rainy season.

Mexico to Paraguay; Cuba. In Panama, known from tropical moist forest in the Canal Zone and Panamá.

Panicum milleflorum Hitchc. & Chase, Contr. U.S. Natl. Herb. 17:494, f. 70. 1915

Perennial, ± erect, to 2 m tall (usually less), nearly glabrous but with hirsute nodes and papillose-hirsute sheaths; culms rooting at lower nodes. Blades 15–35 cm long, 12–20 mm wide, sometimes sparsely scabrous, the margins scabrous. Panicles 25–45 cm long; branchlets numerous, short, densely flowered, angulate, the angles scabrid, the base of the branchlets with longer trichomes; spikelets secund, ca 1.3 mm long, prominently veined; first glume about half as long as spikelet; second glume ± equaling sterile lemma. Fruits indurate, ca 1 mm long, shiny, white. *Croat 6408.*

Uncommon, occurring in swampy places; collected on the sandbar in Fuertes Cove. Flowering and fruiting in the rainy season.

Belize, and Panama to Brazil. In Panama, known from tropical moist forest in the Canal Zone and Panamá.

Panicum pilosum Sw., Prodr. Veg. Ind. Occ. 22. 1788
Grama de camino

Slender, erect perennial, 25–60 cm tall; culms geniculate and rooting at lower nodes, glabrous. Sheaths longer than the internodes, glabrous except for long cilia on margins especially near apex; ligules lacking; blades 5–22 cm long, 6–13 mm wide, glabrous below, sparsely hispid above, the margins scabrid. Panicles terminal, slender, 5–20 cm long, the branches simple, short densely flowered; rachis both scabrid and long-hispid; spikelets 1.3–1.5 mm long, secund, glabrous; first glume about half as long as spikelet; second glume and sterile lemma covering fruit. Fruits ovoid-ellipsoid ca 1 mm long, white, shiny. *Croat 16551.*

Locally abundant to common in clearings; locally common on trails in the forest. Flowering and fruiting throughout the year, more abundantly in the rainy season.

Mexico to Paraguay and Brazil; West Indies. In Panama, known from tropical moist forest in the Canal Zone, San Blas, Chiriquí, Panamá, and Darién, from tropical dry forest in Coclé and Panamá, from premontane wet forest in Panamá and Darién, and from tropical wet forest in Colón.

Panicum polygonatum Schrad. ex Schult., Mant. 2:256. 1824

Slender perennial; culms decumbent at base, rooting at lower nodes, branching, bearded at the nodes. Sheaths shorter than the internodes, glabrous but with long-ciliate margins; blades 5–12 cm long, 5–12 mm wide, cordate at the base, nearly glabrous but with scabrid margins. Panicles terminal or axillary, 10–25 cm long, branched many times, the branches angulate and scabrid; spikelets sessile or pedicellate, 1.3–2 mm long, glabrous but with the median veins scabrid near the apex; fertile floret 1; first glume one-fourth to one-half as long as spikelet; second glume and sterile lemma covering fruit. Fruits white, smooth, ca 1.3 mm long. *Croat 5255.*

Infrequent; collected on the sandbar in Fuertes Cove and on Wheeler Trail in moist areas. It may be locally abundant. Flowering and fruiting late in the dry season and throughout the rainy season.

Similar to *P. milleflorum,* which occurs in similar habitat, but distinguished from it by the smaller blades.

Mexico to Paraguay; Trinidad and Jamaica. In Panama, known from tropical moist forest in the Canal Zone, all along the Atlantic slope, and in Panamá and Darién; also known from premontane wet forest in Coclé (El Valle) and from tropical wet forest in Colón.

Panicum pulchellum Raddi, Agrost. Bras. 42. 1823

Perennial; culms very slender, rooting at lower nodes, creeping at base, ultimately ascending, pubescent at least at nodes. Sheaths shorter than the internodes, pilose with long-ciliate margins; blades ovate-lanceolate, somewhat asymmetrical, 1.5–6 cm long, 8–18 mm wide, sparsely pubescent to glabrous above, usually pubescent throughout below, the margins scabrid. Inflorescence a panicle to 15 cm long of short racemes; racemes 0.5–1.5 cm long; rachis and pedicel scabridulous; spikelets to 2 mm long, pubescent; first glume about one-third the length of the spikelet; second glume and sterile lemma covering fruit; sterile lemma with two conspicuous glands near the middle. Fruits ellipsoid, ca 1.2 mm long, pale, shiny. *Croat 9269.*

Uncommon; collected on steep banks and trails in moist areas of the forest. Flowering and fruiting throughout the year, especially during the dry season.

Southern Mexico to Brazil. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Los Santos, and Panamá and from premontane wet forest in Chiriquí.

Panicum trichanthum Nees, Agrost. Bras. 210. 1829

Perennial, 1–2 m long; culms clambering, geniculate and rooting at nodes, glabrous. Sheaths shorter than the internodes, glabrous, often ciliate; blades 8–15 cm long, 10–25 mm wide, ± asymmetrical, sparsely pubescent on upper and lower surfaces, usually becoming glabrous, the margins scabrid. Panicles diffuse, 20–30 cm long; branches ± terete, nearly smooth; spikelets 1–1.5 mm long on long slender pedicels, glabrous; fertile floret 1; first glume very small; second glume and sterile lemma exceeding fruit. Fruits ellipsoid, indurate, white, shiny. *Croat 5254.*

Rare, occurring on sandbars in deep coves along the shore. Flowers and fruits throughout the year, but especially in the rainy season.

Mexico to Paraguay; Greater Antilles and Trinidad. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Los Santos, Panamá, and Darién.

Panicum trichoides Sw., Prodr. Veg. Ind. Occ. 24. 1788

Annual, 20–60 cm tall; culms slender, decumbent at base, sparsely pubescent. Sheaths except the uppermost much shorter than the internodes, papillose-hispid, prominently ciliate; blades ovate-lanceolate, inequilateral at base, 4–7 cm long, 8–15 mm wide, sparsely pubescent on both surfaces, prominently hispid-ciliate. Panicles terminal, 5–20 cm long, the branchlets many, slender; spikelets 1–1.5 mm long on slender pedicels mostly 4–12 mm long, nearly glabrous; first glume one-third to one-half as long as spikelet; second glume and sterile lemma slightly shorter than mature fruit. Fruits white, shiny. *Croat 10259.*

An infrequent weedy grass found in clearings and open areas. Flowers throughout the year.

Mexico to Peru and Brazil; West Indies. In Panama, known from tropical moist forest in the Canal Zone, all along the Atlantic slope, and from Chiriquí, Veraguas, Panamá, and Darién; also known from tropical dry forest in Panamá (Taboga Island) and from premontane wet forest in Coclé and Panamá.

PASPALIDIUM Stapf

Paspalidium geminatum Stapf in Prain, Fl. Trop. Africa 9:583. 1920

Panicum geminatum Forssk.

Perennial, 0.5–1.5 m tall; culms clumped, decumbent and usually succulent at base, glabrous. Sheaths longer than the internodes, glabrous; blades 10–28 cm long, 3–6 mm wide, glabrous below, scaberulous above, the margins scabrid. Inflorescence a panicle 12–30 cm long, of short ascending racemes 2–4 cm long; rachis of racemes sinuous, scabrid, winged; spikelets 2–2.7 cm long, appressed; first glume about one-fourth as long as spikelet; second glume about half as long as spikelet. Fruits oblong-elliptic, white, shiny, weakly transverse-rugose. *Croat 11808.*

Growing in large clumps atop exposed tree stumps in Gigante Bay and off Gross Point. The plants become quite dried during the dry season, when the water recedes well below the clusters. Apparently flowers sporadically throughout the year.

Throughout the tropics. In Panama, known only from tropical moist forest in the Canal Zone.

PASPALUM L.

Paspalum conjugatum Bergius, Acta Helv. Phys.-Math. 7:129, pl. 8. 1762

Stoloniferous perennial, 30–100 cm or more tall; culms sometimes decumbent at base, simple or sparingly branched, glabrous; stolons long, leafy. Sheaths longer than the internodes, pubescent on collar, ciliate; blades 8–17 cm long, 5–15 mm wide, usually sparsely pubescent throughout, the margins scabrous or ciliate. Inflorescences terminal, or 2 (rarely 3) racemes (conjugate or nearly so), 7–16 cm long; rachis winged, the margins scabrid; spikelets ovate, 1.4–2.2 mm long, solitary, short-pedicellate, plano-convex, long-ciliate; first glume and sterile lemma covering fruit. Fruits plano-convex, ovate, 1.4–2.2 mm long. *Croat 5854.*

KEY TO THE SPECIES OF PASPALUM

Inflorescence of solitary racemes (each borne on a separate peduncle arising from a leaf sheath) . . . . . *P. decumbens* Sw.

Inflorescence a panicle or of more than 1 raceme:

- Inflorescence of 2 (rarely 3) subdigitate racemes:
  - Spikelets usually less than 2 mm long, with long, fine, white trichomes on margins; plants stoloniferous . . . . . *P. conjugatum* Bergius
  - Spikelets usually more than 3 mm long, the margins glabrous; plants rhizomatous . . . . . *P. notatum* Flugge
- Inflorescence a panicle or with racemes not clustered near apex of peduncle:
  - Spikelets with long silky trichomes giving the inflorescence a feathery appearance at maturity . . . . . *P. saccharoides* Nees
  - Spikelets not conspicuously pubescent:
    - Wing of rachis broader than width of spikelet; plants usually aquatic . . . . . *P. repens* Bergius
    - Wing of rachis narrower than width of spikelet; plants not aquatic:
      - Spikelets mostly more than 2 mm long; fruits light to dark brown:
        - Fruits smooth and very shiny; plants usually less than 1 m tall . . . . . *P. plicatulum* Michx.
        - Fruits striate, ± dull; plants usually more than 1 m tall . . . . . *P. virgatum* L.
      - Spikelets usually less than 1.5 mm long; fruits green:
        - Rachis with long hispid trichomes borne sparsely along all of its length; pubescence of spikelets patulous, moderately long; plants rare or possibly no longer present on BCI . . . . . *P. microstachyum* Presl
        - Rachis with long hispid trichomes lacking or restricted to near base; pubescence of spikelets appressed, ± short; plants common in clearings . . . . . *P. paniculatum* L.

Common to locally abundant in clearings. Apparently flowering all year, especially during the late dry season and throughout the rainy season.

Fruits are dispersed by birds and by passing animals, attaching themselves by the long villous trichomes on the margin of the spikelet. Ridley (1930) reported the trichomes to be coated with a viscous substance.

Cosmopolitan tropical weed. In Panama, known from tropical moist forest in the Canal Zone, all along the Atlantic slope, and in Herrera, Panamá, and Darién; known also from premontane wet forest in Chiriquí and Panamá and from tropical wet forest in Colón.

Paspalum decumbens Sw., Prodr. Veg. Ind. Occ. 22. 1788

Small, creeping perennial, usually 10–20(70) cm long; culms decumbent-spreading, rooting at lower nodes, freely branching. Sheaths keeled, the margins usually densely ciliate; blades 2–10(15) cm long, 6–12 mm wide, rounded at base, softly pubescent to nearly glabrous, the margins ciliate and scabrid, 1–8 peduncles arising from upper sheaths. Racemes solitary, 1–3.5 cm long; spikelets paired, plano-convex, short-pedicellate with scabrid pedicels, obovate, 1.3–1.7 mm long, glabrous; first glume ca 0.4 mm long, ciliate at the apex; second glume half as long as spikelet; sterile lemma as long as fruit. Fruits pale, minutely striate. *Croat 8536.*

Infrequent, in open areas of the forest and at the ends of trails along the shore. Apparently flowering and fruiting throughout the year, perhaps more often in the rainy season.

Guatemala to Brazil and Bolivia; West Indies. In Panama, known from tropical moist forest in the Canal Zone, all along the Atlantic slope, in Herrera and Panamá, known also from tropical dry forest in Panamá (Taboga Island), tropical wet forest in Colón, and premontane rain forest in Coclé.

Paspalum microstachyum Presl, Rel. Haenk. 1:215. 1830

Annual, 20–135 cm tall; culms slender, ± erect, geniculate and rooting at lower nodes. Sheaths shorter than the internodes, keeled, glabrous to pubescent; blades 3–30 cm long, 6–20 mm wide, glabrous to pubescent, the margins scabrid. Panicles of 6–35 slender, solitary, or fasciculate racemes 3–8 cm long; rachis narrowly winged, with scattered long trichomes; spikelets paired on slender pedicels, plano-convex, ca 1.5 mm long, short-spreading pubescent; first glume lacking; second glume and sterile lemma covering fruit. Fruits ca 1.5 mm long, pale green, smooth. *Shattuck 465.*

Collected by Shattuck at the end of Miller Trail, probably in the Front Lighthouse Clearing; the species may no longer occur on the island. Flowering and fruiting chiefly at the end of the rainy season.

Guatemala to Brazil. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, and Panamá and from tropical dry forest in Panamá (Taboga Island).

Paspalum notatum Flugge, Monogr. Pasp. 106. 1810

Rhizomatous perennial, 15–50 cm tall; culms glabrous. Leaves crowded; sheaths usually glabrous, ciliate near apex; blades 4–30 cm long, 3–10 mm wide, glabrous, ciliate near the base. Racemes 2 (rarely 3), subconjugate, 3–12 cm long; spikelets solitary, ovate or obovate, 2.5–3.8 mm long, 2–2.7 mm wide, plano-convex, glabrous; first glume lacking; second glume and sterile lemma covering fruit. Fruits 2.5–3.5 mm long, white, shiny, minutely striate. *Croat 16565.*

Infrequent, in the Laboratory Clearing. Flowering and fruiting chiefly in the early rainy season (June to August).

Mexico to Argentina; West Indies. In Panama, known from premontane wet forest in Chiriquí and Coclé, from tropical moist forest in the Canal Zone, Chiriquí, and Panamá, and from lower montane wet forest in Chiriquí (Volcán).

Paspalum paniculatum L., Syst. Nat. ed. 10, 855. 1759

Perennial, 0.3–1(2) m tall; culms ± stout, clumped, erect, glabrous but with bearded nodes. Sheaths keeled, longer than the internodes, usually papillose-hispid throughout; blades 10–50 cm long, 6–25 mm wide, sparsely to densely hispid on upper and lower surfaces, the margins scabrous, the ligules long-ciliate. Inflorescence 5–30 cm long, a panicle of racemes 4–12 cm long; rachis of racemes bearded at the base; spikelets paired, broadly elliptic, 1.3–1.5 mm long, crowded, plano-convex, softly pubescent; first glume lacking; second glume and sterile lemma barely covering fruit. Fruits smooth, shiny, pale green. *Croat 8489.*

Common in the Laboratory Clearing between the dining hall and the dock as well as in the area north of the dock; may occur in other clearings as well. Apparently flowering throughout the year, but less frequently in the early dry season.

Mexico to Argentina; West Indies; West Africa and Australia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, Panamá, and Darién and from tropical dry forest in Panamá (Taboga Island).

See Fig. 49.

Paspalum plicatulum Michx., Fl. Bor. Amer. 1:45. 1803

Cabezona

Erect perennial, mostly 50–100 cm tall; culms in small tufts, rarely branched, glabrous. Sheaths longer than the internodes, keeled, glabrous or sparsely pubescent; blades 15–50 cm long, 3–10 mm wide, glabrous or sparsely pilose above, scabrid on and near the margins. Inflorescence a panicle 20–30 cm long of ascending racemes; racemes often tufted at base, 2–10 cm long; spikelets plano-convex, paired, 2–2.8 mm long, on scabrid pedicels, broadly elliptic, glabrous or appressed-pubescent; first glume lacking; second glume and sterile lemma covering fruit, keeled; sterile lemma weakly cross-wrinkled near the margins. Fruits dark brown, smooth, shiny. *Croat 10333.*

Apparently rare, though locally abundant in the Laboratory Clearing. Flowers most abundantly during the rainy season.

Southern United States to Argentina; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Colón, San Blas, Chiriquí, Herrera, Panamá, and Darién, from tropical dry forest in Coclé and Panamá, from premontane wet forest in Colón, Chiriquí, Coclé, and Panamá, from tropical wet forest in Colón, and from lower montane wet forest in Chiriquí (Volcán).

Paspalum repens Bergius, Acta Helv. Phys.-Math. 7:129, pl. 7. 1762

Aquatic perennial; culms spongy, rooting at nodes. Sheaths longer than the internodes, long-pubescent, becoming glabrous, auriculate at apex; blades 10–27 cm long, 10–25 mm wide, scabrid and with fewer long trichomes. Panicles 10–20 cm long, the racemes spreading or reflexed, 3–6 cm long; rachis winged, the wing wider than spikelets, scabrid throughout; spikelets solitary, plano-convex or sometimes convex on both sides, oblong-elliptic to narrowly ovoid, 1.5–2 mm long, glabrous to short-pubescent, whitish; first glume lacking; second glume and sterile lemma exceeding fruit. Fruits 1.4–1.7 mm long, white, smooth. *Shattuck 403.*

Collected by Shattuck apparently at the margin of the lake at or near the end of Thomas Barbour Trail. Since that area of the shoreline has changed drastically over the years, it is unlikely that the same population still exists. The species could still occur on the island, but it has not been seen in recent years. Flowering throughout the year, especially in the rainy season.

United States south to Paraguay. In Panama, known from tropical moist forest in Canal Zone and Panamá.

Paspalum saccharoides Nees in Trin., Gram. Icon. 1, pl. 107. 1828

Perennial, 1–2 m or more long; culms stout, decumbent or creeping at the base, vinelike and clambering or suberect, glabrous. Sheaths longer than the internodes, glabrous or sparsely pilose, ciliate with long silky trichomes; blades 15–30 cm long (shorter at the base), 8–15 mm wide, tapering to a long-involute apex, finely pilose above, glabrous below, long-ciliate near base. Inflorescences feathery at maturity, 15–30 cm long, composed of many slender, drooping racemes crowded on a short axis; rachis sinuous, the margins scabrid; spikelets 2–3 mm long, solitary, borne in 2 rows on one side of flattened rachis; first glume lacking; second glume thin, sparsely pubescent, fringed with long silky trichomes 5–8 mm long; sterile lemma slightly shorter than the glume, also thin, glabrous. Fruits ca 2 mm long, white, smooth. *Croat 11086.*

Occasional, on steep lakeside banks on the north and east sides of the island, especially along Buena Vista Reach near Fairchild Point. The species is usually restricted to steep banks elsewhere in Panama also. Flowering especially at the beginning of the rainy season (April to October).

Seeds are probably wind dispersed.

Costa Rica to Ecuador and Bolivia. In Panama, known from tropical moist forest in the Canal Zone and Panamá, from premontane moist forest in Chiriquí, and from premontane wet forest in Colón, Coclé, and Panamá.

Paspalum virgatum L., Syst. Nat. ed. 10, 855. 1759
Cabezona

Robust perennial, 1–2 m tall, growing in dense, isolated clumps; culms stout, unbranched, erect. Sheaths longer than the internodes, the lower ones often purplish, the collar and margins glabrous or sparsely hirsute; blades 30–75 cm long, 6–25 mm wide, nearly glabrous but with scabrous margins. Inflorescences 15–30(40) cm long, of few to many thick racemes, the racemes to 15(20) cm long; rachis winged, with a tuft of long trichomes at the base, the margins scabrous; pedicels flattened, the margins scabrid; spikelets obovate, paired, crowded, plano-convex, 2.2–3 mm long, often purplish; first glume lacking; second glume and sterile lemma covering fruit, glabrous or short-appressed pubescent and the margins with longer trichomes especially near the apex. Fruits chestnut-brown, 2–2.7 mm long, minutely striate. *Croat 10244.*

Infrequent, in clearings, especially in the Rear #8 Lighthouse Clearing and on Burrunga Point. Flowering throughout the year, principally in the rainy season.

Texas and Mexico to Brazil; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Panamá, and Darién, from premontane wet forest in Colón, Chiriquí, and Panamá, from tropical dry forest in Panamá (Taboga Island), from tropical wet forest in Bocas del Toro and Colón, and from lower montane wet forest in Chiriquí.

PHARUS P. Browne

Pharus latifolius L., Syst. Nat. ed. 10, 1269. 1759
Pega-pega

Erect, monoecious perennial, 40–80(100) cm tall; culms glabrous. Sheaths longer than the internodes, glabrous; blades oblanceolate to oblong-oblanceolate, acuminate, 10–30 cm long, 2.5–8.5 cm wide, pubescent or glabrous

KEY TO THE SPECIES OF PHARUS

Fruits pubescent only near the tip, curved near apex; blades mostly more than 4 cm wide ..... *P. latifolius* L.

Fruits pubescent nearly to the base, straight; blades less than 4 cm wide ..... *P. parvifolius* Nash

Fig. 49. *Paspalum paniculatum*

Fig. 50. *Pharus latifolius*

Fig. 51. *Streptochaeta sodiroana*

but with scabrid margins, cross-veined, distinctly petiolate at base, the petioles 2–10 cm long. Panicles 10–30 cm long, open; branches slender, densely pubescent; spikelets appressed, brown, paired, one long-pedicellate and staminate, the other nearly sessile, pistillate, and much larger; staminate spikelets 2.7–4 mm long, minutely pubescent, with 6 stamens, the first glume about half as long as spikelet or less; pistillate spikelets 10–18 mm long; glumes dark brown, minutely pubescent, 3–6 mm shorter than the fruit, the second glume a little longer than the first. Fruits narrowly cylindrical, light brown, densely pubescent on exposed tip with gland-tipped trichomes. *Croat 8592.*

Abundant in all parts of the forest. Flowering and fruiting throughout the year.

The gland-tipped trichomes of the fruit disperse by very effectively attaching to animals.

Belize to Peru and Brazil; West Indies. In Panama, known from tropical moist forest in the Canal Zone, all along the Atlantic slope, and in Chiriquí, Panamá, and Darién and from premontane wet forest in Chiriquí and Panamá.

See Fig. 50.

Pharus parvifolius Nash, Bull. Torrey Bot. Club 35:301. 1908

Pega-pega

Monoecious perennial, 60–100 cm or more tall, decumbent at base, rooting at lower nodes, glabrous. Sheaths longer than the internodes, glabrous; blades oblong-lanceolate, acuminate, petiolate, 10–23 cm long, 1.5–3.8 cm wide, cross-veined, glabrous but with minutely scabrid margins. Panicles open, mostly 10–25 cm long; branches slender, pubescent; spikelets appressed, paired, one long-pedicellate and staminate, the other nearly sessile, larger, and pistillate; staminate spikelets 2–3(4.7) mm long, dark brown, glabrous, the first glume about half as long as spikelet; pistillate spikelets 11–14 mm long; glumes dark brown, about half as long as the fruit. Fruits light brown, slender, densely glandular-pubescent throughout. *Croat 8335.*

Occasional, in the older forest, often locally abundant. Flowering and fruiting throughout the year.

Costa Rica to Brazil; West Indies. In Panama, known from tropical moist forest on BCI and in Darién.

PHRAGMITES Trin.

Phragmites australis (Cav.) Trin. in Steud., Nom. Bot. ed. 2, 2:324. 1841

P. communis Trin.

Common reed

Coarse perennial, 2–4(5) m tall, stoloniferous, rhizomatous, usually in large colonies; culms erect, glabrous. Sheaths longer than the internodes, glabrous; blades to 50 cm long, 1–2.5 cm wide, glabrous but with scabrous margins. Panicles 25–55 cm long, plumelike; branches drooping, slender, whorled at base, angulate, scabrous; spikelets 10–20 mm long, bearing several flowers; glumes unequal, dark brown, the first 4–5 mm long, the second 6–8 mm long; lemmas 10–13 mm long, awned-acuminate; rachillas bearded with long white trichomes nearly as long as the spikelet. Fruits not seen. *Croat 12585.*

Occasional, in shallow water at the edge of the island. The populations on the unprotected north and east sides of the island are often very small, while the populations in the protected areas on the south side are larger. Flowering and fruiting principally in the late rainy and early dry seasons.

Fruits usually disarticulate beneath the long-bearded rachilla, which probably aids in wind dispersal. They are also dispersed to some extent by water currents.

Temperate and tropical areas throughout the world. In Panama, known from tropical moist forest in the Canal Zone, Colón, Panamá, and Darién and from premontane wet forest in Chiriquí (Boquete).

POLYTRIAS Hack.

Polytrias amaura (Buse ex Miq.) O. Kuntze, Rev. Gen. Pl. 2:788. 1891

P. praemorsa (Nees) Hack.

Java grass

Stoloniferous perennial, to 35 cm tall; culms decumbent-spreading, slender, glabrous with some nodes pubescent. Sheaths glabrous to pilose, longer than the internodes except near apex; blades 2–6 cm long, 1–3 mm wide, pilose on both surfaces, the margins scabrid. Racemes terminal, solitary, 2.5–5.5 cm long, brown; rachis pubescent; spikelets densely brown-pubescent, 2 or 3 per node, 1 or 2 sessile, 1 pedicellate, all perfect, 3–4 mm long excluding awn; first glume truncate and fimbriate at apex; sterile lemma lacking; fertile lemma awned, the awn 6–8 mm long, geniculate, twisted. *Croat 12827.*

Common along the stairs at the Laboratory Clearing. Generally appearing in large flushes in late rainy and early dry seasons.

The genus is supposed to have two sessile spikelets at each node, but specimens from BCI and other areas of Central America (R. Pohl, pers. comm.) have only one sessile spikelet per node.

Introduced from Java into various parts of the Western Hemisphere. In Panama, known only from tropical moist forest in the Canal Zone (BCI and Summit Garden).

RHIPIDOCLADUM McClure

Rhipidocladum racemiflorum (Steud.) McClure, Smithsonian Contr. Bot. 9:106. 1973

Arthrostylidium racemiflorum Steud.

Carrizo

Slender, arching or clambering, vinelike plant, to 5 m long; culms usually in dense clumps less than 1 m wide with many slender, nodose, and geniculate branches in dense fascicles at broad intervals on culm. Sheaths pubescent, the upper edge extending beyond articulation, with usually 2–4 slender cilia; blades lanceolate, articulate at

base, to 12 cm long, 4–12 mm wide, inconspicuously puberulent on lower surface, the trichomes near the base, glabrous or puberulent on upper surface, sometimes with sparse longer trichomes as well, the veins all about equally prominent, midrib lacking. Flowers very rarely found, in simple racemes 2–8 cm long; spikelets ± crowded, appressed, bearing few flowers; lemmas 6–8 mm long, awned, the awn 1–2 mm long; palea slightly longer than the lemma, the keel pubescent. Fruits not seen. *Croat 8175.*

Abundant in the forest and along the shore. Flowers chiefly in the rainy season, though flowers are rarely seen.

Easily confused with *Chusquea simpliciflora,* but may be distinguished by having blades lacking a distinct midrib. (This flower description is taken from the *Flora of Panama.*)

Southeast Mexico to Colombia. In Panama, known from tropical moist forest in the Canal Zone and Panamá, from tropical wet forest in Panamá (Cerro Azul), and from premontane wet forest in Chiriquí (Boquete).

ROTTBOELLIA L.f.

Rottboellia exaltata (L.) L.f., Nov. Gram. Gen. 40, pl. 1. 1779

Erect perennial, 70–150 cm tall; culms glabrous, with stout roots at lower nodes. Sheaths papillose-hispid; blades 15–45 cm long, 8–16 mm wide, scabrid and sparsely papillose-hispid above, glabrous to scabrid below, the margins scabrous. Racemes terminal or axillary, mostly 5–10 cm long; peduncles scabrous, sheathed; rachis thick, cylindrical, jointed; spikelets appressed, paired, one perfect and sessile, the other staminate and on a thick pedicel; both perfect and staminate spikelets ca 4 mm long, minutely papillate, bifid at apex, the margins scabrid; first glumes indurate; second glume about equal, tightly appressed to rachis. Fruits not seen. *Croat 5853.*

Locally common in the Laboratory Clearing. Flowering and fruiting throughout the year, especially in the rainy season.

Native to the Old World, where it is widespread in tropical Africa, Asia, and Oceania; introduced into Costa Rica, Panama, and the West Indies. In Panama, known only from BCI.

SACCHARUM L.

Saccharum officinarum L., Sp. Pl. 54. 1753
Sugarcane

Erect perennial, to ca 4 m tall; culms to ca 5 cm thick, glabrous; sap sweet. Lower internodes short with overlapping sheaths, the sheaths glabrous or softly pubescent toward the top, densely villous in the throat; ligules truncate, minutely ciliate, ca 5 mm long; blades linear with a prominent midvein, sharply serrate, villous on upper surface at base. Inflorescences very large, of silvery, plumose, panicled racemes, the branches simple, drooping; spikelets all alike, 4–5 mm long, in pairs, one sessile, the other pedicellate, surrounded at the base by long trichomes; rachis disarticulating below spikelets; glumes 1–3-veined, acute to acuminate; sterile lemma similar to glume but hyaline; fertile lemma shorter than glumes, hyaline, awnless, sometimes lacking. Fruits not seen. *Croat 44759.*

Sparsely cultivated by the Panamanian workers in the Laboratory Clearing. Seasonal behavior not determined.

Cultivated throughout the tropics and sporadically in Panama.

Saccharum spontaneum L., Mant. Pl. Altera 183. 1771

Perennial, to ca 3 m tall, sometimes branching; culms stout, glabrous. Sheaths mostly longer than the internodes, glabrous but with villous margins near throat, the old sheaths often persisting on the culms after blades have fallen; blades mostly 25–110 cm long, 5–12 mm wide, glabrous, the margins scabrid. Inflorescences terminal, to ca 25 cm long, bearing very long silky pubescence throughout but especially directly beneath the spikelets; racemes mostly 4–7 cm long; spikelets equal, paired, perfect, 3–4 mm long, one sessile, the other pedicellate; glumes narrowly acute at apex, 1–3-veined, often ± keeled. Fruits not seen. *Croat 11985.*

Collected once along exposed banks on the west side of Peña Blanca Peninsula. Some flowers seen in September. Bor (1960) said that the species flowers in its native range at the end of the rainy season.

The rachilla disarticulates below the spikelets, and the long silky trichomes obviously assist in wind dispersal of the seeds.

Widely distributed in the Old World tropics; introduced into the New World tropics. This is a new report for Panama.

SACCIOLEPIS Nash

Sacciolepis striata (L.) Nash, Bull. Torrey Bot. Club 30:383. 1903

Perennial, 1–2 m tall; culms decumbent-spreading, rooting at lower nodes, glabrous. Sheaths except the uppermost shorter than the internodes, glabrous, the margins ciliate; blades 4–20 cm long, 2–12(15) mm wide, ± glabrous but with scabrid margins. Panicles dense, spikelike, terminal, to 20 cm long; spikelets pedicellate on short

KEY TO THE SPECIES OF SACCHARUM

Culms 3–5 cm thick; plants cultivated at the Laboratory Clearing ..... *S. officinarum* L.
Culms 1–2 cm thick; plants not cultivated ..... *S. spontaneum* L.

KEY TO THE SPECIES OF SCHIZACHYRIUM

Small, decumbent herbs less than 1 m long; leaf blades less than 4 cm long ..... *S. brevifolium* Kunth
Coarse, erect herbs more than 1 m tall; leaf blades more than 10 cm long .....
..... *S. microstachyum* (Desv.) Roseng., Arr. & Izag.

branches, 3–4 mm long; first glume ovate, short; second glume and sterile lemma nearly equal to each other, prominently veined, glabrous; second glume inflated-saccate at the base. Fruits ellipsoid, to 1.7 mm long, whitish, indurate. *Bailey & Bailey 387.*

Collected once on the island; probably no longer present. Seasonal behavior not certain; probably fertile in late rainy and early dry season.

Reported by Standley as *S. myuros* (Lam.) R. & S.

Southern United States and Panama; West Indies. In Panama, known only from BCI.

SCHIZACHYRIUM Nees

Schizachyrium brevifolium Nees ex Kunth, Agrost. Bras. 331. 1829

Andropogon brevifolius Sw.

Usually a weak, slender annual, somewhat decumbent at least at base, to 1 m long, ± glabrous but with scabrous margins. Sheaths shorter than the internodes, compressed; blades 1–4 cm long, 1–5 mm wide. Panicle branches slender; racemes solitary, 1–3 cm long, glabrous but with short beard on callus; spikelets paired, one sessile and perfect, the other reduced to an awned rudiment; sessile spikelet 1.5–3 mm long, the awn geniculate, to 8 mm long. Fruits oblong-linear, pale brown, to 1.4 mm long. *Shattuck s.n.*

Collected once on Orchid Island; though the plant has not been seen for some time, it could easily be overlooked and is to be expected. Apparently flowering and fruiting throughout the year.

Fruits primarily dispersed by adhesion to animals and by hydroscopic action of the awn.

Throughout tropics of Western and Eastern hemispheres. Known in Panama from tropical moist forest in the Canal Zone, Herrera, Coclé, Panamá, and Darién.

Schizachyrium microstachyum (Desv.) Roseng., Arr. & Izag., Bol. Fac. Agr. Montev. 103:34. 1968

Coarse perennial, 1–1.5 m tall, often growing in clumps, glabrous. Sheaths mostly shorter than internodes, compressed and keeled; ligules truncate, to 2.7 mm long; blades 10–30 cm long, 5–10 mm wide, the margins only minutely scaberulous. Inflorescences numerous, large, corymbose, feathery; racemes solitary, 2–3 cm long, the rachis strongly flexuous; rachis and sterile pedicel prominently long-villous; spikelets paired, one sessile and perfect, the other pedicellate, rudimentary, bearing a short awn; sessile spikelets to 4 mm long, awned, the awn ca 1 cm long, geniculate, twisted. Fruits not seen. *Croat 9404.*

Occasional, in clearings, usually in isolated clumps. Flowering and fruiting throughout the rainy season into the early dry season.

Mexico to Brazil; leeward and windward islands of the West Indies. In Panama, known from tropical moist forest on BCI and from premontane wet forest in Chiriquí.

SETARIA Beauv.

Setaria geniculata (Lam.) Beauv., Ess. Agrost. 51:178. 1812

Pajón, Rabo de mono

Perennial, 0.2–1 m tall; culms in dense tufts from short rhizomes, ± erect, branching at the lower nodes, glabrous. Sheaths shorter than the internodes near the base, longer near the apex, glabrous; blades mostly 5–15 cm long, 4–6 mm wide, glabrous to scabrous, often sparsely pilose on the upper surface at the base. Spikelike panicles mostly 2–6 cm long, densely flowered, the axis densely pubescent; bristles 5 or more below each spikelet, usually longer than spikelet; spikelets 2–2.5 mm long, ovoid, glabrous; first glume about one-third as long as spikelet; second glume a little longer than the first; sterile lemma equaling fruit. Fruits white, transversely rugose. *Croat 6811.*

Common in clearings where vegetation is not allowed to grow too tall. Flowering and fruiting throughout the year, especially during the rainy season.

The bristles subtending the spikelets do not appear to aid directly in epizoochorous dispersal, since they remain attached after all fruits have been shed. However, they release the mature disarticulated fruits from the inflorescence upon impact, such as of passing animals, and

KEY TO THE SPECIES OF SETARIA

Leaf blades plicate, more than 4 cm wide ..... *S. paniculifera* (Steud.) Fourn.
Leaf blades not plicate, less than 3.5 cm wide:
  Plant a small grass less than 1 m tall; inflorescences less than 6 cm long; blades less than 1 cm wide ..... *S. geniculata* (Lam.) Beauv.
  Plant a large grass more than 1 m tall; inflorescences more than 15 cm long; blades more than 2 cm wide ..... *S. vulpiseta* (Lam.) R. & S.

perhaps are capable of throwing the fruits out of the inflorescence.

Southern United States to Argentina; West Indies; introduced elsewhere. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Panamá, and Darién, from tropical dry forest in Panamá (Taboga Island), from premontane wet forest in Chiriquí, Coclé, and Darién, and from lower montane wet and rain forests in Chiriquí.

Setaria paniculifera (Steud.) Fourn., Mex. Pl. 2:42. 1886

Pajón, Rabo de mono

Tall perennial, 1.5–3(4) m tall; culms erect, stout, appressed-pubescent at nodes. Sheaths papillose-hispid, more densely near margins; blades plicate, 50–100 cm long, 3–10 cm wide, scabrous. Panicles narrow or loose and open, 40–70 cm long; branches angulate and scabrid; bristles 1 or more below most spikelets, 3–10 times longer than spikelet, antrorsely barbed; spikelets ca 3 mm long, glabrous; first glume about half as long as spikelet; second glume slightly longer than the first; sterile lemma equaling fruit. Fruits lanceolate, finely, transversely rugose. *Croat 6365.*

Forming localized but dense stands in Rear #8 Lighthouse Clearing; also collected along the lakeshore. Flowering and fruiting principally in the rainy season.

Mexico to Colombia and Venezuela; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién and from premontane wet forest in Coclé (El Valle).

Setaria vulpiseta (Lam.) R. & S., Syst. Veg. 2:495. 1817

Large perennial, 1–2 m tall; culms in large clumps, erect or geniculate and rooting at lower nodes, glabrous. Sheaths longer than the internodes, glabrous to densely pubescent, especially along margins; blades 25–50 cm long, 2–3.5 cm wide, scabrous especially on underside of veins and on margins. Panicles 15–30 cm long, often spikelike, dense, the axis densely villous; bristles 1 or 2 below each spikelet, 1–2 cm long; spikelets 2–3 mm long, glabrous; first glume about half as long as spikelet; second glume slightly longer than the first; sterile lemma equaling fruit. Fruits transversely rugose, minutely green-crested, white. *Croat 11717.*

Rare; growing on steep, eroded, lakeside banks south of Fairchild Point, and less often in clearings and at the edge of the forest. Flowering and fruiting from June to December, principally from August to October.

Southern Mexico to Argentina; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Panamá, and Darién, from tropical dry forest in Panamá (Taboga Island), and from premontane moist forest in Panamá (Saboga Island).

SPOROBOLUS R. Br.

Sporobolus indicus (L.) R. Br., Prodr. Fl. Nov. Holl. 170. 1810

Slender perennial, 50–100 cm tall; culms erect in small dense clumps, glabrous. Sheaths glabrous, sometimes ciliate; blades 25–60 cm long, 1–4 mm wide, flexuous, the margins scabrid. Panicles 15–30 cm long; branches short, slender, ± ascending, minutely scabrid; spikelets 1.6–1.8 mm long, glabrous, bearing 1 flower; glumes nearly equal, exceeding fruit. Fruits plump, ellipsoid, ca 1 mm long, brown. *Croat 8657.*

Common in the Laboratory Clearing, especially along the stairs to the dock. Flowering and fruiting sporadically throughout the year, especially during the dry season and the early rainy season.

Southeastern United States and Mexico to Colombia and Brazil; West Indies. In Panama, widespread; known from tropical moist forest all along the Atlantic slope and in the Canal Zone, Veraguas, Herrera, Panamá, and Darién; known also from tropical dry forest in Coclé and Panamá, from premontane wet forest in Colón and Chiriquí, from tropical wet forest in Colón, and from lower montane wet forest in Chiriquí.

STREPTOCHAETA Schrad.

Streptochaeta sodiroana Hack., Oesterr. Bot. Z. 40:113. 1890

Erect, coarse perennial, 60–100 cm tall; culms often with stout roots at lower nodes, the leaves sparse below. Sheaths shorter than the internodes, crowded near the apex, the margins densely long-ciliate near the apex; blades oblong-elliptic, asymmetrical, usually acuminate, 18–30 cm long, 6–9.5 cm wide, ± glabrous, cross-veined; petioles short, densely pubescent at apex. Spikes 20–30 cm long, ca 1 cm thick, densely flowered; spikelets appressed, the lemma bearing awns to 10 cm long, antrorsely barbed, the barbs straight below, twisted and curled toward apex, interconnected with other awns; stamens and styles both prominently exserted at anthesis, both white. Inflorescences usually nodding in fruit, the spikelets disarticulating at the base, hanging suspended by their long awns; the indurate bifid palea somewhat divergent at the apex, useful for dispersal. *Croat 8816.*

Common to locally abundant in dense forest. Flowering in the dry season. The fruits present throughout much of the year.

KEY TO THE SPECIES OF STREPTOCHAETA

Blades 6–9.5 cm wide; spikelets many, densely arranged, ca 14 mm long (excluding awns) . . . . . *S. sodiroana* Hack.

Blades less than 4.5 cm wide; spikelets few, distant, ca 22 mm long (excluding awns) . . . *S. spicata* Nees

Fruits disperse by attachment of the sharp palea to passing animals. The mass of fruits is held together, however, by the tangled awns and often falls to the ground, where seeds may germinate.

Belize to Panama, Ecuador. In Panama, known from tropical moist forest in the Canal Zone and Panamá.

See Fig. 51.

Streptochaeta spicata Schrad. ex Nees, Agrost. Bras. 537. 1829

Erect perennial, 60–90 cm tall; culms simple or branched few times, minutely pubescent especially near nodes. Sheaths long-ciliate and often auriculate at apex; blades 7–15 cm long, 2.5–4.5 cm wide, acuminate, inequilateral at base, scabrid or glabrous, cross-veined. Spikes 10–14 cm long, with 5–11 rather distant spikelets; axes densely pubescent; spikelets 2–2.5 cm long excluding awn, minutely pubescent, bearing 1 flower; 4 bracts at base of spikelet 2–3 mm long; lemma indurate, tapering into an awn 5–10 cm long, the awn coiled in distal half. Fruits brown, cylindrical, ca 8 mm long, covered by 3 acuminate lodicules. *Croat 11832.*

Occasional, in the forest. Flowering and fruiting throughout the year.

Dispersal is similar to that of *S. sodiroana.*

Guatemala to Ecuador and Brazil; Trinidad. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién and from premontane wet forest in Chiriquí (San Félix) and Panamá (Chimán).

STREPTOGYNE Beauv.

Streptogyne americana C. E. Hubb. in Hook.f., Icon. Pl. 5, pl. 3572. 1956

S. crinata Beauv.

Erect perennial, 30–120 cm tall; culms in dense clumps, glabrous. Sheaths longer than the internodes, pubescent especially near apex, auriculate at apex; blades 30–70 cm long, 1–2.2 cm wide, long-acuminate, glabrous or scaberulous. Racemes solitary, spikelike, 20–40(50) cm long; axes angulate, pubescent; pedicels pubescent, 3–4 mm long; spikelets appressed, 3- or 4-flowered, ca 2.5 cm long; first glume to 5(8) mm long, keeled, the keel scabrid; second glume 12–15 mm long, tapered to an awnlike point, the margins scabrid; lemma 2–2.3 cm long excluding awn, scabrid near apex, the awn ca 2 cm long; stigmas elongate, coiled. Mature fruits suspended from coiled stigmas. *Croat 4343.*

Common in the forest, usually not on trails but sometimes on infrequently used trails. Flowering and fruiting mostly in the early dry season.

Fruits are adapted for epizoochorous dispersal by passing animals.

Mexico to northern Brazil; Trinidad. In Panama, known from tropical moist forest in the Canal Zone and Panamá.

18. CYPERACEAE

Aquatic or terrestrial herbs (*Scleria secans* a scandent vine), usually tufted, rhizomatous or stoloniferous, with 3-sided stems. Leaves mostly crowded and basal with a closed sheath; blades simple, entire or sharply serrulate; venation parallel; stipules lacking. Flowers bisexual or unisexual (monoecious or andromonoecious), in bracteate spikelets, the spikelets solitary or variously compound (often umbellate); perianth reduced to several scales or bristles; stamens 1–3, free, hypogynous; anthers 2-celled, basifixed, dehiscing longitudinally, often having a produced connective; ovary 1, superior, 1-locular, 2- or 3-carpellate, with basal placentation; ovule 1, anatropous; style simple, 2- or 3-branched (depending on the number of carpels). Fruits achenes, sometimes in utricles, with albumen.

Easily mistaken for Gramineae (17), but distinguished by having solid, three-sided stems and three-ranked leaves with usually closed sheaths and basifixed anthers.

KEY TO THE TAXA OF CYPERACEAE

Inflorescences simple and unbranched or if compound the heads ± sessile:
- Spikelets solitary, not subtended by leafy bracts; plants usually aquatic ..... *Eleocharis*
- Spikelets numerous, in dense heads subtended by leafy bracts; plants rarely aquatic:
  - Spikelets ovate, flattened ..... *Cyperus luzulae* (L.) Retz.
  - Spikelets not ovate and flattened:
    - Blades usually more than 5 mm wide; heads usually more than 1.5 cm diam ..... *Rhynchospora cephalotes* (L.) Vahl
    - Blades less than 5 mm wide; heads usually less than 1 cm diam:
      - Bracts subtending inflorescence usually white, at least at base; spikelets few, 5–10 mm long ..... *Rhynchospora nervosa* (Vahl) Boeck.
      - Bracts subtending inflorescence always green (sometimes only 1 or 2); spikelets numerous, less than 4 mm long:
        - Spikelets usually ca 3 mm long; scales smooth on keel, blunt at apex with a tiny mucro ..... *Cyperus sesquiflorus* (Torr.) Mattf. & Kuek.
        - Spikelets 1.5–2 mm long; scales spinulose-scabrous on keel, subacute at apex with a short cusp:
          - Plants perennial, the rhizomes elongate, creeping ... *Cyperus brevifolius* (Rottb.) Hassk.
          - Plants annual, rhizomes lacking ..... *Cyperus densicaespitosus* Mattf. & Kuek.

Inflorescences compound, the heads not sessile:
- Spikelets very numerous, in dense, ± globose heads, the heads few, mostly more than 6 mm diam, radiating on short or long rays at apex of stem:
  - Heads whitish, borne on very short rays usually less than 1 cm long, the heads lacking leaflike bracts at base; spikelets markedly flattened with numerous scales easily disarticulating; plants not aquatic ..... *Cyperus luzulae* (L.) Retz.
  - Heads greenish, on rays more than 2 cm long, subtended by short leaflike bracts; spikelets not markedly flattened, the scales few, not disarticulating; plants aquatic ..... *Scirpus cubensis* Kunth
- Spikelets not in dense globose heads radiating from a central point, or if in dense globose heads, the heads less than 6 mm diam:
  - Achenes white, often shiny, exposed at maturity, ± globose:
    - Leaves less than 2 mm wide; plants slender annuals; achenes conspicuously transversely rugose ..... *Rhynchospora micrantha* Vahl
    - Leaves more than 2 mm wide; plants perennials; achenes not transversely rugose:
      - Achenes clustered in small glomerules at apex of slender rays ..... *Calyptrocarya glomerulata* (Brongn.) Urban
      - Achenes solitary, not borne in clusters on slender rays ..... *Scleria*
  - Achenes not as above (if exposed at maturity, not white and shiny):
    - Spikelets, at least in part, solitary on conspicuous peduncles, terete:
      - Blades less than 4 mm wide; peduncles glabrous ..... *Fimbristylis dichotoma* (L.) Vahl
      - Blades more than 1 cm wide; peduncles scabrid ..... *Hypolytrum schraderianum* Nees
    - Spikelets sessile, never solitary on conspicuous peduncles, terete or not, *or* if spikelets borne solitary, then not terete:
      - Plants not aquatic (except sometimes *C. odoratus*); blades less than 1.5 cm wide ..... *Cyperus* (in part)
      - Plants usually aquatic; blades more than 1.5 cm wide (except *Cladium* with very stiff, spinulose margins):
        - Spikelets in racemes, at least some racemes on long rays subtended by a whorl of long, leaflike bracts ..... *Cyperus giganteus* Vahl
        - Spikelets in umbels or corymbs, not borne on long rays subtended by leaflike bracts:
          - Leaf blades usually 5- or more-veined; scales of spikelet pubescent ..... *Fuirena umbellata* Rottb.
          - Leaf blades with only 1 prominent vein; scales of spikelet glabrous or pubescent only on keel:
            - Bracts subtending ultimate clusters of spikes usually acute at apex, the awns, if present, very short; achenes lacking a tubercle at apex; leaves very stiff, the margins very coarsely spinulose-serrate ..... *Cladium jamaicense* Crantz
            - Bracts subtending ultimate clusters of spikes long caudate-acuminate, the awns equaling or longer than remainder of bract; achenes having a cone-shaped tubercle at apex; leaves not very stiff, the margins not coarsely spinulose-serrate ..... *Rhynchospora corymbosa* (L.) Britt.

Flowers are probably all wind pollinated except for *Rhynchospora nervosa* (Leppik, 1955; Baker, 1963), whose pollination is discussed in the systematic treatment. Other species that need to be investigated for possible insect pollination, because they occur deep in the forest where they cannot rely on wind, are *Cyperus simplex, Hypolytrum schraderianum,* and *Calyptrocarya glomerulata.*

Some taxa, such as *Calyptrocarya* and *Scleria,* with shiny white or colored achenes, are well suited for bird dispersal. Adapted also for dispersal by shore birds and by water are the following principally aquatic genera: *Eleocharis, Scirpus, Fuirena,* and some species of *Cyperus.* Taxa occurring on mud flats, such as *Cyperus,* may have seeds dispersed on the feet of birds. Most members of the family have very small diaspores, which could be eaten easily by small birds. Ducks and other shore birds are very important in the dispersal of aquatic Cyperaceae (Ridley, 1930). The seeds of many species occurring in clearings are probably spilled and scattered by the mechanical action of passing animals. Van der Pijl (1968) said that some Cyperaceae seeds are wind dispersed.

About 70 genera and over 3,500 species; widespread, but particularly numerous in high latitudes, usually in wet places.

CALYPTROCARYA Nees

Calyptrocarya glomerulata (Brongn.) Urban, Symb. Ant. 2:169. 1900

Small perennial, to ca 60 cm tall. Leaves linear, longer than culms, 2–9 mm wide, 3-veined, prominently folded along midrib, glabrous but with minutely scabrid margins. Spikelets minute, in small globular heads less than 4 mm diam on rays of compound or simple axillary corymbs; rays to ca 1.5 cm long; pistillate spikelets terminal, minutely puberulent, bearing 1 flower; style bifid; staminate spikelets lateral, bearing 1–4 flowers; stamen 1. Achenes ovoid, weakly compressed, apiculate, whitish, puberulent, ca 1.3 mm long. *Croat 15249.*

Uncommon; known from a few areas along trails in the forest, collected from Zetek and Balboa trails. Seen fertile April through July.

Mexico to Brazil. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Panamá, from premontane moist forest in Panamá, from premontane wet forest in Panamá (Cerro Jefe) and Colón, and from tropical wet forest in Colón.

CLADIUM P. Browne

Cladium jamaicense Crantz, Inst. Rei Herb. 1:362. 1766

Saw grass

Coarse perennial, 1.5–3 m tall; culms ± terete, leafy throughout. Blades to 70 cm long or more, 4–12 mm wide, stiff, the margins and medial rib on lower surface very strongly spinulose-serrulate. Panicles diffuse, to ca 15 cm long, arising from alternate leaf axils; spikelets in clusters of 2–5, terete, ovoid, acute, 4–5 mm long, brown, the uppermost flower perfect; perianth lacking; stamens 2; middle scales of spikelet sometimes with staminate flowers. Achenes ovoid, gradually tapered to a blunt apex, ca 3 mm long, dull, reddish-brown; tubercle lacking.

Reported by Standley to be "common in shallow water at the lake." I have seen no collections, but the plant could be there. Flowers in April and May. The fruits mature during July and August.

This species might be confused with *Rhynchospora corymbosa,* which grows in the same places and has a similar habit; it is possible that Standley confused the two species. *Cladium* can be most easily distinguished from *Rhynchospora corymbosa* by its much coarser leaf margins, its fruits lacking a cone-shaped tubercle at the apex, and its inflorescence lacking antrorsely barbed, attenuate bracteoles.

Throughout tropical and subtropical America. In Panama, known from tropical moist forest on the Atlantic slope in the Canal Zone and from tropical wet forest in Colón (Portobelo).

CYPERUS L.

The styles of *Cyperus* may be cleft two or three times, usually corresponding to whether the achenes are two-sided (lenticular) or three-sided.

Cyperus brevifolius (Rottb.) Endl. ex Hassk., Catal. Hort. Bogor. 24. 1884

Kyllingia brevifolia Rottb.

Very similar to *Cyperus densicaespitosus,* except perennial, the rhizomes usually elongate, and the spikelets slightly smaller. *Croat 12011.*

Occasional, in the Laboratory Clearing. Seasonality uncertain; probably flowers and fruits throughout the year. It has been seen fertile from January to September.

The habit of growth is noteworthy. Since the plant is perennial and develops elongate rhizomes, a whole series

KEY TO THE SPECIES OF CYPERUS

Spikelets clustered in dense, ± globose heads:
- Heads borne on short rays ..... *C. luzulae* (L.) Retz.
- Heads sessile:
  - Scales of spikelets smooth; the headlike spikes often cylindrical, usually 3 in number ..... *C. sesquiflorus* (Torr.) Mattf. & Kuek.
  - Scales of spikelets spinulose-scabrous on keel; the headlike spikes round or ellipsoid, frequently solitary:
    - Plants annual, caespitose, lacking elongate rhizomes ..... *C. densicaespitosus* Mattf. & Kuek.
    - Plants perennial, the rhizome elongate, creeping ..... *C. brevifolius* (Rottb.) Hassk.

Spikelets in open, diffuse inflorescences:
- Ultimate clusters of spikelets forming simple umbels:
  - Umbels on rays usually less than 5 cm long; culms long, weak, and flexuous, with most leaves reduced to sheaths; plants growing in swamps ..... *C. haspan* L.
  - Umbels on rays usually 10–20 cm long; culms not weak and flexuous, erect, the leaves not reduced to sheaths; plants not growing in swamps:
    - Inflorescences simple; spikelets 1–3 at apex of long, unbranched rays, the rays longer than culms ..... *C. simplex* H.B.K.
    - Inflorescences compound; spikelets several on compound rays, the rays much shorter than culms ..... *C. diffusus* Vahl
- Ultimate clusters of spikelets racemose:
  - Spikelets purple to black ..... *C. rotundus* L.
  - Spikelets green to brown:
    - Culms terete, naked; plants aquatic, usually 1.5–2 m tall ..... *C. giganteus* Vahl
    - Culms ± trigonous, leafy at least at base; plants usually terrestrial and less than 1 m tall:
      - Spikelets usually more than 1 cm long, sparse along rachis, decurrent, the scale bases becoming corky, the rachilla breaking into 1-fruited joints; inflorescences usually compound ..... *C. odoratus* L.
      - Spikelets less than 1 cm long, very dense on rachis (usually contiguous), the rachilla wings not becoming corky; inflorescences simple ..... *C. tenuis* Sw.

of plants may be produced in succession. The species thus tends to be more locally gregarious than is *C. densicaespitosus,* which it very closely resembles, except for being somewhat more robust and having creeping rhizomes. Reportedly the most common species of *Cyperus* in Panama, growing in all but the drier areas of the west.

Southern United States to Argentina. In Panama, known from tropical moist forest on both slopes of the Canal Zone and in Bocas del Toro, from premontane wet forest in Chiriquí and Coclé, from tropical wet forest in Colón, and from lower montane wet forest in Chiriquí.

Cyperus densicaespitosus Mattf. & Kuek., Pflanzenr. IV.20(Heft 101):597. 1936
Kyllingia pumila Michx.

Small annual, 4–30(40) cm tall; culms very slender. Leaves linear, usually shorter than culms, 1–3 mm wide. Bracts subtending inflorescence 3–9 cm long, 2–4 mm wide; heads globose to ovoid, terminal, usually solitary (to 3), sessile, 4–6 mm long; spikelets 1.5–2 mm long; scales membranaceous, pale, keeled, the apex subacute with a short cusp, the keel spinulose-scabrous; stamens 1 or 2; style bifid. Achenes lenticular, elliptic, pale, 1–1.5 mm long. *Croat 5910.*

Occasional, in the Laboratory Clearing. Flowering and fruiting throughout the year, especially in the dry season.

Easily confused with *C. sesquiflorus.* Plants tend to be taller, more slender, and more widely spaced than those of *C. sesquiflorus,* and have spikes tending to be greenish rather than whitish.

Widely distributed in the United States from New York to Ohio and south to Argentina; Africa. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién, from premontane moist forest in the Canal Zone, and from lower montane wet forest in Chiriquí.

Cyperus diffusus Vahl, Enum. Pl. 2:321. 1806

Perennial, 30–60 cm tall; culms slender. Leaves linear, 4–12 mm wide, the underside of midrib and the margins scabrid. Inflorescences subtended by several, long, leaflike bracts, compound; spikelets both at base of inflorescence and on long, spreading rays, the ultimate clusters forming simple umbels, greenish, 10–24-flowered, 5–15(20) mm long; scales green only on keel, with a narrow, incurved tip. Achenes obovate to globose, brown, trigonous with concave sides, smooth, 1–1.5 mm long. *Croat 6912.*

Abundant in clearings, especially near the laboratory. Apparently flowers throughout the year.

Throughout warmer regions of Western and Eastern hemispheres. In Panama, widespread and ecologically variable; known from tropical moist forest all along the Atlantic slope as well as in Chiriquí, Herrera, Panamá, and Darién, from tropical dry forest in Panamá (Taboga Island), from premontane moist forest in the Canal Zone and Panamá, from premontane wet forest in Chiriquí, Coclé, Panamá, and Darién, from tropical wet forest in Panamá and Darién, and from lower montane wet forest in Chiriquí.

Cyperus giganteus Vahl, Enum. Pl. 2:364. 1806

Stout aquatic perennial, 1–2(2.5) m tall; culms terete. Leaves reduced to basal sheaths. Bracts subtending inflorescence leaflike, 10–40 cm long, 0.5–2 cm wide, the margins and the underside of midrib scabrous; inflorescences large, compound; spikes elongate, lax, on spreading rays; spikelets 3–10 mm long, slender, cylindrical, 8–14-flowered; scales straw-colored, green on keel. Achenes minute, 1 mm long, trigonous with 1 face concave, pale yellow or white. *Croat 6168.*

Forming dense stands in a few places along the shore, especially in quiet coves. Flowers in the rainy season, with the fruits persisting into the dry season.

Mexico to Argentina. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Panamá, from premontane wet forest in Bocas del Toro, and from tropical wet forest in Colón.

Cyperus haspan L., Sp. Pl. 45. 1753

Slender, glabrous perennial, mostly 50 cm to more than 1 m tall; culms mostly slender, glabrous. Leaves mostly short or reduced to sheaths, sometimes with longer basal leaves usually to 3 mm wide. Bracts subtending inflorescence 2, usually shorter than inflorescence; inflorescences usually compound with several spikelets at apex of simple or branched, umbellate rays; spikelets 5–10(15) mm long, bearing many flowers, flattened, brownish; scales 1.2–1.7 mm long, obtuse and minutely apiculate at apex. Achenes usually white, ca 0.5 mm long, obovoid to ellipsoid, trigonous, with a rough granular surface. *Croat 13241.*

Infrequent, in swamps at the edge of the lake in some areas of the south shore. Flowers and fruits throughout the year, perhaps principally in the rainy season.

Warmer regions of Western and Eastern hemispheres. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Veraguas, and Panamá, from tropical dry forest in Coclé, from premontane moist forest in Panamá, from premontane wet forest in Chiriquí, Panamá, and Coclé, from tropical wet forest in Colón and Panamá, and from lower montane wet forest in Chiriquí.

Cyperus luzulae (L.) Retz., Obs. Bot. 4:11. 1786

Perennial, 0.5–1 m tall. Leaves linear, 3–7 mm wide, glabrous or the margins and the underside of midrib scabrous. Bracts subtending inflorescence leaflike, to 30 cm long; spikelets in dense globose heads about 1 cm diam, mostly on short rays, numerous, ovate, flattened, 2–5 mm long, bearing up to 10 or more flowers; scales whitish, membranaceous, boat-shaped, easily disarticulating; stamen 1. Achenes oblong, 1 mm long, trigonous, smooth, light brown. *Croat 5810.*

Common in the Laboratory Clearing. Flowers and fruits throughout the year.

Throughout tropical America. In Panama, known from tropical moist forest all along the Atlantic slope as well as in Veraguas, Los Santos, Herrera, Panamá, and Darién; known also from premontane moist forest in the Canal

Zone and Panamá, from premontane wet forest in Chiriquí, Coclé, Panamá, and Darién, and from tropical wet forest in Coclé (Atlantic slope) and Colón.

Cyperus odoratus L., Sp. Pl. 46. 1753
C. ferax L.

Annual, usually (10)50–100 cm tall. Leaves linear, (1.5)5–14 mm wide. Bracts subtending inflorescence large and leaflike, mostly 15–50 cm long; inflorescences compound (rarely simple), the racemes sessile or on short to long rays (to 20 cm long); spikelets linear, subterete, mostly 7–22 mm long, brownish at maturity; scales 2–3 mm long, striate, ± divergent in age; rachilla strongly winged, the wings becoming corky in age, the spikelets breaking up into single segments. Achenes oblong, 1.5–2.7 mm long, weakly trigonous, dark brown, densely papillose. *Croat 9563, 13239.*

An occasional weed of clearings and marshes. Flowers throughout most of the year.

Well-developed or fruiting specimens are not confused with any other species. Depauperate epiphytic plants on floating logs in the lake may be only 10–25 cm tall and with leaves 1.5–2.5 mm wide. These specimens have a simple inflorescence, but may be distinguished from *C. tenuis* by having corky rachilla wings.

Tropics and subtropics throughout the world. In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Los Santos, Panamá, and Darién; known also from tropical dry forest in Coclé, from premontane moist forest in Panamá, from premontane wet forest in Veraguas and Panamá, from tropical wet forest in Colón, and from lower montane wet forest in Chiriquí.

Cyperus rotundus L., Sp. Pl. 45. 1753
Nut grass, Purple nutsedge, Junco

Slender perennial, 10–60 cm tall. Leaves linear, 2–6 mm wide, usually much shorter than culms. Bracts subtending inflorescence leaflike, short, 1–5 cm long; spikes several, lax, on rays to 6 cm long or very short; spikelets linear, 1–3 cm long, bearing 12–30 flowers; scales purplish to black, keeled, obtuse, Achenes ca 1.5 mm long, obovate-ellipsoid, dark, bluntly trigonous. *Kenoyer 152, Shattuck 357.*

Not seen recently, but to be expected in clearings. Often abundant elsewhere in open areas of the Canal Zone, especially along railroad tracks. Flowers in the rainy season.

Throughout warmer regions of the world. In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién; known also from premontane dry forest in Los Santos and from premontane moist forest in the Canal Zone and Panamá.

Cyperus sesquiflorus (Torr.) Mattf. & Kuek., Pflanzenr. IV.20(Heft 101):591. 1936
Kyllingia odorata Vahl

Small caespitose perennial, 5–40 cm tall; culms very slender. Leaves linear, shorter or slightly longer than culms, 2–3 mm wide. Bracts subtending inflorescence linear, leaflike, 3–8 cm long; spikes 1–3, terminal, head-like, ovoid to cylindroid, sessile and confluent, 5–12 mm long, the terminal spike tending to be cylindrical, the lateral ones usually ovoid; spikelets 3–3.5 mm long; scales opaque, keeled, the apex blunt with a tiny mucro, the keel smooth; style bifid. Achenes lenticular. *Croat 6458.*

A weedy sedge locally common in the Laboratory Clearing. May be found in flower and fruit throughout most of the year.

The spikes are usually whitish, compared to the greenish color of *C. densicaespitosus.*

Widespread distribution from southern United States to Uruguay; West Indies; tropical areas of Africa and Asia. In Panama, known from tropical moist forest in the Canal Zone and Darién, from premontane moist forest in Panamá, and from lower montane wet forest in Chiriquí.

Cyperus simplex H.B.K., Nov. Gen. & Sp. 1:207. 1816

Small perennial, 5–35 cm tall; culms slender, glabrous. Leaves linear, 3–6 mm wide, purplish at ground level. Bracts subtending inflorescences leaflike, to 30 cm long; inflorescences simple, with 1–3 sessile spikelets at apex of a ray 10–20 cm long; spikelets 5–15(20) mm long, many-flowered, compressed; scales with a green keel, acuminate; stamen 1. Achenes subglobose, trigonous, ca 1 mm long, brownish, densely papillose, roughened. *Croat 15157.*

Frequent in the forest. Flowers and fruits principally in the rainy season (April to October).

Southern Mexico to Bolivia and Brazil. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién and from premontane moist, premontane wet, and tropical wet forests in Panamá.

See Fig. 52.

Cyperus tenuis Sw., Prodr. Veg. Ind. Occ. 20. 1788
C. caracasanus Kunth

Perennial, the culms 15–60 cm tall, the underground part purplish. Leaves mostly basal, linear, to 4(5.5) mm wide. Bracts subtending inflorescence long and leaflike; inflorescences of 5–15, simple, loosely cylindrical or flattened spikes; spikes sessile or on short rays, less than 7 cm long including rays; spikelets 5–7(10) mm long, subterete, 3–8-flowered; scales having green median stripe, the margin broad and thin. Achenes subcylindric-trigonous, slightly curved, beaked at both ends, brownish, minutely papillose, 1.5–1.8 mm long. *Croat 11866.*

Very abundant during part of the year in the Laboratory Clearing. May be found in flower throughout the year.

Mexico to Brazil; West Indies; tropical Africa. In Panama, known from tropical moist forest in the Canal Zone, San Blas, Panamá, and Darién, from tropical dry forest in Panamá (Taboga Island), from premontane wet forest in Chiriquí and Coclé, and from lower montane wet forest in Chiriquí.

See Fig. 53.

Fig. 52. *Cyperus simplex*

Fig. 53. *Cyperus tenuis*

KEY TO THE SPECIES OF ELEOCHARIS

Spikelets ovoid, 3–5 mm long; mature achenes less than 1 mm long, shiny black, smooth, the tubercle (style base) minute, depressed ..... *E. caribaea* (Rottb.) S. F. Blake
Spikelets oblong to oblong-linear, 8–25 mm long; mature achenes more than 1 mm long, green to brown, minutely striate, faintly reticulate, the tubercle lanceolate ..... *E. plicarhachis* (Griseb.) Svens.

ELEOCHARIS R. Br.

Eleocharis caribaea (Rottb.) S. F. Blake, Rhodora 20:24. 1918

Glabrous and leafless aquatic, to 45 cm tall, densely tufted with numerous long roots; culms stiff, ca 1 mm wide. Spikelets solitary, at apex of culms, ovoid, obtuse, 3–5 mm long; scales obtuse, yellow-brown, thin, weakly keeled, the lowermost sterile; bristles subtending achene to twice as long as achene; flowers perfect; stamens 1–3; style 2-cleft, exserted. Achenes obovate, weakly compressed, less than 1 mm long, smooth, black, shiny; tubercle (style base) short, depressed. *Ebinger 583.*

Rare; in quiet areas along the south shore of the island in marshes and on tree stumps in the lake. Probably flowers and fruits throughout the year.

Distinguished from *E. plicarhachis* by its much smaller, ovoid spikelets and by its smooth, black, obovate achenes with a depressed tubercle.

Throughout most tropical areas of the world. In Panama, known from tropical moist forest in the Canal Zone and Bocas del Toro, from premontane moist forest in the Canal Zone and Panamá, and from premontane wet and tropical wet forests in Colón.

Eleocharis plicarhachis (Griseb.) Svens., Rhodora 31:158. 1929

Stoloniferous, leafless herb growing on wet soil; culms 20–60 cm long, 2–3 mm thick. Spikelets solitary at apex of culms, oblong to oblong-linear, 8–25 mm long; scales greenish, stiff, striate but central keel lacking; flowers bisexual; stamens 1–3; style 2-cleft. Achenes rounded to obovate, longitudinally striate, green to brown, 1–1.5 mm long; tubercle prominent, lanceolate. *Croat 13230, 13971.*

An occasional component of floating masses of vegetation on the south side of the island. Seen fertile throughout most of the year.

This was mistakenly reported by Standley (1933) as *E. variegata* Presl var. *laxiflora* (Thwaites) Ridley.

Mexico to Paraguay; Cuba. In Panama, known only from tropical moist forest in the Canal Zone and Panamá.

FIMBRISTYLIS Vahl

Fimbristylis dichotoma (L.) Vahl, Enum. Pl. 2:287. 1805

F. annua (Allioni) R. & S.; *F. diphylla* (Retz.) Vahl

Annual or perennial, nearly glabrous, 5–60 cm tall; culms terete, leafy near base. Leaves linear, ca 3 mm wide, mostly arising from base of culm, the margins scabrous. Inflorescences branched, usually loose and open, subtended by few bracts, the bracts longer than inflorescence; spikelets numerous, 5–10 mm long, solitary on peduncles, acute, brownish; scales having a green keel and minute apiculum; flowers perfect; stamens 1–3; style bifid, prominently fimbriate. Achenes obovate, terete, ca 1 mm long, white to brown, with a minute projection at base, sculptured with both vertical grooves and transverse wrinkles. *Croat 8566.*

Common in clearings. Flowers throughout the year, principally in the rainy season.

Low altitudes in temperate and tropical areas of the world. In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Herrera, Panamá, and Darién; known also from tropical dry forest in Coclé and Panamá (Taboga Island), from premontane moist forest in the Canal Zone and Panamá, from premontane wet forest in Chiriquí and Coclé, from tropical wet forest in Colón, and from lower montane wet forest in Chiriquí.

FUIRENA Rottb.

Fuirena umbellata Rottb., Descr. & Icon. 70, pl. 19, fig. 3. 1773

Aquatic herb, 0.5–1.5 m tall; culm often aerenchymatous, several-sided at base, becoming 3-sided above, with creeping rhizomes. Leaves to 40 cm long and 3.5 cm wide, usually minutely scabrid, the veins usually 5 or more. Inflorescences terminal or axillary, branched; spikelets oblong to lanceolate, 4–7(10) mm long; scales scabridulous and sparsely hispidulous, the keel strong, 3-ribbed, extending into an awn, the scale being shed with achene at maturity, the outer bristles filiform, the inner bristles thin, obovate, caudate at apex, enveloping the achene; stamens 3; style trifid. Achenes trigonous, broadly elliptic, light brown, smooth, to 1.3 mm long including their slender apex. *Croat 5340.*

Abundant at the edge of the lake, usually growing in shallow water or on tree stumps. Flowers and fruits throughout the year.

Standley (1933) also reported *Fuirena robusta* Kunth based on *Woodworth & Vestal 464.* This specimen was misidentified and is actually *F. umbellata.*

Throughout the tropics of Western and Eastern hemispheres. In Panama, known from tropical moist forest all along the Atlantic slope and from the Canal Zone and Panamá on the Pacific slope; known also from premontane moist forest in the Canal Zone, from premontane

wet forest in Coclé and Panamá, and from tropical wet forest in Colón and Coclé.

See fig. on p. 12.

HYPOLYTRUM L. C. Rich.

Hypolytrum schraderianum Nees in Mart., Fl. Brasil. 2(1):65, t. 5. 1842

H. nicaraguense Liebm.

Wide-leaved perennial herb, to 1.2 m tall. Leaves longer than culms, 2–3 cm wide, 3-ribbed, the margins scabrous, the outermost leaves basal and bractlike. Inflorescences corymbose-paniculate, mostly 5–8 cm long, often as broad as or broader than long, the lowermost bracts leaflike, to 40 cm long; branches densely scabrid; spikelets oblong, terete, ca 4 mm long, brown, nearly sessile or peduncles to 5 mm long; the peduncles scabrid; scales rounded at apex; stamens 2; style bifid. Achenes ovoid, ca 2.5 mm long, brown, beaked. *Croat 5932, 8349.*

Occasional in the forest, usually in somewhat open areas. Flowers from the late rainy season to the early dry season. The fruits mature in the late dry and early rainy seasons.

Throughout Central America and south to Brazil. In Panama, known from tropical moist forest in the Canal Zone and Darién and from premontane wet forest in Panamá.

See Fig. 54.

RHYNCHOSPORA Vahl

Rhynchospora cephalotes (L.) Vahl, Enum. Pl. 2:237. 1805

Paja macho de monte

Perennial, usually 75–100 cm tall, with a coarse rhizome. Leaves linear, 5–15 mm wide, the margins scabrous. Bracts subtending inflorescence usually 2 or 3, long, leaflike; spikelets in a dense, terminal, sessile, ovoid head 1.5–4 cm long; flowers numerous, ca 7 mm long, the upper ones staminate, the lower ones bisexual; scales greenish to light brown with a stout tip; stamens 3; style bifid. Achenes subglobose, weakly flattened, 1.5–2 mm long, light brown, capped by persistent green tubercle and subtended from base by 6 persistent bristles to ca 5 mm long. *Croat 8554.*

Occasional in the forest, but locally common along the shore, usually near water. Flowers from the late rainy season through the dry season. The fruits mature in the late dry and early rainy seasons.

The species is quite variable elsewhere.

Mexico to Trinidad and Brazil; Jamaica. In Panama, known from tropical dry forest in Herrera, Coclé, Panamá, and Darién, from premontane moist forest in the Canal Zone, from tropical moist forest in the Canal Zone and Colón, from premontane wet forest in Panamá, and from tropical wet forest in Colón and Panamá.

See Fig. 55.

Rhynchospora corymbosa (L.) Britt., Trans. New York Acad. Sci. 11:85. 1892

Coarse herb, to 1.5 m tall, usually aquatic; culms triangular. Leaves linear, to 1 m long, 1–2 cm wide, the midrib scabrous on the underside, the margins scabrous. Dense corymbs arising from each of the upper leaves, to 12 cm long, the bracts caudate-acuminate, the upper flowers staminate, the lower flowers bisexual; spikelets numerous, brown at maturity, 7 mm long, containing a single achene; scales thin, brown, glabrous, the keel green; stamens 3; style bifid. Achenes 2–3 mm long, obovate, brown, with corky conic beak, the bristles exceeding achene. *Croat 13981.*

Uncommon, but locally abundant in some marshes on the south edge of the island. Flowers and fruits principally during the dry season and the early rainy season.

Sometimes the dominant plant in a localized area.

Throughout tropics of Western and Eastern hemispheres. In Panama, known from tropical moist forest in the Canal Zone (Atlantic slope), Bocas del Toro, and Colón, from premontane wet forest in Panamá and Chiriquí, and from tropical wet forest in Colón.

Rhynchospora micrantha Vahl, Enum. Pl. 2:231. 1805

Weak, slender annual, 10–35(50) cm tall, glabrous throughout; culms leafy. Leaves linear, mostly 10–20 cm long, 1–2 mm wide. Bracts slender, scabrid; spikelets in lax, slender corymbs to 1.5 mm long, the upper flowers staminate, the lower flowers bisexual; scales 1-veined, awn-pointed; bristles lacking; stamens 3, style bifid. Achene rounded to obovate, biconvex, white, ca 1 mm long, transversely rugose, the style base slender. *Kenoyer 153.*

Collected once on Orchid Island. Flowers and fruits throughout the rainy season.

The plant grows in similar locations as and looks similar to *Bulbostylis junciformis* (H.B.K.) Lindm., which does not occur on BCI.

KEY TO THE SPECIES OF RHYNCHOSPORA

Inflorescence a single, dense, terminal head:
- Heads less than 1 cm long, usually white; scape bracts usually white at base, less than 15 cm long and 5 mm wide; leaves usually less than 5 mm wide ..... *R. nervosa* (Vahl) Boeck.
- Heads more than 1.5 cm long, greenish; scape bracts green, usually more than 15 cm long and 5 mm wide; leaves more than 5 mm wide ..... *R. cephalotes* (L.) Vahl

Inflorescence compound:
- Spikelets less than 2 mm long in widely scattered clusters on slender branches ... *R. micrantha* Vahl
- Spikelets more than 5 mm long, in a usually congested dense corymb ..... *R. corymbosa* (L.) Britt.

Fig. 54. *Hypolytrum schraderianum*

Fig. 55. *Rhynchospora cephalotes*

Throughout Central America; West Indies; tropical Africa. In Panama, known from tropical moist forest in the Canal Zone, San Blas, and Panamá, from premontane moist forest in the Canal Zone, from premontane wet forest in the Canal Zone and Panamá, and from tropical wet forest in Colón.

Rhynchospora nervosa (Vahl) Boeck. in Vid., Medd. Nat. For. Kjobenh. 1869:43. 1870.

Dichromena ciliata Vahl; *D. radicans* sensu auct.

Junco menudo, Clavo

Weak herb, 10–70 cm tall. Leaves 10–45 cm long, 3–5 mm wide, glabrous or villous on upper surface. Bracts subtending inflorescence 4–6, unequal, 1–15 cm long, usually white near base on upper side; inflorescence a dense head held well above leaves; spikelets 3–15, narrowly ovoid, 5–10 mm long, the flowers bisexual; scales thin, brown to whitish, glabrous or rarely scabrid on keel and margin; stamens 3; style 2-cleft, exserted and white at anthesis. Achenes obovate, weakly flattened, white to brownish, with numerous transverse wrinkles, the style base brown or greenish, ± flattened. *Croat 6808.*

Common in clearings. May be found in flower and fruit throughout the year.

Svenson (1943) in the *Flora of Panama* reported this species to have black or brown achenes, but I have found them to be white or more rarely light brown at maturity. Achenes are exposed along the rachis as the bracts become deciduous, beginning at the base. *Standley 40831,* reported by Svenson as *Dichromena pubera* Vahl, should probably be included here despite the fact that the scales are scabrid on the keel and margins; its achenes are like those of *R. nervosa,* and it does not differ in any other way.

In Central America, flowers open between 9:00 and 11:00 A.M. and are visited by the bees *Trigona* sp., *Bombus mexicanus,* and *Apis mellifera* (Leppik, 1955).

Throughout most tropical areas of the Western Hemisphere. In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Chiriquí, Veraguas, Panamá, and Darién; known also from tropical dry forest in Los Santos, Herrera, Coclé, and Panamá, from premontane dry forest in Los Santos, from premontane moist forest in the Canal Zone and Panamá, from premontane wet forest in Chiriquí and Panamá, and from tropical wet forest in Chiriquí.

SCIRPUS L.

Scirpus cubensis Kunth, Enum. Pl. 2:172. 1837

Stout, glabrous perennial, 30–100 cm tall, usually aquatic. Leaves basal, long and narrow, equaling or exceeding culms and inflorescences, to 1 cm wide except wider at sheathing base, the midrib raised above and usually scabrous, the margins scabrous; leaves drying with numerous minute rectangular reticulations at least near base. Bracts subtending inflorescence leaflike, often more than 60 cm long; inflorescences of dense globose heads, 1–1.5 cm diam on rays 1–10 cm long; spikelets 4–8 mm long; scales acuminate; stamens 2 or 3; style bifid or trifid. Achenes narrowly obovoid, smooth, pale. *Croat 13974.*

Apparently quite rare, though perhaps overlooked in sterile condition; locally abundant in marshes along the shore. Flowers throughout the year, mostly during the dry season.

Throughout most of tropical America. In Panama, known only from tropical moist and premontane moist forests in the Canal Zone.

SCLERIA Bergius

Scleria eggersiana Boeck., Cyp. Nov. 2:41. 1890

Stout herb, 1.5–2 m tall; culms ± smooth or scabrid near apex, often clustered and connected by a ± woody rhizome; ligules broadly to narrowly triangular, to 1 cm long, glabrous or the margins bearing short trichomes. Leaves linear, mostly 1–2.5 cm wide, glabrous or scabrid especially on margins and ribs. Panicles to 35 cm long, sparse, with relatively few ascending branches; spikelets sparse, unisexual; staminate spikelets many-flowered; pistillate spikelets 1-flowered with several empty scales;

KEY TO THE SPECIES OF SCLERIA

Plants climbing and vinelike, often suspended on low shrubs or trees to 3 m or more; leaves 2–7 mm wide; plants generally on lakeshore ..... *S. secans* (L.) Urban

Plants erect or leaning but never vinelike:

Plants less than 1 m tall; leaves less than 1 cm wide; inflorescences often purplish; achenes purple or white; hypogynia (cuplike structures beneath fruit) glabrous or weakly ciliate; plants of clearings ..... *S. pterota* Presl

Plants 1–3 m tall; leaves more than 1 cm wide; inflorescences not purple; achenes white; hypogynia with upper margin conspicuously ciliate; plants usually growing near water:

Cilia purple, moderately long ..... *S. mitis* Bergius

Cilia brown or tan, usually short or inconspicuous:

Inflorescences glabrate; achenes to 3 mm long; cilia of hypogynium conspicuous ..... *S. eggersiana* Boeck.

Inflorescences conspicuously pubescent; achenes 3.5–6 mm long; cilia of hypogynium inconspicuous ..... *S. macrophylla* Presl

bracts inconspicuous; hypogynia obscurely 3-lobed, the margins densely ciliate with short brown trichomes (occasionally longer). Achenes white (sometimes brownish), globose, 2.5–3 mm long, often tipped with persistent tubercle. *Croat 11309.*

Occasional, usually in water at the edge of the lake. May be found in fruit throughout much of the year but principally in the rainy season.

Probably more abundant than *S. mitis,* with which it is easily confused; *S. mitis* apparently prefers not to grow directly in water.

Central America to northern South America; West Indies. In Panama, known only from tropical moist forest on the Atlantic slope of the Canal Zone and from tropical wet forest in Colón.

Scleria macrophylla Presl, Rel. Haenk. 1:200. 1828
S. paludosa (?)Kunth

Stout herb, 1–3 m tall; culms with usually smooth margins; ligules blunt, often pubescent, the veins stout, meeting a collecting vein, the margins thick, glabrous. Leaves linear-lanceolate, 15–60 cm long, 1–7 cm wide, minutely pubescent or glabrous, the margins scabrous. Inflorescences paniculate, terminal or axillary, densely puberulent; spikelets unisexual; staminate spikelets many-flowered; pistillate spikelets with 1 flower and several empty scales; bracts narrow and conspicuous; hypogynia very thick, 3-lobed, the margins minutely ciliate. Achenes rounded, white, shiny, 3.5–6 mm long, often with large, conic, persistent tubercle. *Croat 12815, 13156.*

Uncommon, in marshes on the lakeshore. Probably flowers and fruits toward the beginning of the dry season.

Distinguished by its densely pubescent inflorescence, large achenes, and broad leaves.

Mexico to Brazil and Bolivia. In Panama, known from tropical moist forest in the Canal Zone and Panamá and from premontane moist forest in Panamá.

Scleria mitis Bergius, Kongl. Vetensk Acad. Handl. 26:145. 1765

Stout herb, 1–2 m tall, nearly glabrous; culm margins smooth; ligules narrowly triangulate, glabrous to pubescent, 1–1.5 cm long. Leaves 30–50 cm long, mostly 1.5–2.5 cm wide, somewhat scabrid especially on margins. Panicles narrow, 20–50 cm long, much-branched; spikelets congested, unisexual; staminate spikelets many-flowered; pistillate spikelets with 1 flower and several empty scales; bracts inconspicuous; hypogynia truncate, the rims densely ciliate with long purplish-brown trichomes. Achenes ovoid to ellipsoid, ca 2(4) mm long, smooth and white, often tipped with a persistent, conic tubercle. *Croat 5251, 8010.*

Uncommon; occurring at the edges of clearings, near the shore, and on silt deposits in coves such as the one in Fuertes Cove. Flowers and fruits as early as December, but usually from February to July.

Distinguished by the long, purplish-brown cilia of the hypogynium.

Guatemala to Paraguay; Cuba. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Colón, from premontane moist forest in Panamá, and from tropical wet forest in Colón.

Scleria pterota Presl, Isis (Oken) 21:268. 1828
S. melaleuca Schlecht. & Cham.; *S. pterota* var. *melaleuca* Uitt.

Herb, 30–90 cm tall; culms ± scabrid, the trichomes ascending; ligules triangulate, ca 5 mm long, the veins extending almost to margin; margin thin, ciliate. Leaves to 40 cm long, mostly less than 12 mm wide, ± scabrid. Panicles terminal or axillary, often brown to purplish, the branches short, scabrid, bearing few spikelets; spikelets unisexual; staminate spikelets many-flowered; pistillate spikelets with 1 flower and several empty scales; bracts inconspicuous; hypogynia with 3 broad, rounded, glabrous or weakly ciliate lobes. Achenes globose, 1.5–2.5 cm long, bearing white trichomes in lower half. *Croat 6482.*

Abundant in clearings and open areas of the forest. Flowers and fruits throughout the year.

The BCI material would contain also the variety *melaleuca* Uitt. with black achenes, but the character of fruit color is of doubtful taxonomic value.

Throughout the tropics of the Western Hemisphere. In Panama, known principally from tropical moist forest in the Canal Zone, all along the Atlantic slope, and on the Pacific slope in Chiriquí, Veraguas, Los Santos, Herrera, Panamá, and Darién; known also from tropical dry forest in Panamá, from premontane moist forest in the Canal Zone and Panamá, and from tropical wet forest in Colón.

Scleria secans (L.) Urban, Symb. Ant. 2:169. 1900
Cortadera

Climbing, vinelike herb, 3–6 m tall; culms with sharp, retrorsely scabrous to hispid trichomes on angles; ligules blunt, usually to 6 mm long, brown and thin above, thick at base, the conspicuous connecting veins generally pilose. Leaves generally less than 30 cm long, 2–7 mm wide, sparsely pubescent with longer trichomes but the margins and underside of ribs retrorsely scabrous. Panicles usually purplish, terminal or axillary; branches sparsely villous; spikelets unisexual; staminate spikelets many-flowered; pistillate spikelets with 1 flower and several empty scales; bracts conspicuous, filiform; hypogynia inconspicuous, glabrous, the margins reflexed, becoming undulate on drying. Achenes usually few, ± ovoid, 2–4 mm long, white, shiny. *Croat 13013.*

Locally quite common along the shore; occasional in the forest and open areas. Flowers and fruits throughout the year.

Of all the plants on the island this is the one most appropriately avoided. It usually grows over low trees at the margin of the lake, and once one is entangled every move worsens the situation. The edges of the culms cut like razors, and someone struggling to get free may pull large masses of the plant down on top of him. White-

faced monkeys have been seen eating the fruits during the latter part of the rainy season when food is scarce.

Mexico to Bolivia and Brazil; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Chiriquí, and Panamá, from tropical dry forest in Panamá (Taboga Island), from premontane wet forest in Colón and Panamá, and from tropical wet forest in Colón.

19. PALMAE (ARECACEAE)

Unbranched trees, shrubs, or lianas, rarely subacaulescent and appearing herbaceous, often with spiny stems. Leaves alternate, basal or clustered at the apex of the stem, petiolate, the base of the petiole sometimes persistent, usually deciduous leaving a narrow scar ring on the trunk; blades pinnately or palmately compound (sometimes simple and pinnately veined in *Geonoma* or in juveniles); blades and leaflets pleated, the margins usually entire; venation principally parallel, appearing pinnate or palmate; stipules lacking. Inflorescences of spicate or branched interfoliar or intrafoliar spadices; flowers bisexual or unisexual (monoecious or dioecious), actinomorphic, often immersed in a cavity, subtended by 2 envelopes, the primary one usually short and soon falling, the secondary one (the spathe) often persisting until maturation of the fruits; sepals 3, free or united, imbricate; petals 3, usually briefly connate and imbricate, or tepals 6; floral envelopes sometimes accrescent, forming cupule at base of fruit; stamens 6 (many in *Socratea*; 8 or 9 in *Desmoncus*; 3 in *Synechanthus warscewiczianus*), free, in 2 whorls of 3 each; anthers 2-celled, dehiscing longitudinally; ovary superior, 3-locular, 3-carpellate, the carpels united (elsewhere rarely with 3 free carpels); placentation basal or axile (parietal in *Oenocarpus*); ovules 3, 1 per loculus, but usually with only 1 developing, anatropous; styles usually 3, free or fused, or stigmas sessile. Fruits drupes; seeds 1(3), with endosperm.

Because of the characteristic leaves, the Palmae are confused only with the Cyclanthaceae. Leaves of both families are pleated, or the individual pinnae V-shaped. The Palmae may be distinguished from the Cyclanthaceae by generally being caulescent and by having six perianth segments, usually few ovules, and frequently compound inflorescences with a persistent spathe, by lacking conspicuous staminodia, and by having usually large, one-seeded fruits. Palms are unique in being the only monocots tall enough to compete with trees in the forest.

Little is known of the pollination systems of palms. *Astrocaryum* and *Scheelea,* which produce abundant amounts of pollen and are tall enough to be affected by wind currents, are possibly wind pollinated. However, I have seen *Trigona* bees visit the inflorescence of *Scheelea zonensis* in great numbers while it is in flower. The same may be true of *Socratea,* which is one of the tallest species of palm on the island, but it produces relatively small amounts of pollen. *Bactris* flowers are protogynous and all pollinated by small beetles that feed on staminate flowers (Essig, 1971, 1973); no nectar is produced. Studies by Essig (1971) on *Bactris major* in Costa Rica show numerous flower visitors, but he concluded that only nitidulid and curculionid beetles play any role in pollination. *Geonoma* is protandrous. *Asterogyne,* a closely related genus, is pollinated by syrphid flies in Costa Rica (Schmid, 1970). Self-pollination is generally prevented where staminate and pistillate flowers share the same spike by a well-marked protandry.

Fruits are animal dispersed. *Geonoma* as well as possibly *Chamaedorea wendlandiana, Synechanthus warscewiczianus, Cryosophila warscewiczii,* and *Desmoncus isthmius* are partly bird dispersed. Fallen fruits of *Scheelea* are fed upon by vultures, but it is not known if they are carried away (Foster, pers. comm.). *Astrocaryum standleyanum* is taken by bats (Bonaccorso, 1975). White-faced monkeys eat the mesocarp of *Astrocaryum standleyanum, Scheelea zonensis, Socratea durissima,* and *Oenocarpus panamanus* without breaking through the tough endocarp. They are also known to swallow whole the fruits of *Desmoncus isthmius* (Hladik & Hladik, 1969; Oppenheimer, 1968). Spider monkeys are reported to eat *Astrocaryum* and *Socratea* fruits (Hladik & Hladik, 1969). *Scheelea zonensis* and *Astrocaryum standleyanum* are taken by monkeys and coatis (Kaufmann, 1962) and by squirrels (Enders, 1935). While fruits of *Astrocaryum, Scheelea, Socratea,* and *Oenocarpus* may be taken in large part by arboreal frugivores, many find their way to the ground and are further dispersed by rodents and other ground animals. Perhaps most fruits are dispersed by rodents such as spiny rats and agoutis, and by peccaries (Enders, 1935), which are the only groups of animals capable of breaking through the stony endocarp. Agoutis scatterhoard fruits of *Astrocaryum, Bactris, Scheelea,* and *Socratea* (N. Smythe, pers. comm.; C. C. Smith, 1975). Smith has found that *Scheelea* often has a second or third ovule develop, and even if the fruit is bitten open by a rodent it is still possible that one seed will remain for germination. On the other hand Janzen (1971) reported that the widespread bruchid beetle *Caryobruchus buscki* Bridw. can be responsible for the destruction of all seeds by eating through carpel walls.

About 236 genera and 2,650 species; widespread, principally in the tropics and subtropics.

KEY TO THE TAXA OF PALMAE

Leaves palmately compound (segments radiating from central point); at least the base of trunk armed with branched spines ..... *Cryosophila warscewiczii* (H. Wendl.) Bartl.

Leaves pinnately compound or simple and pinnately veined (leaflets radiating from 2 sides of a central rachis):

Trunk of stem long and slender, vinelike, erect only as a juvenile; leaflets replaced on end of leaf by large recurved spines ..... *Desmoncus isthmius* Bailey

Trunk erect or, if stemless, leaves without retrorse spines:
Plants armed with long needlelike or flattened spines; leaflet margins usually with tiny sharp setae (sparse on some juvenile *Bactris;* sometimes lacking on *B. gasipaes*):
Trunks less than 7 cm diam; trunkless juvenile leaves with leaflets mostly of same width (if leaflets entire or of different widths, then the cross-veins prominent or the lower surface not densely white-scurfy) ..... *Bactris* (in part)
Trunks more than 10 cm diam (trunkless juvenile leaves of *Astrocaryum* with leaflets of greatly different widths or entire, the lower surface densely white-scurfy):
Lower surface of blades covered with a dense whitish, scurfy pubescence able to be scraped off, but the trichomes themselves completely indistinguishable; spathe more than 80 cm long; staminate flowers in part aggregated distally, solitary or in pairs, the subtending bractlets coherent with adjacent bractlets, forming a cupule sometimes as long as the flower ..... *Astrocaryum standleyanum* Bailey
Lower surface of blades sparsely pubescent with erect, simple trichomes; spathe less than 70 cm long; staminate flowers not densely aggregated distally but associated with pistillate flowers in triads or irregularly dispersed among triads, the flowers subtended by short, distinct bracteoles ..... *Bactris gasipaes* H.B.K.
Plants not armed with long, needlelike or flattened spines; leaflet margins without tiny sharp setae:
Leaf blades not deeply divided ..... *Geonoma cuneata* Spruce
Leaf blades variously pinnate:
Leaflets narrow at base, broadened to 10 cm or more, the lower edge straight, the upper and outer margins irregularly toothed; trunks with large spiny stilt roots ..... *Socratea durissima* (Oerst.) H. Wendl.
Leaflets of essentially same width for most of their length, the ends tapering to a point:
Leaflets regularly arranged and of nearly same width throughout:
Leaflets falcate (the ends curved toward apex); lower side of rachis with broad cream-colored band the full length of the leaf; trunks usually with adventitious roots at base ..... *Chamaedorea wendlandiana* (Oerst.) Hemsl.
Leaflets straight, the ends not curved toward apex; rachis not with light-colored band along full length of leaf on underside; trunks without adventitious roots:
Plants rare, persisting in old cultivations; lateral costae all equally inconspicuous, the surface flat; trunk more than 20 cm diam ..... *Cocos nucifera* L.
Plants common, occurring throughout forest or in swampy areas; lateral costae at least in part raised, the surface sometimes prominently pleated; trunk more than 30 cm diam or less than 12 cm diam:
Rachis of leaf glossy beneath, green when fresh; petioles round at apex, unarmed; trunks less than 12 cm diam, erect, 8–20 m tall ..... *Oenocarpus panamanus* Bailey
Rachis of leaf densely furfuraceous beneath, brown; petioles canaliculate at apex, sharply armed; trunks more than 30 cm diam, decumbent at base, to 2 m tall ..... *Elaeis oleifera* (H.B.K.) Cort.
Leaflets irregular, either irregularly spaced or of irregular widths or both:
Leaflets inserted on rachis at different angles, some held higher than others; inflorescences massive, ca 2–3 m long; fruits ca 3 cm diam; trees at maturity over 30 cm diam ..... *Scheelea zonensis* Bailey
Leaflets inserted on rachis at same angle, none raised considerably more than others; inflorescences less than 1.5 m long; fruits less than 1 cm wide:
Leaf scars on trunks ca 1 cm apart; costae of leaflets in outer half of blade (below terminal lobe) decurrent onto rachis and obscuring the central midrib; secondary costae of leaflets scarcely if at all raised on upper surface; trunks seldom more than 1.5 m tall; inflorescences simple, unbranched ..... *Geonoma procumbens* Spruce
Leaf scars on trunk mostly 5 cm or more apart; costae of leaflets in outer half of blade (below terminal lobe) not merging with or obscuring central rib of rachis; secondary costae of leaflets much raised on upper surface; trunks usually 2 m tall or more; inflorescences branched:
Petiole and rachis flattened near base of blade on upper surface with the lateral margins sharp; leaflets in about 25 pairs, spaced 1–4 cm apart near apex; leaf scars mostly ca 5 cm apart in middle of trunk; inflorescence branches 2–3 mm thick, branched; fruits 4–6 mm long ..... *Geonoma interrupta* (R. & P.) Mart.
Petiole rounded, the rachis prominently ridged just above base of blade; leaflets in 4–6 pairs, spaced up to 10 cm apart near apex; leaf scars to 15 cm apart in middle of trunk; inflorescence branches ca 1 mm thick, unbranched; fruits ca 15 mm long ..... *Synechanthus warscewiczianus* H. Wendl.

Fig. 56. *Astrocaryum standleyanum*

Fig. 57. *Astrocaryum standleyanum*

Fig. 58.
Bactris barronis

ASTROCARYUM G. Meyer

Astrocaryum standleyanum Bailey, Gentes Herb. 3:88 1933

Black palm, Chunga

Monoecious tree to 15 m tall; juveniles trunkless, the trunk of mature plants to 20 cm dbh, the internodes 30–40 cm long, prominently spiny, the spines slender, 10–15 cm long, flattened, shiny and black or with margins thin and brown, often furfuraceous; spines of petiole, rachis, peduncle, and outer surface of spathe much shorter than of internodes; leaf scars 2–3 cm long. Leaves 2–4 m long; petioles 1 m or more long, canaliculate above; leaflets to 75 cm or more long and 3.5 cm wide (broader on juvenile leaves), with small marginal setae, irregularly spaced and inserted at staggered angles, the apex oblique or cleft, the midrib prominently raised on upper and lower surfaces, the upper surface glabrous, the lower surface covered with a dense whitish scurf; juvenile leaves at first entire, later with few, widely spaced leaflets, these narrow or to 10 cm wide (especially at apex), the petiole at first furfuraceous, its spines to 25 cm long and 8 mm wide. Spathe armed on outer surface, 84–145 cm long, deciduous (rolling inward on drying); spadix somewhat shorter than spathe, ± erect to spreading at anthesis; peduncles terete, armed, equaling rachis; staminate flowers crowded on the outer part of rachilla, solitary or in pairs, falling soon after anthesis; subtending bractlets forming a cupule sometimes as long as flower; stamens 6, exserted; pistillate flowers few, on lower part of rachilla, 15–18 mm long; fruiting spadix pendent. Fruits ± obovoid, orange, 4–4.5 cm long (including the prominent beak), held in a massive pendent cluster, the surface coarsely papillate; nutlets 1–3, with longitudinal black stripes. *Croat 5391, 16626.*

Very common in the younger forest; less abundant in the older forest except on steep ravines. Flowering mostly from May to September. Plants may flower while some fruits are still present on old inflorescences. By the end of the rainy season fruits are one-half to two-thirds full size. They begin to be eaten by the animals when they attain mature size even if still green, beginning in January, with most being removed between March and June.

The species is similar to *A. aculeatum* G. Meyer of northern South America and Trinidad, but that species is described as attaining a height of 25 m with a trunk to 30 cm diam.

Nicaragua to Colombia. In Panama, known from low elevations in wet and very wet regions (Holdridge, 1970); few collections exist but I have seen the species in tropical moist forest in the Canal Zone, Panamá, Colón, and Darién.

See Figs. 56 and 57.

BACTRIS Jacq.

The genus is most easily distinguished by its usually slender (broad in *B. gasipaes*), spiny-ringed trunks and often spiny leaves and spathes. Leaflets usually bear small marginal spicules as well. Flowers have six to twelve anthers and are not sunken in the rachis. Two staminate flowers are usually associated with a single pistillate flower. Floral envelopes often enlarge to form a cupule on the fruit; these may be in two separate series or may be united to form a single series.

Bactris barronis Bailey, Gentes Herb. 3:101. 1933

Small, monoecious tree, to 8 m tall, forming small clusters; trunks to 5 cm diam; internodes prominently spiny. Leaves regularly pinnate but sometimes interrupted (especially on juvenile leaves), usually spineless except on vaginate part of petiole, occasionally with a few spines higher on petiole and rachis; petioles usually more than

KEY TO THE SPECIES OF BACTRIS

Leaflets regularly arranged (or nearly so) on rachis, all directed in about the same plane (sometimes irregular on juvenile plants of *B. barronis,* but these can be recognized by being blackish-green with prominent cross-veins):
- Petioles armed only at the base; rachis usually unarmed; leaflets with prominent cross-veins; rachillae of inflorescence numerous, slender (1–2 mm wide), to 12 cm long; fruits depressed-globose, ca 1 cm diam, prominently short-bristled, held in a close, compact, ± globular cluster, orange at maturity ..... *B. barronis* Bailey
- Petioles and rachis armed ± throughout; leaflets lacking prominent cross-veins; rachillae of inflorescence usually 9–17, thick (more than 3 mm wide), more than 12 cm long; fruits ± obovate, ca 3 cm diam, not short-bristled, held in a diffuse cluster, purplish at maturity ..... *B. major* Jacq.

Leaflets irregularly arranged on rachis, directed at different angles (regular only near apex):
- Trunks 10–15 cm diam; spathe 50–70 cm long ..... *B. gasipaes* H.B.K.
- Trunks less than 5 cm diam; spathe less than 35 cm long:
  - Leaflets with prominent cross-veins, the marginal setae conspicuous, mostly 5–10 mm long or longer; fruits orange, the beak obscure to blunt, the cupule with a single ± entire envelope ..... *B. coloradonis* Bailey
  - Leaflets lacking any obvious cross-veins, the marginal setae inconspicuous or absent, mostly 1–3 mm long; fruits not orange, the beak prominent, slender; cupules of 2 series, their margins crenate ..... *B. coloniata* Bailey

Fig. 59. *Bactris coloniata*

Fig. 61. *Bactris major*

Fig. 60. *Bactris coloradonis*

1 m long, green, terete; spines on petiole and sheath variable in length, mostly 1–9(15) cm long; leaflets 30 or more pairs, 75–100 cm long, 1.5–4.2 cm broad (the uppermost pair often much broader), spaced 2.5–5 cm apart near apex and 7–10 cm apart near base, dull, conspicuously cross-veined between the prominent side ribs, strongly setose marginally, the setae 2–6 mm long; midrib prominently raised on upper surface, the oblique apex 2.5–5 cm long, held ± straight; juvenile leaves blackish-green with prominent cross-veins, at first entire, becoming irregularly pinnate, some leaflets (especially apical pair) much broader than others. Spathe 15–30 cm long, usually persisting in fruit, bearing dense, coarse, black spines usually 1 cm long or less; spadix to 28 cm long, the floriferous part to 15 cm long, rachillae numerous, slender, densely flowered, to 12 cm long, the peduncle very short and stout, tightly curved; flowers cream-colored; staminate flowers not available; pistillate flowers with the calyx cup-shaped, 2 mm wide, 1 mm high, weakly 3-lobed, the corolla tubular, 2.5 mm long, ca 1.5 mm wide, weakly 3-lobed, sparsely appressed-spiculate. Fruits turbinate to pyriform, ca 1 cm diam, usually ± flattened on top with a short beak, green with short bristles, becoming orange and losing most bristles at maturity; mature fruit clusters tight, ± globular, 6–10 cm diam; cupule nearly flat, in 2 unequal series, at least the larger series shallowly lobed; seed 1. *Croat 9272.*

Common in the forest. Flowering in the late dry to early rainy seasons (March to May). Fruits mature in the wet season, June to September.

Distinguished from other *Bactris* by occurring in dense clusters, often associated with juvenile plants, and by having petioles usually spiny only at the base and with very dense, short spadices. Pinnae of adult blades are regular and are inserted at the same angle; in juvenile plants the pinnae may be unequally spaced and stagger-angled.

Known only from Panama in tropical moist forest in the Canal Zone and Panamá.

See Fig. 58.

Bactris coloniata Bailey, Gentes Herb. 3:106. 1933
Uvito

Small, monoecious tree, 3–4(6) m tall, forming open colonies; plants connected by subterranean stems; trunk 3–4 cm diam; internodes weakly spiny, the spines 1–4 cm long. Leaves 2–3.3 m long, irregularly pinnate, spiny all over or only on base of petiole; petioles terete, to 1.4 m long, furfuraceous on lower side only or all over with only the upper surface near base glabrous, the vaginate base to 40 cm long, spiny throughout its length, the spines solid black to stramineous and black-tipped, 1–7 cm long (mostly 4 cm); rachis ribbed at base, becoming triangulate distally, sparsely spiny, the spines like those of the longer type on petiole; leaflets ca 23 pairs, 30–75 cm long, 2.5–6 cm broad, thin, glossy, lacking prominent side ribs or cross-veins, usually with narrow furfuraceous bands near margins on lower surface, prominently setose at apex, the apex falcate, oblique, very long-caudate and drooping, the acumen to 6 cm long on upper leaflets, to 14 cm long on lower leaflets; upper leaflets ± regularly arranged, the lower becoming arranged in groups of 4–12, each group 5–20 cm apart, the leaflets of each group inserted at staggered angles, the lowermost pair of pinnae at base of blade often held almost vertical forming nearly a right angle with rachis. Spathe 20–35 cm long, ± caudate at apex, often persisting in fruit, densely setose, the trichomes brown to sienna, at first appressed, later ± erect, the slender, unarmed base nearly as long as broadened part of spathe; spadix with usually 15–20 well-spaced branches, the branches to 25 cm long, 1.5–3.0 mm thick; staminate flowers pedicellate, the pedicel to 1 mm long, slender; sepals 3, very slender, ca 1 mm long; petals 3, accrescent in lower half, acute, ca 4 mm long; pistillate flowers ca 4 mm long, the envelopes striate, the inner ones short and truncate, the outer with 3 acute lobes. Fruits turbinate, 1.5–2.5 cm long, with abrupt, short, slender beak, green to black, sparsely hirtellous, becoming ± glabrous at maturity; cupule double with bluntly scalloped edges; seed 1. *Croat 6772, 8787.*

Abundant in the forest, usually in small or large stands; juveniles often very abundant. Plants are not commonly seen in flower, apparently not flowering every year; numerous individuals flower, but only a small part of the adult population. Flowers in the middle to late dry season, with fruits maturing in the early rainy season, mostly in August and September.

The most abundant and most variable *Bactris* on the island. Included here are *Bailey 505* and *521,* which Bailey considered distinct species.

Known only from Panama in tropical moist forest on the Atlantic slope in the Canal Zone and from premontane wet forest in Panamá.

See Fig. 59.

Bactris coloradonis Bailey, Gentes Herb. 3:104. 1933
B. coloradensis Burr.

Small, monoecious tree, 5–8 m tall, often growing as single plants; trunk less than 5 cm diam; internodes obscurely spiny, the spines 1–6 cm long, dull, black, broadened at base. Leaves 2.5–3 m long; petioles usually ca 1 m long, round, canaliculate above, slightly rufous beneath, spiny only at base or rarely throughout its length (especially true of juvenile plants), the spines 1–8.5 cm long; rachis usually unarmed, green above, rufous below; leaflets 25 or more pairs, to 70 cm long, 2–4 cm wide, glabrous, gray-green, dull, the midrib very prominent above, scarcely more prominent than strong lateral veins below, the cross-veins very prominent on both surfaces, the upper surface with occasional setae, the lower surface sometimes with rufescent bands, the margins usually sparsely but prominently setose, especially near apex, the setae 5–10 mm long or more; apex of leaflets oblique, 3–4 cm long in the middle and distal parts of leaf, to 12 cm long on proximal leaflets; distal leaflets regularly arranged, becoming clustered in groups of 3 or 4, the groups 2–6 cm apart, but with gaps to 30 cm on either side, the proximal leaflets of each group inserted at a

higher angle and held above the plane of the leaf, the lowermost pair of leaflets at base of blade sometimes inverted with the bottom side up, the apex of leaflet pointing toward apex of blade; juvenile leaves at first entire, becoming pinnate, the outermost pair broad, the leaflets characterized by having extremely long spines on margin and on upper surface. Spathe 25 cm long, densely brown-spiny, usually falling before fruit matures; peduncle short, somewhat flattened, closely curved, densely covered with short, stiff, brown trichomes at least toward apex; fertile part of spadix 15–25 cm long, widely branched, the branches 20–30, to 2 mm thick. Fruits orange, fading on drying, glabrous, ± round to obovoid, 1–2 cm long, obtuse and beakless at apex but drying with a blunt beak; cupule small and shallow, almost entire, the outer series very reduced; seed 1. *Croat 15422.*

Apparently rare on the island, known only from the older forest. Time of flowering unknown. Fruiting individuals have been seen only during June and July.

Easily distinguished by its solitary habit, its irregular leaflets with very prominent cross-veins, and its orange, nearly beakless fruit.

Known only from Panama in tropical moist forest on BCI.

See Fig. 60.

Bactris gasipaes H.B.K., Nov. Gen. & Sp. 1:302. 1816

Gulielma gasipaes (H.B.K.) Bailey; *G. utilis* Oerst.

Pejibaye palm, Pixbá

Monoecious tree, 5–20 m tall; trunk solitary or clustered, 10–15 cm diam, the internodes ca 20 cm long, densely armed with spines to 10 cm long. Leaves irregularly pinnate, to 3 m long; rachis 2 m long or more, sparsely armed; leaflets to 120 pairs, in clusters of 4 each, staggered-angled, 50–60 cm long, ca 3 cm wide, sparsely short-pilose on underside of veins, the margins entire or very sparsely setose, the cross-veins prominent. Inner spathe woody, less than 70 cm long, finely tomentose and armed with spines ca 1 cm long; spadix 30 cm long above branches; peduncle unarmed; rachis short; rachillae 25–30, minutely ferruginous-puberulent, 20–30 cm long, densely flowered, the pistillate flowers interspersed among the staminate ones, often associated with staminate flowers in triads, the flowers subtended by short distinct bracteoles; staminate flowers white, 4–5 mm long, broad and flat at apex, puberulent as on rachillae; petals 3, stout, concave, acute at apex; floral envelope truncate, 8–10 mm long, ca 9 mm wide, the flowers weakly sunken. Fruits orange-red, ovoid, to ca 5 cm long; seed 1. *Croat 11798, 14479.*

Cultivated at the Laboratory Clearing. Flowers in the late dry and early rainy seasons. The fruits mature in the rainy season. The plant at the Laboratory Clearing flowered in mid-May, and though the fruits developed normally for a time, they all fell off without ripening before August.

Similar to *Astrocaryum standleyanum,* but distinguished by the smaller spathe and spadix.

Widely cultivated in Central America and northern South America. In Panama, known from low elevations in very wet regions (Holdridge, 1970); few collections exist, but the species is expected to occur throughout Panama and is perhaps in all provinces.

Bactris major Jacq., Select. Stirp. Am. 280, t. 171, f. 2. 1763

B. balanoidea (Oerst.) H. Wendl.; *B. augustinea* Bailey; *B. superior* Bailey

Mongo lolo, Palma brava

Small, monoecious tree, 3–10 m tall, forming small and dense to large and open thickets (usually small and dense in open areas), sometimes leaning; trunk 4–6 cm diam; leaves often persisting until plants are as much as 5 m tall; internodes 13–26 cm long, prominently spiny, the spines 1–8 cm long, with spineless leaf scars ca 5 cm long; petiole, rachis (especially lower side), and often parts of lower leaf surface ± furfuraceous-scaly. Leaves regularly pinnate, variable, 0.7–4 m long, densely spiny on petiole and most of rachis with spines mostly 1–6.5 cm long, black or brown, the longest near base of petiole to 11 cm long; petioles 1–1.5 m long, the rachis round on lower side (drying sulcate), triangular along most of its length on upper side; pinnae on ± same plane, 30–60 cm long, 0.8–3 cm wide, the sides ± parallel, the lower surface sometimes with furfuraceous bands, the apex oblique, very short or to 10 cm long, the margins prominently dark-setose with small setae 1–3 mm long. Spathe 40–60 cm long, ± woody and persisting in fruit, the broadened part 22–32 cm long, sparsely to densely black-setose with the setae 5–20 mm long, the narrow base of spathe usually lacking setae; spadix with 9–17 stout branches, the peduncle furfuraceous-scaly, the floriferous part 20–30 cm long; flowers cream-colored; staminate flowers sessile, 7–8 mm long, the petals 3, thick, ovate, acuminate, the filaments connate to about the middle; staminodial ring ca 2 mm high; pistillate flowers ca 6 cm long, their calyx accrescent, cuplike, the outer envelope ca 3 mm long at anthesis, the inner envelope ca 1 mm long, soon becoming much larger than the outer ones. Fruits held in a diffuse cluster, ellipsoid to ovoid, to 4 cm long and 3 cm broad, obtuse to rounded at apex with a small point, furfuraceous-scaly, becoming dull purple at maturity; exocarp thick; mesocarp fibrous, sweet; cupule bluntly crenate, the outer series much smaller than the inner; seed 1. *Bailey 162* (type of *B. superior*), *Croat 8567, 10740.*

Common throughout the island; locally very abundant. Usually flowering in the dry season, with the fruits maturing in the rainy season or early dry season. A typical individual flowered in March and lost its fruits in late December. The species may also flower during the middle of the rainy season.

Bactris augustinea Bailey, which represents a more depauperate form of this species, grows in more exposed places, such as along the margin of the lake and on roadsides (e.g., the type locality near Summit Garden, Canal Zone). These plants are much shorter, are colored a lighter green, and have leaves that are much smaller, with leaflets closer together and directed somewhat upward,

compared to those plants occurring in the forest. No other differences have been detected between those plants inhabiting the shore and those in the forest. The specimen of *B. superior* described by Bailey (1933) from BCI is no doubt also *B. major;* it has unusually well-developed leaves and probably represents the other extreme from *B. augustinea,* having been collected within the forest. Otherwise the plant falls well within the limits of variability of *B. major.* Bailey (1933) described his collection *293* as being 15 m tall. I have seen no *Bactris* on BCI as tall as that, but Bailey's photographs, which accompany the type specimen, show a plant that is probably not more than 10 m tall.

Abundant along coasts of Central America and northern South America; Trinidad and Tobago. In Panama, known principally from tropical moist forest on both slopes of the Canal Zone and in Panamá and Darién; known also from tropical dry forest in Los Santos.

See Fig. 61.

CHAMAEDOREA Willd.

Chamaedorea wendlandiana (Oerst.) Hemsl., Biol. Centr.-Amer. Bot. 3:407. 1885

Bodá, Bolá, Caña verde, Nurú, Pacaya

Dioecious shrub or small tree, to 5(7) m tall, growing as individuals or in open colonies; trunk to 5 cm diam with pronounced leaf scars, usually with adventitious roots at base (rarely higher on trunk). Leaves ca 2.5 m long, glabrous; petioles 40–50 cm long, canaliculate at base, rounded, with cream-colored band on lower surface extending along rachis to tip of blade; blades mostly less than 2 m long; leaflets regular, ca 17 pairs, 40–60 cm long, shortest at both ends of blade, 5–9.8 cm wide, abruptly tapered toward both ends, falcate at distal end; costae several, some prominently raised on upper surface; juvenile leaves entire. Inflorescences 1–3 per plant, in various stages of development, erect until maturity of fruit; spathes to ca 40 cm long, thin, narrow, long-acuminate, soon weathering; spadix branched once, densely flowered, white; rachillae 8–20, strongly divaricate, mostly less than 18 cm long, becoming orange and prominently pitted in fruit; staminate flowers crowded, ca 2 mm long; petals and sepals 3 each, ± equal, ovate; stamens 6, slightly longer than petals; anthers held perpendicular to filament, dehiscing upward; pistillodes about as long as filaments; pistillate flowers similar to staminate flowers but somewhat larger, thicker, and much less crowded, the pistils about as long as petals; stigmas prominent. Fruits oblong, 14–20 mm long, usually light green and shiny but turning black at maturity; exocarp thin; mesocarp fleshy and edible but bitter prior to maturity; seed 1. *Croat 6504, 6506.*

Uncommon, sometimes locally abundant in low areas near streams, such as near Lutz Creek south of the Laboratory Clearing. Flowers mostly late in the rainy season to early in the dry season (September to February), but flowers have also been seen in May. Fruits mature from April to October, but chiefly in the early rainy season (May to July).

The bee *Trigona tataira* (Diptera) was observed collecting pollen. The weevil *Cholus* sp. (Curculionidae, subf. Cholinae) also frequents flowering inflorescences, but does not collect pollen.

Nicaragua, Costa Rica, and Panama. In Panama, known from tropical moist forest in Bocas del Toro, San Blas, both slopes of the Canal Zone, Panamá, and Darién; known also from premontane wet forest in Panamá and Darién.

See Fig. 62.

COCOS L.

Cocos nucifera L., Sp. Pl. 1188. 1753

Coconut, Palma de coco

Monoecious tree, 7–20(30) m tall; trunk usually more than 20 cm diam, unarmed; leaf scars prominent. Leaves green, 2–6 m long, the rachis and midrib prominently raised, yellowish or light green; petioles including leaf sheath ca 1 m long; leaflets regular, in a single plane, 60–110 cm long, to 5 cm wide, the shorter ones on either end of blade. Spathes ca 1 m long, striate, acuminate; rachillae 30–40, to 40 cm long; staminate flowers to 12 mm long, borne on upper part of interfoliar branching spadices; stamens 6; pistillate flowers globose, ca 3 cm diam, restricted to lower part of spadices; ovary 3-celled. Nuts many, in bunches, obtusely triangular, to 30 cm long, covered by a thick fibrous husk, the interior shell very hard; endosperm solidified into an edible, white substance; interior containing a liquid, whitish endosperm; seed 1. *Croat 7484.*

Rare; cultivated in the Laboratory Clearing and persisting in the forest at old settlement sites. Flowers in February. The fruits require 9 or 10 months to develop.

Pantropical in cultivation. In Panama, most abundant in coastal areas, especially along the Caribbean coast; few collections exist, but probably in cultivation in all provinces.

CRYOSOPHILA Blume

Cryosophila warscewiczii (H. Wendl.) Bartl., Publ. Carnegie Inst. Wash. 461:38. 1935

Acanthorrhiza warscewiczii H. Wendl.; *C. albida* Bartl.; *C. guagara* P. H. Allen

Noli, Palma de escoba

Tree, to 10 m tall; trunks 10–15 cm diam above the enlarged base, much of the trunk bearing spines, at least when young, the spines simple or branched, to 16(35) cm long, sometimes restricted to base of older plants. Petioles longer than blade, broadly canaliculate; blades round in outline, 1.5–2 m diam or more, palmately veined and irregularly lobed almost to base, lobed completely to base on lower margin, green and glabrous on upper surface, densely whitish-pubescent on lower surface, the trichomes so small and appressed as to appear glaucous

Fig. 62. *Chamaedorea wendlandiana*

Fig. 63. *Cryosophila warscewiczii*

(sometimes arachnoid with brown trichomes on veins); juvenile blades triangular in outline, deeply 2- or 3-lobed (more in age), densely arachnoid-pubescent. Inflorescences interfoliar, nodding, the spathelets (nodifronds) short, acuminate, densely woolly on outside, ultimately deciduous, the outer ones coriaceous, the outermost usually bearing 2 keels, the inner ones longer, each subtending a branch of the spadix, to 15 or 30 cm long, closely enveloping at least lower part of branch; spadix branches at least as long as broad, 30–75 cm long, the main axis stout, the branches very short or to ca 30 cm long, densely flowered; flowers bisexual, 3-parted, glabrous; sepals oblong; petals broadly obovate to rounded, concave, 2.5–4 mm long, the margins thin, the sepals and petals stiff, erect, forming a narrow tube; stamens 6; filaments in pairs, flattened, broad and united at base, slightly longer than petals and cernuous near apex; anthers ca 1 mm long, pendent on outside of corolla just above apex; pistils 3, narrowly ovoid, long-tapered to apex, curved outward just above apex; stigmas held just above throat of corolla. Fruits round to obovate, mostly 1–2 cm diam, smooth, fleshy and white at maturity; pericarp thin; seed 1, round, 8 mm or more diam. *Croat 17017.*

Common in some areas of the younger forest, especially on the east side of the island. Flowers from May to October in Panama (as late as December elsewhere in Central America), chiefly in August. The fruits develop in 2 to 3 months, mostly between August and December. Populations may flower twice in a year; those seen in flower in October had mature-sized fruits as well.

Recognized by the palmate leaves, the white fleshy fruits, and the branched spines on the trunk, which Bailey (1943) considered to be root thorns. *Cryosophila albida* Bartl. and *C. guagara* P. H. Allen cannot be considered distinct from *C. warscewiczii,* since key characters such as pubescence and fruit size are very variable.

Belize to Panama, no doubt also Colombia. In Panama, known from tropical moist forest on both slopes of the Canal Zone and in Panamá and Darién; known also from premontane wet forest in Coclé (El Valle) and Panamá (Cerro Campana) and from tropical wet forest in Darién.

See Fig. 63.

DESMONCUS Mart.

Desmoncus isthmius Bailey, Gentes Herb. 6:211. 1943

Matamba

Slender, monoecious, widely spreading climber, growing into canopy but usually lower than 8 m; trunk 3–5 cm diam; juveniles usually erect. Leaves usually ca 2 m long; petioles short; rachis with black, flattened spines, often recurved, their bases swollen; base of petiole and sheath with denser, shorter spines, the leaf sheaths extending 3–12 cm above petiole; leaflets alternate, long-lanceolate, acuminate, 12–27 cm long, 2.5–4 cm wide, broad at middle, the margins unarmed, the surfaces glabrous or puberulent, the upper surface sometimes with weakly elevated cross-lines, the midrib pronounced but the side veins indistinct, the underside often with 1 or more acicular spines; pinnae becoming opposite toward apex of blade, finally replaced by large, opposite, stout, reflexed spines. Spathes to ca 24 cm long, the rachillae 15 or more, slender (less than 2 mm wide), flexuose in fruit, the peduncle and lower part of rachis armed with short prickles (sometimes with pustular bases); flowers either in triads with 1 pistillate between 2 staminate or with staminate flowers solitary near end of rachilla; staminate flowers soon deciduous, ca 8 mm long; calyx short, tridentate; petals 3, ovate, oblique, acuminate, fleshy; stamens usually 8 or 9; filaments fused to petals at base; pistillate flowers with a small annular calyx; corollas much longer than calyx, urceolate, tridentate, with very small, adnate staminodia; pistils ovoid, 3-celled; styles short; stigma trifid. Fruits bright red at maturity, ellipsoid, 1.5–2 cm long, glabrous; exocarp thin; mesocarp fleshy; seed 1, ca twice as long as broad, obscurely 3-sided with a pore on each side and with dark lines radiating from each pore; cupule inconspicuous. *Croat 7759, 11288.*

Frequent in the forest; most abundant in dense thickets and along the shore where vegetation is sufficiently dense to provide support. Flowers in the rainy season. Fruits in the dry season and early rainy season.

Fruits are eaten by white-faced monkeys from April to August (Hladik & Hladik, 1969).

The species is similar to and perhaps inseparable from *D. orthacanthos* Mart. of South America, which was described as a plant forming dense thickets in clearings, with a spathe more than 50 cm long, whereas *D. isthmius* is always in forests and has a much shorter spathe. In addition, the type illustration by Martius (1824) showed the recurved spines to have long filiform appendages. Probably the Panamanian plants will not be found to be distinct from other Central American plants from Mexico south, which are now known as *D. chinanthlensis* Liebm.

Known only from Panama in tropical moist forest in the Canal Zone, Panamá, and Darién and from tropical wet forest in Colón.

ELAEIS Jacq.

Elaeis oleifera (H.B.K.) Cort., Fl. Colomb. 1:203. 1897

Corozo oleifera (H.B.K.) Bailey

Corocito, Corozo, Corozo colorado, American oil palm

Monoecious tree, 4–5 m tall; trunk at first decumbent, the upright part to 2 m high, 30 cm or more thick, bearing old leaf bases; crown usually broader than tree height. Leaves broadly spreading, the tips of the lower leaves often touching the ground; petioles 1–2 m long, 9–12 cm broad near base, broadly canaliculate, the sharp edges bearing spinelike teeth; rachis roughened on underside with brown scales; blades 2–4 m long; leaflets regular, in 60–110 pairs, to ca 1 m long, 4–6 cm wide, the apex oblique, the midrib prominent on upper surface with 2 faint marginal ribs on lower surface. Inflorescences borne among leaf axils; spathes thin, obscure, soon becoming a mass of dilacerating fibers, the outer spathes to 30 cm

Fig. 64. *Elaeis oleifera*

Fig. 65. *Elaeis oleifera*

long, the inner to 50 cm long in staminate flowers, to 60 cm long in pistillate; staminate inflorescences soon weathering, the peduncles 20–35 cm long, ca 1 cm thick, the rachillae numerous, 20–25 cm long, ca 1 cm thick; stamens 6, the filaments partly united into a staminal tube ca 3 mm long; pistillate inflorescences 30–40 cm long, the peduncles ca 40 cm long, the rachillae stout, irregular, 4–9 cm long, closely compacted, pointed at apex; flowers white, sunken in rachillae, subtended by 2 or 3 bracts; tepals 6, ca 8 mm long; staminodial rings 6-dentate, ca 2 mm high; styles white, exserted and receptive for about a day, then becoming black; fruiting inflorescences usually broader than high, to 30 cm wide. Fruits orange, of irregular shapes due to mutual pressure, 2–3.5 cm long, often with persistent styles; seeds 1–3. *Croat 5203, 5539.*

Common only at the margin of the lake, but seen also in the seasonally swampy area near Standley Trail 500 and below the escarpment south of Armour Trail 700. Seasonal behavior uncertain. Flowers have been seen only during the early rainy season, but since flowers last for such a short time with the old inflorescences persisting, it cannot be said that flowering does not occur over a longer period of time. The fruits are present all year on some individuals, but most mature during the late dry or early rainy seasons. Individuals may bear more than one fruiting inflorescence in different stages, indicating the possibility that the plant flowers more than once a year.

Standley's plate VI in the *Flora of Barro Colorado Island* (1933), labeled *Corozo oleifera,* is *Scheelea zonensis.*

Bailey (1943) reported that fruits are black at maturity. My observations indicate that the fruits become loose and fall while still orange. However, fruits that are not able to fall free do become black.

Central America to Colombia and the Guianas (perhaps only introduced into northern South America). In Panama, a characteristic element of premontane wet forest (Tosi, 1971); known also from tropical moist forest on BCI and in Darién. Collected from tropical wet forest in Costa Rica (Holdridge et al., 1971).

See Figs. 64 and 65.

GEONOMA Willd.

The genus is distinguished by its slender spadices, which are enveloped at the base of the peduncle by two tubular bracts (spathes) and by its sunken, bilabiate flower pits. Usually there are three unisexual flowers in each pit, one pistillate between two staminate, though the upper ends of the spadix (or rarely the entire spadix) may be exclusively staminate. Flowers have six tepals in two series. Staminate flowers are white and somewhat exserted, appearing before the pistillate but lasting only a short time. Filaments are united into a tube and anther cells are well separated and spreading. Pistillate flowers are usually purplish with six staminodia and three white stigmas; the stigmas are exserted at anthesis but soon wither.

Geonoma cuneata H. Wendl. ex Spruce, J. Linn. Soc., Bot., 11:104. 1869

G. decurrens H. Wendl. ex Burr.

Small, monoecious shrub. Leaves few, simple, nearly sessile or borne on a narrow trunk 3–4 cm diam and 2 m tall; internodes 1.5–2 cm long; petioles 10–25 cm long; blades deeply 2-lobed at apex (the long acuminate lobes straight or curved inward), 1–1.5 m long, 20–35 cm wide at apex, narrowed toward base, strongly pleated especially near rachis, decurrent on petiole, the margin entire, the veins 3–15 mm apart, variously furfuraceous (at least when young). Spadix simple, held erect or drooping; peduncles 50–70 cm long, glabrous, ensheathed by tubular, densely tomentose spathes at base; rachis 25–40 cm long, 5–9 mm wide, minutely rugose and obscurely appressed-pubescent; flower pits in 7–10, ± oblique series 1–2 mm apart; staminate flowers whitish, exserted; pistillate flowers shorter, embedded. Fruits mostly ellipsoid, 7–8 mm long, somewhat smaller on drying, glabrous, greenish to yellow or pale orange at maturity; exocarp hard; seed 1. *Croat 10825.*

Common in deep woods, particularly in the older forest. Flowering and fruiting data are inconclusive, but most flowering occurs in the rainy season, especially the early rainy season. Fruits develop in both the rainy and the dry seasons. Flowering and fruiting inflorescences may occur on the same plant, indicating either that the fruits require more than a year to develop or, probably more likely, that the plants flower more than once a year.

The only palm in the flora with an entire adult leaf. It may be confused with juveniles of many other palms, which also have entire leaves, but the juvenile leaves of other species are usually much smaller.

Nicaragua to Colombia; elevations below 100 m. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, and Panamá and from premontane wet forest in Coclé (El Valle).

See Fig. 66.

KEY TO THE SPECIES OF GEONOMA

Leaf blades simple ..... *G. cuneata* Spruce
Leaf blades pinnately compound:
  Inflorescences unbranched; plants usually to 1.5 m tall ..... *G. procumbens* Spruce
  Inflorescences compound, branched many times; plants usually more than 3 m tall .....
  ..... *G. interrupta* (R. & P.) Mart.

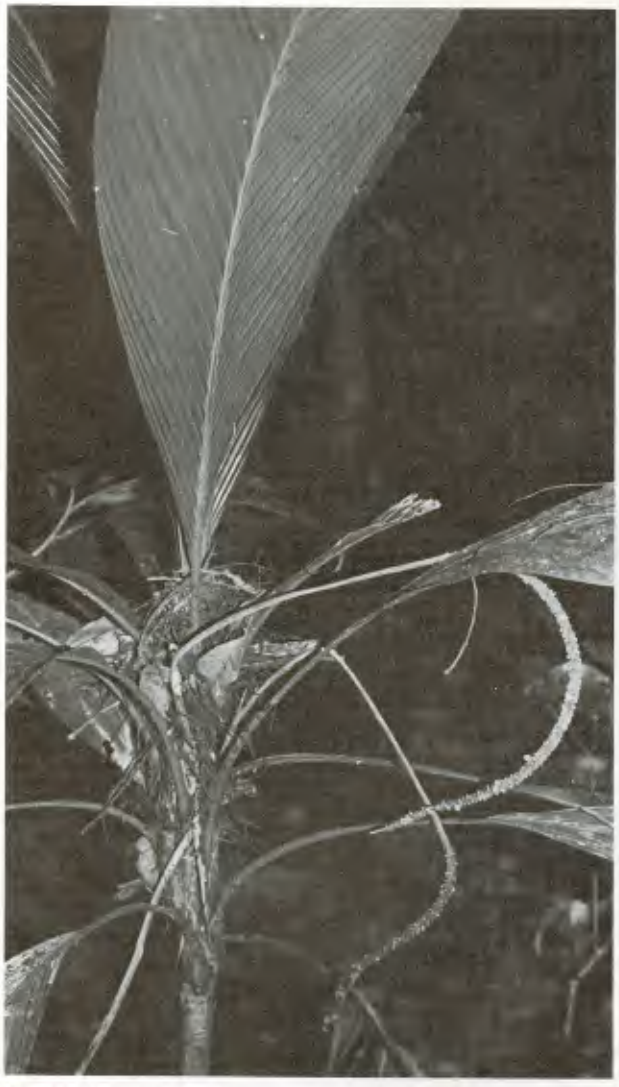

Fig. 66. *Geonoma cuneata*

Fig. 68. *Oenocarpus panamanus*

Fig. 67. *Geonoma procumbens*

Geonoma interrupta (R. & P.) Mart., Hist. Nat. Palm. 2:8, t. 7. 1823

G. oxycarpa Mart.; *G. binervia* Oerst.

Small, monoecious tree, to 6 m tall; trunk to 6.5 cm diam; leaf scars prominent, to 8 cm apart. Leaves glabrous, irregularly pinnate, ca 2.5 m long; petioles 40–65 cm long, vaginate at base, flattened above with sharp edges; blades often more than 2 m long; leaflets in 20–30 pairs, abruptly long-acuminate, held in a single plane, 45–60 cm long, 1–9 cm wide (except terminal), spaced 1–10 cm apart, with 1–7 ribs prominent on upper and lower surfaces; rachis flat below, becoming triangulate by middle of blade; juvenile leaves entire. Spadix somewhat maroon, compound, branched many times, 60–75 cm long, often about as broad as long, lightly pubescent; flower pits spirally arranged in 5 series ca 3–6 mm apart; staminate flowers whitish, exserted, ca 4 mm long; pistillate flowers shorter, embedded. Fruits globular-ellipsoid, 4–6 mm long; pericarp slightly fleshy, becoming reddish and finally purple to black at maturity; seed 1. *Croat 7432, 9303.*

Occasional and usually widely dispersed in the forest. Flowering data is inconclusive. Flowers and fruits may be seen in most months of the year, but the flowers appear principally in the dry and early rainy seasons, with the fruits maturing during the rainy season.

Possibly confused with *Synechanthus warscewiczianus,* a plant of similar habit with irregular leaves but with an inflorescence of many slender undivided branches. Some plants possibly are entirely staminate, since the inflorescences wither after flowering. I am using here the broader interpretation of this species used in the *Flora of Surinam* (Wessels-Boer, 1965) and not the narrower interpretation used in the monograph of geonomoid palms (Wessels-Boer, 1968).

Mexico to Panama and northwestern South America; Haiti. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Darién, and Panamá.

Geonoma procumbens H. Wendl. ex Spruce, J. Linn. Soc., Bot. 11:105. 1869

Monoecious shrub, acaulescent or with trunk to 1.5 m tall and 5–6 cm thick; leaf scars 1 cm or less apart. Leaves glabrous, clustered at apex, continuously pinnate but somewhat irregular, to 2 m long; petioles ca 50 cm long or more, vaginate ca 20 cm at base, otherwise terete; rachis becoming sharply ridged above; leaflets in 10–24 pairs, 25–50 cm long, shortest at apex of plant, 2–5 cm wide except terminal pair, the apex long-acuminate and falcate, ± decurrent on rachis at base, the major ribs 1–3, equal, the others smaller; juvenile leaves entire and much smaller but otherwise like adult leaves. Inflorescences about as long as leaves but drooping below them; peduncles enveloped at base by 2 persistent spathes, the inner spathe much longer; spadix simple, maroon, the fertile part to ca 50 cm long, 12–15 mm thick; flower pits in 10–12 almost vertical series and in almost regularly alternating whorls ca 1 mm apart; rachis minutely rugose and appressed-pubescent; tepals oblong to spatulate, oblique, acute at apex, to 4 mm long, at least the outermost keeled, thickened, concave, and violet-purple at apex; stamens ca 6 cm long, the tube to 4.3 mm long, the free parts spreading. Fruits ovoid-ellipsoid, 9–11 mm long, about half as broad as long, purplish-black at maturity; pericarp hard; seed 1. *Croat 6607, 9790.*

Occasional, preferring the deep shade of areas adjacent to creeks or creek beds. Seasonal behavior uncertain. Flowering is known only in the late dry season and early rainy season. Fruits are seen most of the year, but most mature in the rainy season.

Recognized by the usually short trunk, pinnate leaves, and unbranched spadix. *G. interrupta* has a much longer trunk and a compound inflorescence.

Nicaragua to Colombia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Panamá, and Darién, from premontane wet forest in Colón and Coclé (El Valle), and from tropical wet forest in Panamá and Darién.

See Fig. 67.

OENOCARPUS Mart.

Oenocarpus panamanus Bailey, Gentes Herb. 3:71. 1933

Maquenque

Slender, monoecious tree, 8–20 m tall, 6.5–12 cm dbh, in small clumps of 3–10 individuals, usually with plants of different ages in each clump; trunk smooth, with widely spaced, narrow, discolored leaf scars; crownshaft blackish-green, to 80 cm long. Leaves to 6 m long; petioles short, canaliculate; sheaths very broad, to 75 cm long; rachis near base of blade canaliculate on upper surface, rounded on lower surface, becoming triangulate before apex of blade; leaflets in 30–70 pairs, regular, 2–6 cm apart, 50–88 cm long, the longest at middle of blade, 4.5–6 cm wide, the midrib prominent above, the surface pleated, the apex oblique, its extension 3–5.5 cm long on central pinnae, to 9 cm long on basal ones; juvenile leaves sometimes irregularly pinnate (the youngest with only 2 lobes), glaucous on underside, the petiole with abundant brown persistent fibers at base. Inflorescences borne at base of crownshaft; spathes 2, deciduous at anthesis, the outer spathe of 2 woody valves to ca 30 cm long, the inner spathe a tube that splits on one side, 65–75 cm long; spadix scurfy, 15–25 cm long; peduncles short and stout, ± bulbous at base, the numerous slender flexuose rachillae 40–75 cm long, drooping; flowers unisexual, interspersed on rachillae, usually 1 pistillate flower between 2 staminate flowers but pistillate flowers usually lacking near end of rachillae; some spadices apparently entirely staminate; staminate flowers ca 3 mm long; sepals and petals valvate; stamens 6; filaments short; anthers versatile; pollen dry and powdery; pistillate flowers smaller than staminate flowers, the 3 recurved style lobes often persisting in fruit. Fruits dark blackish-green

Fig. 69. *Scheelea zonensis*

Fig. 70. *Scheelea zonensis*

Fig. 71. *Socratea durissima*

(drying brown), 2–2.5 cm long, with an abrupt short point, slightly longer than broad, the lower third enveloped by the enlarged, irregularly crenate perianth lobes; seed 1. *Bailey 75* (type), *Croat 8093, 9517.*

Very common on all parts of the island. Flowering and fruiting season undetermined. Apparently flowers more than once a year, at least one wave of flowering occurring in the late rainy to early dry season, mostly November to March. Most fruits apparently mature from the middle of the dry season to early in the rainy season (March to July). Flowers also occur in the early rainy season from June to August, perhaps constituting a second wave of flowering. Plants often bear both flowering and fruiting inflorescences.

Costa Rica and Panama. In Panama, known from moist and wet regions at low elevations (Holdridge, 1970); known from tropical moist forest in the Canal Zone, Panamá, and Darién. Known from premontane wet forest in Costa Rica (Holdridge et al., 1971).

See Fig. 68.

SCHEELEA Karst.

Scheelea zonensis Bailey, Gentes Herb. 3:36. 1933
Palma real, Manaca

Monoecious or dioecious tree, to 30 m or more tall with trunk 30 cm or more diam, the upper part of the trunk very broad with old leaves and inflorescences persisting for several seasons. Blades unarmed, 5–10 m long, often held in a vertical plane; petioles 30–60 cm long, canaliculate on upper surface; rachis canaliculate on upper surface at base of blade, becoming sharply triangular toward apex; leaflets very irregular, 1 m or more long, 1–4.5 cm wide, blunt and inequilateral, one side of apex 2.5–3.5 cm longer than the other, the midrib prominent on upper surface, the reticulate veins drying prominent, the pinnae inserted at staggered angles and often in clusters of 2 or 3, the lowermost of each cluster almost erect; juvenile leaves at first entire, the surface much pleated, soon splitting into separate, ± regular pinnae, the uppermost ± united. Spathe to 3 m long, woody, deeply grooved on outside, with a long point, persisting; peduncles massive, usually longer than fertile part of spadix; spadix yellowish-white, over 1 m long, with numerous simple branches usually less than 20 cm long, usually bearing staminate flowers near the end and pistillate flowers closer to peduncle (some trees bear only staminate flowers and others only pistillate flowers); staminate flowers soon falling, their petals subulate, 1.5–2 cm long; stamens 6, often exserted from between petals, less than 5 mm long; filaments short and thin; anthers to ca 4 mm long; pistillate flowers with petals imbricate at base, narrowed toward apex; fruiting inflorescences massive, the rachillae coarse and heavily scarred by old fruit attachments. Fruits ± oblong, brownish-orange, 6 cm or more long, about 3 cm thick, enveloped at base by the large accrescent calyx, the surface minutely longitudinally striate, the beak abrupt, 5–8 mm long; seeds 1–3. *Croat 6100.*

Common throughout the island, especially near the shore and in younger areas of the forest; juvenile plants more abundant than adult. Flowers from April to September with most flowers appearing in the early rainy season. By the end of the rainy season fruits are already of mature size, but green. Many mature by the middle of the dry season, then begin to disappear slowly, and are mostly gone by July. The fruits are usually present and mature at the time of flowering.

Probably most plants bear both staminate and pistillate flowers on the same inflorescence; however, staminate plants (and pistillate, *fide* Bailey, 1943) occur in smaller numbers.

This species does not appear to be different from *S. rostrata* (Oerst.) Burr. from Costa Rica. Standley's plate VI in the *Flora of Barro Colorado Island* (1933), labeled *Corozo oleifera,* is the species; *C. oleifera* is treated here as a synonym of *Elaeis oleifera.*

A variety of small insects visit the huge flowering inflorescences. The heavy fruit crop provides a large portion of the diet of a number of larger animals, including white-faced monkeys and agoutis. The agoutis bury the fruits indiscriminately for later retrieval (Smythe, 1970). Vultures also feed on fallen fruits (R. Foster, pers. comm.).

Costa Rica and Panama; additional field work will probably show the species to range from at least Belize to Colombia. In Panama, common in and characteristic of tropical moist and premontane wet forests (Tosi, 1971); as for most palms, few collections exist, but the species has been seen or collected on both slopes of the Canal Zone and in Colón, Panamá, and Darién.

See Figs. 69 and 70.

SOCRATEA Karst.

Socratea durissima (Oerst.) H. Wendl., Bonplandia 8:103. 1860
Stilt palm, Jira

Monoecious, slender, stilt-rooted tree, 25–30 m tall; wood very hard; trunk to 15 cm diam, ringed; stilt roots 1–3 m high, often replacing the trunk at base, bearing short spines; crownshaft bluish-green, very long and bulging at base. Blades 2 m long or more; petioles rounded on underside; leaflets ± regular, in 8–14 pairs, narrow at base, greatly broadened to deeply toothed at apex (the terminal pair united, truncate), inserted on rachis at an angle (the proximal edge higher on rachis, the distal edge lower on rachis), often splitting in age, the various parts then directed at different angles, the ribs numerous, raised on lower surface; juvenile plants much like adults, the blades entire or with few pinnae. Inflorescences borne below the crownshaft; spathes 2, thin, 40–50 cm long, both deciduous as a single unit; spadix stout with up to 16 stout branches, to 60 cm long; peduncles about as long as or longer than rachis, stout, flattened laterally, drooping in fruit; staminate flowers to 1.2 cm long and 1.5 cm wide, soon falling; sepals 3, minute; petals 3, thick, concave; stamens numerous (ca 50), about as long as petals, the filaments very short; pistillate flower usually borne between 2 staminate flowers, much smaller and

obscured by them. Fruits oblong, 2.5–3 cm long, with a small subapical point, the cupule bowl-shaped, to 1 cm wide; seeds 1–3, to 2.5 cm long, beaked at base and marked with anastomosing lines, enveloped very loosely by thin woody husk at maturity. *Croat 8160, 8638.*

Common throughout the forest; sometimes locally abundant. Seasonal behavior uncertain. Flowering chiefly in the early rainy season (May to August), but sometimes in the dry season as well. Most fruits mature in the middle to late dry season. Juvenile or mature-sized fruits may be found on the ground at most times of the year. Oppenheimer (pers. comm.) reports that fruits are eaten by white-faced monkeys during March and April.

Socratea, Scheelea, and *Desmoncus* are the only palms that are seen regularly in the canopy. *Socratea durissima* is not confused with any other species on BCI, although Bailey (1943) stated that its identification is not positive. However, it has been confused with *S. exorrhiza* (Mart.) H. Wendl., which ranges from Colombia to Brazil, and it is possible the two species are not distinct.

Both spider monkeys and white-faced monkeys eat the thin pulp between the seed and the husk (Oppenheimer, 1968).

Nicaragua, Costa Rica, Panama, and possibly Colombia. In Panama, widely distributed in wet regions at low elevations (Holdridge, 1970) and appearing as a characteristic tree species of tropical moist forest (Holdridge & Budowski, 1956, as *Iriartea exorrhiza* Mart.) and of tropical wet forest (Tosi, 1971); collected from tropical moist forest in the Canal Zone, Panamá, and Darién and from tropical wet forest in Colón and Panamá. Common in premontane wet and premontane rain forests in Costa Rica (Holdridge et al., 1971).

See Fig. 71.

SYNECHANTHUS H. Wendl.

Synechanthus warscewiczianus H. Wendl., Bot. Zeitung (Berlin) 16:145. 1858

S. angustifolius H. Wendl.; *S. ecuadorensis* Burr.; *S. panamensis* H. E. Moore

Palmilla, Bolá

Monoecious tree, to 5 (6) m tall; trunk 4–5 cm dbh, sometimes with prop roots at base; internodes 6–8 cm long; leaf scars to 15 cm apart. Leaf blades ca 10, spreading, usually less than 2 m long; petioles becoming rounded or obscurely flattened near base of blade, 50–75 cm long including sheath, sheathing at base, the sheath two-thirds to three-fourths as long as petiole; rachis prominently ridged just beyond base of blade; pinnae few, in 4–6 pairs, irregular in shape, 1.5–2 cm wide, 29–41 cm long, irregularly spaced, to 10 cm apart, the apex long-acuminate, falcate, the terminal pair often irregularly united, the costae many, in part slightly raised on upper surface (sharply so on drying), the larger ones 15–18 mm apart; juvenile leaves entire, bilobed as adults at apex, becoming pinnate with 2 or 3 lobes, often on one side only, with the other side entire. Inflorescences usually below leaves, ± erect in flower, drooping in fruit, to nearly 1 m long; spathe thin, tightly sheathing peduncle, persisting and becoming weathered; spadix broomlike, on a long slender peduncle to 70 cm long, with many long thin branches mostly at right angles to axis when open; flowers tiny, in biseriate clusters of 4–13, on alternate sides of rachis, only the lowermost of each group pistillate; staminate flowers ca 0.6 mm long, the calyx much less than half as long as petals; stamens 3; filaments elongate, exserted at anthesis; staminodia usually present; pistillate flowers ca 1 mm long, the pistil as long as petals; pistillodes lacking. Fruits oblong, ca 1.5 cm long, light yellow to orange at maturity (drying black); seed 1. *Croat 7010, 11020.*

Occasional, especially in the old forest, preferring shady moist areas near streams. Flowering mostly in the early to middle rainy season (June to September), and fruiting in late rainy to dry season. Less frequently flowering in late dry season, with fruits maturing in the early rainy season.

Recognized by its broomlike inflorescence and irregularly pinnate leaves.

Costa Rica to Colombia and Ecuador; mostly low elevations but to 1,200 m. In Panama, known from tropical moist forest on both slopes in the Canal Zone and in San Blas and Darién, from premontane wet forest in Veraguas (Cerro Tute) and Panamá (Lago Cerro Azul), and from premontane rain forest in Panamá (Cerro Jefe) and Darién (Cerro Pirre).

20. CYCLANTHACEAE

Epiphytic vines or terrestrial, acaulescent or short-stemmed, palmlike herbs arising from a rhizome. Leaves alternate or forming a rosette, petiolate, the petioles dilated at base forming a clasping sheath; blades simple, entire to cleft, often plicate; venation palmate; stipules lacking. Flowers unisexual (monoecious), actinomorphic, the sexes interspersed and closely congested on a simple, axillary spadix subtended by several spathes; perianth cupular or lobed or rudimentary in staminate flowers, many-lobed or rudimentary in pistillate flowers; stamens many; filaments connate at base, epitepalous if a perianth is present; anthers 2-celled, dehiscing longitudinally; staminodia 4 in pistillate flowers, short or flexuously filiform; ovary inferior, 1-locular, 2–4-carpellate; placentation parietal; ovules numerous, anatropous; style none or 1, with 1–4 stigmas. Fruits fleshy syncarps of separate or connate berries; seeds numerous, with copious endosperm.

The Cyclanthaceae may be confused with the Palmae (19), but are distinguished by having conspicuous staminodia, several usually deciduous spathes subtending the simple spadix, and a fleshy syncarpous fruit with numerous small seeds.

Most Cyclanthaceae are visited by small weevils (*Coleoptera*) and other insects. The first day after anthesis the staminodia appear to yield some fragrance, which probably acts as an attractant. Harling (1958) reported that

KEY TO THE TAXA OF CYCLANTHACEAE

Plants vines; leaf blades entire ..... *Ludovia integrifolia* (Woods.) Harl.
Plants not vines; leaf blades cleft to divided:
  Leaf blades becoming deeply 2-parted, almost divided, the segments usually entire; fruiting spadix like a series of concentric rings ..... *Cyclanthus bipartitus* Poit.
  Leaf blades not deeply 2-parted, either 2-cleft or 4-parted, the segments dentate to deeply split; fruiting spadix not a series of concentric rings:
    Leaf blades broadly obovate, bifid halfway at most (the segments often irregularly split); petioles winged, at most half as long as blade; plants short-stemmed ..... *Asplundia alata* Harl.
    Leaf blades rounded in outline, 4-parted; petioles at least half again as long as blade; plants acaulescent ..... *Carludovica*

during this stage the stigmas are receptive and the anthers are unopened, but most species I have observed have the stigmas completely covered by a mass of anthers until later. Moreover, I have seen anthers open and *Trigona* bees collecting pollen at this stage on *Carludovica palmata*. Usually by the following day the staminodia have withered, and Harling reported that the pleasant aroma is replaced by a "sweetish, somewhat sickening" smell but that the weevils are still present on the spadices among the staminodia. He said the weevils are often very destructive but are nevertheless probably the legitimate pollinators of most Cyclanthaceae. *Trigona* bees collecting pollen might also effect pollination, and visits by xylocopid bees were also reported by Harling.

Fruits are mostly bird dispersed, perhaps except for *Cyclanthus,* but they may also be taken by lizards, mammals, and perhaps even ants (van der Pijl, 1968). Fruits of *Carludovica palmata* are eaten by the bat *Micronycteris hirsuta* (Phyllostomidae) (Wilson, 1971) and by the tamarin (Hladik & Hladik, 1969).

According to Harling (1958), a family of 11 genera and 178 species ranging from southern Mexico and Lesser Antilles throughout Central America and the Amazon basin; also in eastern Brazil.

ASPLUNDIA Harl.

Asplundia alata Harl., Acta Horti Berg. 18:223–224. 1958

Large terrestrial herb, ca 2 m tall; stems to 30 cm high and 12 cm thick. Leaves to 1.8 m long, closely spiraled, clustered at apex; petioles about half the length of blade; blades broadly obovate, to ca 1 m long and 60 cm wide near apex, bifid, tapering to narrow base, decurrent onto petiole and continuous with broadly vaginate wing of petiole, becoming very much dissected in age, the surfaces pleated, the ribs 3, the lateral ribs branching from the midrib near base, the segment ribs prominently raised on upper surface, with furfuraceous scales scattered on lower surface; juvenile leaves similar to adults in shape, at first entire, splitting in maturity. Inflorescences from leaf axils, often several; peduncles to ca 20 cm long; spathes usually 3 or 4, ± oblong, 6–10 cm long, widely spaced below spadix, the outer one keeled; spadix cylindrical, blunt at apex, 4.5–6 cm long, white in flower, becoming green in fruit; staminate flowers alternating with short, conical pistillate flowers, densely covering spadix, but soon falling free; perianth lobed; pistillate flowers with tepals thick, longer than style at anthesis, light green; staminodia to ca 6 cm long, caducous; stigmas medial, narrow, elongated, dark green. Seeds ca 1.5 mm long and ca 1 mm wide. *Croat 10204, 14088.*

Uncommon, on creek banks and in ravines in the vicinity of the Laboratory Clearing. Flowers from late dry season to the middle of the rainy season, March to August. Mature fruits have been seen from June to September.

Known only from Panama in tropical moist forest in the Canal Zone, San Blas, and Chiriquí and from tropical wet forest in Colón.

CARLUDOVICA R. & P.

Carludovica drudei Mast., Gard. Chron. n.s. 8:714. 1877

Large, acaulescent herb, 2–3 m tall. Petioles to 2.5 m long, terete, vaginate only near base; blades to 1.8 m wide, palmately and unequally 4-lobed, the lobes to 75 cm long, 35–60 cm wide at apex, with 9–16 teeth per lobe, the teeth 5–13 cm long, glabrous and shiny above, dull below; juvenile leaves entire, the apex V-shaped, becoming 4-lobed, the lateral lobes more deeply divided. Peduncles 40–50 cm long; spathes 4, congested immedi-

KEY TO THE SPECIES OF CARLUDOVICA

Lobes of blade toothed less than one-fourth the way to base; blades shiny on upper surface, dull on lower surface; stigmas laterally compressed; tepals clearly exceeding stigmas even in flower ..... *C. drudei* Mast.
Lobes of blade toothed deeply, often past middle; blades shiny on both surfaces; stigmas ovate to suborbicular; tepals scarcely, if ever, exceeding stigmas ..... *C. palmata* R. & P.

Fig. 73. *Carludovica drudei*

Fig. 72. *Carludovica drudei,* inflorescence with staminodia exserted from pistillate flowers

Fig. 74. *Carludovica drudei,* cross section of spadix

ately below spadix; spadix narrowly cylindrical, 11–12 cm long, 1.5 cm thick in flower, to 22 cm long and 4.5 cm thick in fruit; staminate and pistillate flowers alternating spirally on spadix; staminate flowers in clusters of 4, lacking perianth, the stamens numerous, closely congested, obscuring all of pistillate flower but the staminodium, falling within a few days after anthesis; pistillate flowers sunken into fleshy axis of spadix; tepals 4, 5–6 mm long in flower, distinctly surpassing length of stigmas (to 8 mm long in fruit); staminodium slender, flattened, very long and showy, white, falling soon after anthesis; stigmas 4, laterally compressed; fruiting spadices rupturing at maturity, beginning at apex, to expose bright orange matrix with embedded fruits. Fruits oblong to rounded, ca 10 mm long, 6–8 mm broad; seeds numerous, ± ovoid, ca 2 mm long, flattened. *Croat 10838, 12305.*

Occasional, in the forest, usually along streams, possibly preferring steep banks. Flowers in June. The fruits mature from July to October.

Distinguished by having the leaf lobes toothed much less than halfway to the base.

Lowland forests in Mexico (Chiapas and the Yucatan Peninsula), Costa Rica, Panama, and possibly Colombia. In Panama, known from tropical moist forest on both slopes in the Canal Zone and in Chiriquí and Darién.

See Figs. 72, 73, and 74.

Carludovica palmata R. & P., Syst. Veg. 291. 1798

Panama hat palm, Palmita, Jipijapa, Portorrico, Atadero, Rampira, Iraca, Guachiban, Canagria

Large, glabrous, acaulescent herb, to over 3 m tall. Petioles to 3.5 m long, round; blades palmately lobed, pleated, usually light green in color, to 1 m long and 1.9 m wide, usually with 4 ± irregular lobes to 80 cm long and 85 cm wide at apex, the lobes irregularly toothed to past middle, with 10–16 teeth per lobe. Peduncles 20–45 cm long; spathes usually 3(4), congested just below spadix, ca 25 cm long, greenish to white, maroon near apex; spadix cylindrical, white in flower, ca 15 cm long and 2.5 cm thick, to 25 cm long and 6 cm thick in fruit; staminate and pistillate flowers alternating spirally as in *C. drudei;* tepals scarcely if at all exceeding stigmas; staminodia 4–6 cm long; stigmas ovate to suborbicular. Fruits orange, ca 1 cm long; seeds many, white, 2 mm long. *Croat 10385.*

Common locally, primarily in clearings and on steep banks of the shoreline, but also in the forest on Orchid Island; common and widespread in the Canal Zone. Flowers mostly in January and February, possibly March. The fruits mature from April to June, rarely later in the rainy season.

Except for leaf differences, tepal length, and shape of stigma the species is very similar to *C. drudei,* which is treated in much greater detail. The leaf segments of *C. palmata* are at least in part toothed more than halfway to base.

Native from Guatemala to Bolivia; introduced in the West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Coclé, Panamá, and Darién.

See Figs. 75 and 76.

CYCLANTHUS Poit.

Cyclanthus bipartitus Poit., Mém. Mus. Hist. Nat. 9:36. 1822

Portorrico, Lengua de buey

Acaulescent, monoecious herb, to 3.5 m tall. Petioles 1.5–2 m or more long; blades to 1.6 m long, almost completely bisected, occasionally trifid, each segment 15–24 cm wide, the base of each lobe oblique, the midrib near upper edge at base, becoming centered by apex. Peduncles 40–90 cm long; spathes 5–7, broadly ovate, 15–25 cm long, the inner cream-colored or pinkish, the outer ± foliaceous; spikes 5–11 cm long when flowering, 1.5–2.5 cm broad, with staminate and pistillate flowers in 10–15 separate alternating whorls, the flowers of each whorl connate; staminate flowers naked; pistillate flowers enclosed by two rims of fleshy tissue, these becoming much enlarged; fruiting syncarps to 6 cm diam, ± pendent. Each segment of syncarp falling off individually, with many seeds in a fleshy matrix; seeds to 1.5 mm long and 1 mm wide. *Croat 5386, 6016.*

Occasional, inhabiting chiefly stream banks and the lakeshore, though numerous juvenile plants are found within the forest away from any streams. Flowers mostly April and May, but also sometimes in June and perhaps later as well. The fruits mature throughout the rainy season, mostly by October.

The soft fleshy segments of the syncarp float and are dispersed in part by water currents and in part by animals or birds.

Guatemala to Peru and Brazil; Lesser Antilles. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, Panamá, and Darién and from tropical wet forest in Panamá (beyond Cerro Jefe) and Colón.

See Fig. 77.

LUDOVIA Brongn.

Ludovia integrifolia (Woods.) Harl., Acta Horti Berg. 18:338. 1958

Carludovica integrifolia Woods.

Nonrosulate epiphytic vine; stems 9–12 mm diam, at first green, becoming brown, forming long, ± tough, brown roots at most nodes; internodes mostly 5–7 cm long. Leaves drying thin, all but the upper 3–8 withering but often persisting; petioles 10–15 cm long, narrowly canaliculate; sheaths thin, extending one-third to almost entire length of petiole; blades narrowly elliptic to oblanceolate, acuminate, cuneate and often ± unequal at base (one side slightly shorter), 13–23(33) cm long, 4–7(17) cm wide, weakly bicolorous, the lower surface dull, with 4–7 major veins running almost parallel to the midrib but extending to the blade margin; margins weakly toothed at termination of each veinlet, the midrib raised on both surfaces but most prominent in basal third of blade. Spathes 3, enveloping spadix, acuminate, greenish to white, the outer 6–8 cm long, the inner to 5 cm long, all caducous, breaking loose from base at anthesis and carried

Fig. 75. *Carludovica palmata*

Fig. 76. *Carludovica palmata*

Fig. 78. *Ludovia integrifolia*

Fig. 77. *Cyclanthus bipartitus*

Fig. 79. *Ludovia integrifolia*

upward by the enlarging spadix; spadix ca 3 cm long at anthesis; staminodia widely dispersed in clusters of 4 (rarely 5), to ca 3 cm long; staminate flowers ca 3.5 mm long, the perianth 20–30-lobed, glandular; pistillate flowers connate with each other, the tepals much reduced, the long, immersed stigmas sessile, longer than broad; fruiting spadices 8.5–9.5 cm long, ca 1.5 cm diam, blunt, becoming orange, fleshy and tasty at maturity, the peduncles with 3 prominent spathe scars; stipes 5–7 mm long; stigmas round, ca 0.5 mm diam. Fruits diamond-shaped, 11–17 mm long, 9–12 mm wide, conical; seeds numerous, ± ovoid, ca 1.5 mm long, embedded in a sweet, sticky, gelatinous matrix at maturity. *Croat 12560.*

Occasional, in the old forest. Reportedly flowers in June. Mature fruits have been recorded in November and December.

Obscurely resembling *Stenospermation* (21. Araceae), but distinguished by having more than one spathe.

Panama to Ecuador on the Pacific slope. In Panama, known from tropical moist forest in the Canal Zone and Darién.

See Figs. 78 and 79.

21. ARACEAE

Epiphytic (two-thirds of BCI species), terrestrial, or rarely aquatic herbs, sometimes with suffruticose parts, occasionally scandent; rarely with milky sap (*Syngonium*), caulescent or acaulescent, glabrous or rarely pubescent or prickly on petioles. Leaves alternate or clustered, petiolate with sheathing bases, simple or divided; blades entire, occasionally perforate; venation parallel or pinnate- or palmate-netted; cataphylls usually present. Flowers bisexual or unisexual and plants monoecious, in terminal or axillary cylindrical spadices, the spadix suspended and sometimes enclosed by an herbaceous spathe; spadix uniform, bearing bisexual flowers or consisting of pistillate and staminate parts, the staminate part above the pistillate and deciduous or rotting away after anthesis; perianth lacking in unisexual flowers (also in bisexual flowers of *Rhodospatha* and *Stenospermation*) or with segments 4 (*Anthurium*), (2)3(4) (*Spathiphyllum*) or 4–8 (*Dracontium*); stamens free or united in unisexual flowers, usually 4, or (2)3(4) (*Spathiphyllum*), 4–6 (*Xanthosoma*), 2–4(6) (*Homalomena*), 3 or 4 (*Syngonium*), and 2–6 (*Philodendron*); anthers 2-celled, dehiscing by apical slits or pores; staminodia sometimes present; ovaries many per spadix, sessile or immersed in spadix (and thus inferior), with 1, 2, or several locules; placentation basal, parietal, axile, or apical; ovules 1 to many; style 1; stigma massive, usually capitate. Fruits berries, free or connate at maturity, usually protruding from tepals in bisexual flowers or exposed by rupturing of the spathe in unisexual flowers; seeds with endosperm.

Araceae are best characterized by the fleshy, cylindrical spadix subtended by a leafy spathe borne on a peduncle. In general, members of the family are not confused with any other, though *Ludovia integrifolia,* a simple-leaved Cyclanthaceae (20), looks much like an aroid.

Flowers of most species with closed spathes are pollinated primarily by large awkward ruteline scarab beetles, which are attracted to the inflorescence by the white spathe and/or the odor. It is not known what they get from their visits. They are often found crawling on the pistillate part of spathate inflorescences even when these are nearly closed. (See the discussion of *Dieffenbachia pittieri.*) In *Anthurium* and *Spathiphyllum* the open spathes also form the attractant organ, but do not trap insects as do closed spathes. The spadix of some species, e.g., *A. ochranthum,* is colored bright yellow or white and may itself attract attention. I have seen male euglossine bees visiting *Anthurium* and *Spathiphyllum* inflorescences in great numbers in the Canal Zone. Dressler (1968a) reported that *Eufriesa pulchra* visits *Anthurium.* Bees are believed to effect pollination of orchids, and it is possible they gather scent compounds from these two genera

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KEY TO THE TAXA OF ARACEAE

Plants small floating aquatics; inflorescences inconspicuous; leaves spongy, covered with short, few-celled trichomes ..... *Pistia stratiotes* L.

Plants rooting in soil or epiphytic; inflorescences conspicuous:

Leaves peltate; blades usually reddish near center and spotted with white, red, or yellow; plants terrestrial; flowers unisexual ..... *Caladium bicolor* (Ait.) Vent.

Leaves with petioles basifixed; blades entirely green in color:

• Leaf blades variously divided:

Plants with one very large, deeply divided leaf arising from a subterranean caudex ..... *Dracontium dressleri* Croat

Plants not as above, either epiphytic or with entire leaves, the leaves several to many:

Leaves pinnatifid, with pinnate divisions in blade at approximately right angles to midrib:

Blades with basal lobes, the lowermost vein with a prominent branch into each segment; spathe persistent; flowers unisexual; stigmas round ..... *Philodendron radiatum* Schott

Blades without basal lobes, the lowermost vein unbranched; spathe deciduous; flowers bisexual; stigmas linear ..... *Monstera dilacerata* C. Koch

Leaves variously parted, not pinnatifid, the lobes not primarily at right angles to midrib:

Blades with 6–18 lobes:

Plants terrestrial; peduncles arising from the ground; spathe enveloping spadix; spadix of distinct staminate and pistillate parts ..... *Xanthosoma helleborifolium* (Jacq.) Schott

Plants epiphytic; peduncles not arising from the ground; spathe free; spadix uniform:
Leaf segments lobed, usually more than 50 cm long ..... *Anthurium clavigerum* Poepp. & Endl.
Leaf segments entire, usually less than 30 cm long .. *Anthurium bombacifolium* Schott
Blades with 3–5 lobes:
Blades round in outline; leaflets of approximately the same size and shape ..... *Anthurium bombacifolium* Schott
Blades not round in outline; leaflets not of uniform size and shape:
Plants juvenile; caudex short; leaves clustered at apex, commonly directly associated with entire leaves ..... *Anthurium clavigerum* Poepp. & Endl.
Plants adult; long vines; leaves well spaced, not directly associated with entire leaves:
Leaf veins all parallel, none impressed on upper surface, collecting veins lacking; milky sap lacking; spathe persistent; spadix lacking a sterile staminate part ..... *Philodendron tripartitum* (Jacq.) Schott
Leaf veins interconnected between major laterals, not parallel, the major veins impressed above, the collecting veins 2 or 3; milky sap common; spathe deciduous; spadix bearing a sterile staminate part above the pistillate part ..... *Syngonium*

• Leaf blades simple and entire, though often lobed at base:
◆ Leaf blades conspicuously cordate, sagittate, or hastate, lobed at base, the sinus at least one-fourth as long as blade:
Plants epiphytic:
Spathe linear-lanceolate, free; spadix uniform; reticulate venation prominent ..... *Anthurium brownii* Mast.
Spathe enclosing spadix; spadix divided into staminate and pistillate parts; reticulate venation lacking or not prominent (except *P. hederaceum,* which is also puberulent on petioles) ..... *Philodendron* (in part)
Plants terrestrial or aquatic, rooted in soil:
Plants acaulescent or with subterranean stem, sometimes pubescent:
Petioles puberulent, armed with short prickles in basal half ..... *Homalomena wendlandii* Schott
Petioles glabrous or pubescent, but not armed with short prickles ..... *Xanthosoma*
Plants with definite stem or caudex (the leaves sometimes closely clustered and appearing acaulescent):
Plants commonly growing in standing water, the stem erect, at least 1 m tall, armed with short prickles at least in basal part; spathe deciduous in fruit ..... *Montrichardia arborescens* (L.) Schott
Plants never in standing water, the stem usually creeping over the ground, short, unarmed; spathe persistent in fruit:
Petioles conspicuously flattened on upper surface; veins all parallel or at least without conspicuous reticulate veins; spathe enveloping spadix; spadix of staminate and pistillate parts ..... *Philodendron grandipes* Krause
Petioles terete; veins not all parallel, the reticulate veins prominent, forming a collecting vein near margin; spathe free, narrow; spadix uniform with bisexual flowers:
Blades thick; sinus narrow or closed, the lobes often overlapping (at least when flattened out); fruits ± orange; plants growing usually at the margin of the lake on exposed areas (rarely in the forest except as an epiphyte) ..... *Anthurium brownii* Mast.
Blades thin; sinus always broad, the lobes never overlapping; fruits violet-purple at apex, white at base; plants growing in forest ..... *Anthurium ochranthum* C. Koch

◆ Blades never conspicuously lobed at base, or if cordate, with basal sinus much less than one-fourth the length of blade:
■ Plants terrestrial (including those in standing water):
Plants acaulescent or nearly so, the caudex nearly subterranean; flowers bisexual (spadix thus uniform); spathe remaining open and persistent ..... *Spathiphyllum*
Plants caulescent with a thick stout stem, usually short, creeping along the ground then erect; flowers bisexual or unisexual; spathe rather tightly enveloping spadix and persistent or caducous:
Major lateral veins close together, at ca 90° angle from midrib; petioles hard, nodose and geniculate at apex; spathe free, soon deciduous; spadix uniform (i.e., flowers bisexual) ..... *Rhodospatha moritziana* (Schott) Croat
Major lateral veins not close together, directed decidedly upward; petioles succulent, not nodose or geniculate; spathe persistent, attached to lower part of spadix; spadix with staminate and pistillate parts; sap with odor of oxalic acid ..... *Dieffenbachia*

- Plants epiphytic, never terrestrial at maturity except by accident:
  - Plants with fertile parts:
    - Spadix divided into staminate and pistillate parts; spathe persistent and enveloping spadix after opening; plants long epiphytic vines ..... *Philodendron* (in part)
    - Spadix uniform; spathe either deciduous or narrow and free after opening:
      - Spathe narrow, free at anthesis, usually persistent; leaf blades with or without collecting veins near margin; stigmas round or square; plants with or without elongate caudices ..... *Anthurium* (in part)
      - Spathe broad or convolute, usually surrounding spadix at anthesis (at least at base), soon deciduous; leaf blades lacking collecting veins; stigmas oblong or linear; plants with elongate caudices:
        - Blades small, less than 7 cm wide, the veins ± parallel to midrib; peduncles recurved at apex before anthesis ..... *Stenospermation angustifolium* Hemsl.
        - Blades very much larger, the veins not parallel to midrib; peduncles always ± erect:
          - Leaves entire, never perforate or pinnately lobed; primary lateral veins often 1 cm or less apart; caudex and petioles not finely tuberculate; stigmas round or ellipsoid ..... *Rhodospatha wendlandii* Schott
          - Leaves often perforate; primary lateral veins 1.5 cm or more apart; caudex and petioles usually finely tuberculate; stigmas linear ..... *Monstera*
  - Plants sterile:
    - Blades with ± prominent reticulate veins between major lateral veins:
      - Blades perforated or pinnately lobed; plants long slender vines with many short roots at most nodes ..... *Monstera*
      - Blades entire, not perforated; plants usually with short caudices ..... *Anthurium* (in part)
    - Blades with all lateral veins parallel or subparallel:
      - Lateral veins ± parallel to midrib ..... *Stenospermation angustifolium* Hemsl.
      - Lateral veins never almost parallel to midrib:
        - Leaves pinnately lobed ..... *Monstera dilacerata* C. Koch
        - Leaves entire:
          - Petioles continuously canaliculate to base of blade ..... *Rhodospatha wendlandii* Schott
          - Petioles winged-vaginate but the sheath always ending short of blade (free part of sheath may extend beyond base of blade in *P. guttiferum*) ..... *Philodendron* (in part)

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similar to the scent compounds they seek in orchids (Dodson et al., 1969; Hills et al., 1972). A male bee of *Eulaema cingulata* has also been reported to visit inflorescences of *Xanthosoma nigrum* without taking either pollen or nectar (Dodson, 1966). The implication is that bees may be attempting to collect scent compounds from this species as they probably do from *Spathiphyllum* and *Anthurium.* Probably a similar system will be found for other genera with bisexual flowers, such as *Monstera, Rhodospatha,* and *Stenospermation.*

Rhodospatha moritziana has a whitish, syrupy substance covering the spadix just after anthesis that may attract such insects as euglossine bees. Faegri and van der Pijl (1966) reported that these nectarlike substances are secreted by the stigmatic papillae but that the cell contents soon disintegrate. See *Dracontium dressleri* for a discussion of probable fly pollination (Croat, 1975c).

Fruits are endozoochorous, probably predominately ornithochorous, except perhaps those of *Pistia* and *Spathiphyllum.* This is especially true of *Anthurium,* which has colorful fruits that suddenly emerge from the tepals and may later be suspended slightly from two to four threadlike structures. All of the fruits of the spike may emerge at nearly the same time, as in *A. bakeri* and *A. friedrichsthalii,* or they may be considerably staggered, as in *A. tetragonum.* Once exposed, they are quickly removed. The seeds (usually two to four) are easily forced from the lower end of the berry and are embedded in a clear, jellylike, sticky mesocarp. After eating the sweet mesocarp (no doubt many seeds as well), the bird probably has some seeds stuck to its bill. Whetting its beak on a distant tree, the bird deposits the seeds at an appropriate germination site, where they stick. Bats are also known to take fruits of *Anthurium* (Yazquez-Yanes et al., 1975).

Fruits of *Dracontium* are probably dispersed in a manner similar to *Anthurium.* All genera with unisexual flowers, except *Montrichardia,* have the spathe completely covering at least the lower part of the spadix until the fruits mature. In the case of *Dieffenbachia* and *Philodendron* the pistillate part of the spadix is fused to the spathe, and the fruits are free. At maturity the inflorescence curls, rupturing the spathe and exposing the fruits. Seeds of *Dieffenbachia* seem well suited for bird dispersal, but are probably taken by larger animals as well. In *Philodendron* the fruits are closely aggregated and are probably eaten by monkeys as well as birds. Leaf-cutter ants have been seen carrying the tiny seeds also, and no doubt some are dropped along the way. It is important to point out that, except in the case of *Philodendron radiatum,* seeds germinate on the ground. Later stages of the plant become hemiepiphytic or even truly epiphytic by climbing trees and losing their ground connection.

Caladium and *Xanthosoma* have closely congested fruits that are no doubt dispersed in a manner similar to *Philodendron,* though the spathe seems to fall more by decomposition than by arching of the inflorescence. In *Syngonium* the fruit is syncarpous, and the spathe falls free at maturity of the fruit. Fruits, while not colorful, are fleshy and sweet. The few, relatively large seeds may be swallowed when the tasty mesocarp is eaten. Fruits are probably taken mostly by monkeys but possibly by other animals as well. In *Montrichardia,* the only species having unisexual flowers and lacking a persistent enveloping spathe, the fruits are held in an irregular aggregate much larger than the fruits of any other genus. They are usually water dispersed, but are also reported to be eaten by the Hoatzin bird (*Opisthocoma cristatus*) in South America (Ridley, 1930).

All members of the tribe Monsteroideae, including *Stenospermation, Monstera, Rhodospatha,* and *Spathiphyllum,* have fruits that are apparently unprotected by any structural modification such as a protective spathe. Nicolson (1960) reported that all these genera contain trichosclereids; since in masses these cells may give hardness and mechanical protection (Eames & MacDaniels, 1947), it is possible that they play a part in preventing predation on immature inflorescences.

Monstera and *Stenospermation* have bisexual flowers with uniform inflorescences like *Anthurium,* but the pistils become united and form a syncarpous fruit. At maturity the periphery of the fruit exfoliates in sheets or smaller segments, exposing the soft fleshy locules containing many small seeds. Fruits are probably taken by arboreal frugivores, including birds.

Fruits of *Spathiphyllum* are fully exposed and closely congested like the kernels of a cob of corn, becoming rather loose and easily removed at maturity. They are probably taken by birds and other animals; I have seen large segments of an inflorescence removed as though from a single bite. Bunting (1965) reported that the fruits may be water dispersed. Vegetative reproduction of new plantlets that later split off is a clear possibility for the aquatic *Pistia.*

About 120 genera and 1,800 species; widely distributed but most numerous in the tropics and subtropics.

ANTHURIUM Schott

The genus *Anthurium* appears to be considerably more plastic in its variation in morphological characters than are most genera in the family, with the result that a large number of species have been described more than one time.

Anthurium may be distinguished by having a free spathe that is usually persistent. The spadix is cylindrical and uniform with bisexual flowers having four tepals; the tepals are opposite the four stamens and more or less three-sided at the apex. Fruits have two locules with one or two ovules per locule.

KEY TO THE SPECIES OF ANTHURIUM

Leaves compound:
- Leaflets sessile, undulate or lobed; largest leaflets more than 50 cm long (on adult plants); spadix more than 40 cm long ..... *A. clavigerum* Poepp. & Endl.
- Leaflets petiolulate and entire; largest leaflets less than 30 cm long; spadix less than 15 cm long ..... *A. bombacifolium* Schott

Leaves simple:
- Leaves ovate to triangular and cordate, with large basal lobes and a prominent sinus:
  - Blades coarse and leathery, drying very stiff, the margins wavy or folded, the sinus narrow or closed by overlapping basal lobes (at least on flattening); fruits ± orange; plants usually epiphytic except at lake margin ..... *A. brownii* Mast.
  - Blades thin, the margins never strongly wavy or contorted, the sinus usually open (sometimes closed), broad; fruits violet-purple at apex, white at base; plants always terrestrial on BCI ..... *A. ochranthum* C. Koch
- Leaves without basal lobes or sometimes moderately cordate at base but without large basal lobes and a deep sinus:
  - Blades without a collecting vein, the primary lateral veins extending apically near the margin and closely approaching or merging with it; large epiphyte with obovate to oblanceolate leaves and large, ± pendent inflorescences ..... *A. tetragonum* Schott*
  - Blades with a collecting vein (the primary lateral veins joining before reaching the margin):
    - Plants scandent or with elongate, often branched, creeping caudices:
      - Blades acute at base, often punctate on lower surface; fruits white at maturity ..... *A. scandens* (Aubl.) Engler
      - Blades rounded at base, epunctate; fruits orange or red at maturity ..... *A. flexile* Schott
    - Plants not scandent, acaulescent or with short unbranched caudices:
      - • Plants lacking punctations:
        - Blades broadest at or about middle; cataphylls weathering, becoming fibrous, persisting on all but the oldest part of stem; spadix lavender at anthesis; fruits white ... *A. scandens* (Aubl.) Engler
        - Blades broadest usually well above middle; cataphylls not weathering into fibers, ultimately deciduous; spadix not lavender at anthesis; fruits red ..... *A. gracile* (Rudge) Lindl.

- Plants conspicuously punctate, at least on underside of leaf:
  - Blades usually more than 10 times longer than wide, of ca equal width throughout; plants often pendent or at least the leaves not held stiffly erect; fruits truncate at apex, broader than long, pale yellow-orange ..... *A. friedrichsthalii* Schott
  - Blades usually less than 10 times longer than wide, considerably broader in distal half; plants not pendent, the leaves held stiffly erect; fruits not as above:
    - Blades more than 11 cm wide; peduncles usually more than 30 cm long; blades ± thick, broadest at middle, gradually tapered to both ends .. *A. acutangulum* Engler
    - Blades usually less than 11 cm wide; peduncles usually less than 30 cm long;
      - Blades thin, conspicuously acuminate at apex; collecting vein much more prominent than the lateral veins; spadix less than 11 cm long in flower (to 15 cm in fruit); fruits bright red ..... *A. bakeri* Hook.f.
      - Blades thick, obtuse to acute at apex (often with short apiculum); collecting vein scarcely if at all more prominent than the lateral veins; spadix usually more than 11 cm long in flower; fruits yellowish or orange ..... *A. littorale* Engler

*Discovered too late for treatment: *A. concolor* Krause, Notizbl. 107:617. 1932. *Croat 8154* from Pearson Peninsula. Like *A. tetragonum,* but spadix violet-purple and petioles three-ribbed on lower side.

Anthurium acutangulum Engler, Bot. Jahrb. Syst. 25:371. 1898

A. porschianum Krause

Epiphyte; caudex short and thick, usually surrounded by a dense mass of roots; internodes short; cataphylls thin, short, weathering into brown fibers. Petioles stout, 9–18 cm long, with a deep narrow channel on upper surface, geniculate at apex; blades elliptic or oblong-elliptic, rounded or obtuse at apex and cuspidate-acuminate, mostly obtuse at base, 20–40 cm long, 11–15 cm wide, often arching with the tip curved downward, punctate on underside, ± thick, the major lateral veins in 10–15 pairs, forming a prominent collecting vein near the margin. Inflorescences spreading-pendent; peduncles 30–45 cm long; spathe green (pinkish elsewhere), lanceolate-acuminate, 9–11 cm long, less than 2 cm wide, withering in age; spadix sessile or short-stipitate, linear, weakly tapered to apex, 15–30 cm long, 7–10 mm broad (4–5 mm when dried); tepals truncate at apex, sharply triangular, 2–3 mm wide. Mature fruits apricot-orange, ca 5 mm long, 5 mm wide (slightly wider in direction of axis), drying with small depression at apex. *Croat 4347b, 6740.*

Apparently rare, occurring in the forest and seen only on small trees within 2–3 m of the ground. Individuals produce successive inflorescences and may be found in flower all year, especially during the rainy season. The fruits probably develop promptly.

Perhaps most easily confused with *A. littorale,* which has narrower blades, often broadest below the middle, with reticulate venation usually as prominent on dry specimens as the lateral veins. Elsewhere in Panama the species is most easily confused with *A. ramonense* Engler ex Krause, a species with thick, oblanceolate-elliptic leaves, thicker petioles, and stouter spadices.

Honduras to Panama; sea level to 900 m. In Panama, known from tropical moist forest in the Canal Zone and Bocas del Toro, from premontane wet forest in Bocas del Toro, and from tropical wet forest in Colón and Panamá.

See Fig. 80.

Anthurium bakeri Hook.f., Bot. Mag. 32, pl. 6261. 1876

Epiphyte; caudex short and thick, usually less than 10 cm long and 1.5 cm wide; internodes short, moderately slender-rooted; cataphylls ± thick, 3–5 cm long, soon reduced to coarse, brown, persistent fibers. Petioles 3–17 cm long, to 5 mm thick, broadly canaliculate and straight to moderately geniculate near apex, broadened and shortly vaginate at base; blades elliptic-lanceolate, broadest at or about middle, rather abruptly acuminate at apex, acute at base and weakly decurrent onto margins of petiole, 19–44 cm long, 2.8–9 cm wide, bicolorous, only moderately thick when fresh, thin on drying, held erect largely by V-shaped construction of blade and by midrib, the midrib thick, prominently raised on underside, the lower surface densely punctate; collecting vein 3–8 mm from margin, prominent on both surfaces, especially the lower, the lateral veins obscure (moderately prominent on dried specimens). Inflorescences held ± erect; peduncles slender to moderately stout, 8–29 cm long, shorter than leaves; spathe green, reflexed, 2–5.5 cm long, 7–20 mm wide, acute and apiculate at apex, the margin often turned in, decurrent onto peduncle at base; spadix sessile to shortly stipitate, bluntly rounded at apex, 2–11 cm long and 5–7 mm wide in flower, to 15 cm long and 2.5 cm wide in fruit. Fruits obovate, acute to rounded at apex, ca 6 mm long, bright red, emerging from tepals and pendent, suspended on 2 slender white fibers; seeds 2, oblong, white, ca 3 mm long, somewhat flattened, embedded in a sticky, clear matrix. *Croat 6627, 10882.*

Uncommon, in the forest, usually at low elevations on reasonably small branches. Probably rare other places as well, since the plant has seldom been collected despite its prominently colored inflorescences and frequent flowering. Plants produce a continuing series of inflorescences throughout the year, especially during the rainy season, and fruits mature in 3–6 weeks.

Though possibly confused with *A. littorale,* which has thick leaves lacking a prominent collecting vein, *A. bakeri* is recognized by its thin, punctate blades, which are broadest at or about the middle, by the short spadix, which is scarcely if at all tapered toward the apex, and by its bright red berries.

Guatemala to Panama (in Costa Rica on the Atlantic slope as well as from the Osa Peninsula on the Pacific slope). In Panama, known from tropical moist forest on BCI and at Summit Garden in the Canal Zone and from premontane wet forest in Colón (Santa Rita Ridge).

See Fig. 81.

Fig. 80. *Anthurium acutangulum*

Fig. 81. *Anthurium bakeri*

Anthurium bombacifolium Schott, Oesterr. Bot. Z. 8:182. 1858

Creeping epiphyte; caudex long and slender; internodes elongate; cataphylls caducous or weathering to persistent tough fibers. Leaves palmately compound; petioles 24–44 cm long; leaflets 6–11, nearly sessile or on petiole to 5.5 cm long, broadest at about middle, tapered abruptly to cuspidate-acuminate apex and gradually to cuneate-attenuate base, 15–30 cm long, 5–9 cm wide, entire; lateral veins forming 2 collecting veins, 1 marginal, 1 more remote. Peduncles mostly 20–53 cm long; spathe green, 6–10 cm long, 1–2.5 cm wide at base; spadix maroon, short-stipitate or sessile, 3–15 cm long, 7–13 mm broad, attenuate; tepals 6–7 mm long, 4–5 mm wide in fruit. Fruits maroon, 7–8 mm long, 5–6 mm wide; seeds ovoid to oblong, ca 5.3 mm long and 4 mm wide. *Croat 7090, 11700.*

Occasional in the forest in trees, often within 3 m of the ground. May be found in flower or fruit much of the year with most flowering in the dry season. Most fruits develop in the late dry season and in the early rainy season.

Recognized by its thin, palmately compound leaves and elongate caudex.

This species would be considered *A. undatum* Schott from South America if that species is distinct from *A. bombacifolium,* since all the leaflets are subequal and radiate equally from the apex of the petiole. Typical material collected in Honduras, Belize, and Mexico has leaflets pedately arranged, the lateral ones with a distinct auricle on the outer margin.

Mexico to Panama. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, and Darién; known also from premontane moist forest in Panamá, from premontane wet forest in Colón; and from tropical wet forest in Colón and Panamá.

Anthurium brownii Mast., Gard. Chron. n. s. 7:744, f. 139, 140. 1876

Epiphyte, or perhaps secondarily growing terrestrially, often flowering when still rather small; caudex moderately long and densely rooted, 2–5.5 cm thick; cataphylls 5–17 cm long, 2–6 cm broad, soon turning brown, persisting. Leaves coarse and thick, clustered at apex; petioles 25 cm to rarely more than 1 m long, shortly sheathed at base and becoming triangular-canaliculate above, ca 1 cm wide, the geniculum dark, 2 cm long, 1.5 cm wide; blades hastate to trilobate, mostly 27–66 cm long, to 48 cm wide, thick-coriaceous (at least when dried), the upper lobe abruptly acuminate, 10–28 cm broad, the margins broadly undulate, the basal lobes directed outward on young plants, inward on older plants, often overlapping sinus, the sinus to 23 cm deep; major veins above sinus 5–8 pairs, the larger vein of each basal lobe joined by 8 or 9 smaller veins. Peduncles terete, 88–102 cm long, usually longer than petioles; spathe 8–23 cm long, cordate to truncate and 1.5–4.5 cm wide at base, long-acuminate, green, persisting in fruit, often ± twisted; spadix maroon, short-stipitate, 7–28 cm long, long-tapered, 4–15 mm wide in flower, heavy and to 38 cm long and 2.5 cm wide in fruit. Fruits dense, ± ellipsoid to obovoid, 5–8 mm long, 5 mm wide, orange or orange tinged with red, becoming mostly exserted from tepals and ultimately entirely exserted and dangling on 2 slender filaments; seeds 2, whitish, 4.5–5.3 mm long, 3–3.3 mm wide, embedded in a sticky, transparently whitish matrix. *Croat 8252, 10389.*

Abundant, usually rather high in forest trees or epiphytic on tree roots or old tree stumps at the margin of the lake. Those plants along the lakeshore generally are more massive than those in the forest. Apparently flowers and fruits all year.

Distinguished by the thick, cordate, very undulate blades. Immature plants have been known to flower when the leaves were no longer than 14 cm, scarcely revolute, and almost triangular in shape. Such plants might be thought to be another species.

Costa Rica to Colombia. In Panama, known from tropical moist forest in the Canal Zone, San Blas, and Panamá, from premontane moist forest in the Canal Zone (Ancón), from premontane wet forest in Chiriquí, Coclé, and Panamá, and from tropical wet forest in Colón and Panamá.

See Fig. 82.

Anthurium clavigerum Poepp. & Endl., Nov. Gen. Sp. Pl. 3:84. 1845

A. holtonianum Schott; *A. wendlandii* Schott; *A. panduratum* Mart. non Schott

Large epiphyte; caudex often 1 m or more long, to 5 cm thick, with large, irregular leaf scars. Leaves closely congested near apex of stem, palmately compound, often 1–2 m broad, shorter than petiole; petioles terete, shortly vaginate at base, geniculate at apex; leaflets 7–12, ± sessile, acuminate, the margins sinuate or with 2 to 5 deep lobes, the middle leaflet 50–100 cm or more long, the lateral leaflets becoming progressively shorter; juvenile leaves simple, entire, thick, at first lanceolate, long-caudate, acute at base, later truncate to cordate at base, to 29 cm long and 10 cm wide, becoming palmately compound with 3 or 5 sessile leaflets, the lower pair of leaflets asymmetrical. Inflorescences very stout, usually drooping below leaves; peduncles terete, shorter than petioles; spathe 30–65 cm long, 3–11 cm wide, maroon; spadix 40–80 cm long, 2 cm wide at base tapering to apex, the apex usually withering in fruit; fruiting spadices heavy, to 6 cm wide. Fruits obovate, 6–7 mm long, violet-purple to red-violet, exserted from tepals at maturity; tepals triangular in cross section, thickened and truncate at apex, to 5 mm long at maturity of fruit; seed 1(2), oblong, 3–4 mm long, white, sticky, embedded in a jellylike mesocarp. *Croat 4230, 4654, 8328.*

Common, usually growing at 2–7 m from the ground. Flowering early in the dry season (December) to as late as March (rarely later); juvenile inflorescences may be seen as early as October. The fruits develop from April to October, mostly in June and July. Individuals usually bear no more than two inflorescences, and fruits require about 4 months to develop.

Distinguished from any other plant by its large, pedately compound leaves with lobed leaflets.

Fig. 82. *Anthurium brownii*

Fig. 83. *Anthurium clavigerum*

Fig. 84. *Anthurium clavigerum*

Costa Rica to Peru and Brazil; low elevations. In Panama, known from tropical moist forest on both slopes in the Canal Zone and in Darién, from premontane moist forest in Panamá, from premontane wet forest in Chiriquí, and from tropical wet forest in Coclé (Atlantic slope) and Chiriquí.

See Figs. 83 and 84.

Anthurium flexile Schott, Oesterr. Bot. Z. 8:180. 1858

Epiphyte; caudex slender, usually less than 4 mm diam, creeping or scandent, usually with short, fleshy roots at nodes; internodes mostly 2–5 cm apart; cataphylls few, slender, acuminate, to 4 cm long. Petioles slender, 2.5–15 cm long, not obviously geniculate, vaginate only near base or to midlength; blades ovate-elliptic to oblong-oblanceolate, acuminate, narrowly rounded to subcordate at base, 10–20 cm long, 3.5–11 cm wide, thin, epunctate; venation pinnate, the principal lateral veins arising near the base of the blade and uniting with other lateral veins to form a slender collecting vein remote from the margin, often also with an indistinct submarginal collecting vein, the smaller veins distinct on dried specimens. Inflorescences borne from uppermost leaf axils; peduncles very slender, 7–15 cm long (to 20 cm in fruit); spathe lanceolate, acuminate or long-attenuate, rounded or subcordate at base, spreading, 4–8 cm long, 1–1.8 cm wide, pale green; spadix violet-purple at anthesis, sessile to stipitate, 5–9 cm long, of ± equal width throughout but narrowed at apex, less than 5 mm diam at anthesis, to ca 2 cm diam in fruit. Fruits usually developing at base first, ovoid to ellipsoid, often weakly beaked, mostly 8–10 mm long, orange or red. *Starry 60.*

Apparently rare; it has not been seen in recent years. Seasonal behavior uncertain; may be seen in fertile condition most of the year, but with most fruits maturing in the rainy season. Plants produce successive inflorescences over a long period of time, but possibly have two different periods of flowering activity.

Mexico to Colombia. In Panama, known from wetter parts of tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, and Darién and from premontane wet forest in Coclé and Darién.

Anthurium friedrichsthalii Schott, Oesterr. Bot. Wochenbl. 5:65. 1855

A. linearifolium Engler; *A. gracile* sensu Standley (1944) non (Rudge) Lindl.

Epiphyte, usually pendent, often loosely attached; caudex usually less than 15 cm long, 1–1.5 cm diam; nodes very close together, moderately rooted, the roots brownish, 3–4 mm wide; leaf scars prominently raised; cataphylls soon reduced to brown fibers, the fibers persistent at upper leaf bases. Leaves crowded; petioles 1.5–14 cm long, mostly less than 10 cm long, ca 2–3 mm wide, moderately to very strongly geniculate at apex, the base enlarged to 1 cm diam, the sheath 12–30 mm long; blades linear, long-acuminate at apex, subacute at base, 12–56 cm long, 0.8–4(5.8) cm wide (mostly less than 3 cm wide), strongly bicolorous (when fresh), the lower surface light green with numerous brown punctations; midrib prominently raised above, the lateral veins obscure on both surfaces (moderately prominent below when dried), the collecting vein 3–4 mm from margin. Inflorescences pendent, shorter or longer than leaves; peduncles to ca 2.5 mm thick, (9)19–30 cm long (to 40 cm in fruit); spathe linear, 1–5 cm long, 3–5 mm wide, not reflexed; spadix sessile (elsewhere distinctly stipitate), narrowly cylindrical, 3–15 cm long and 4–5 mm wide, to 25 cm long and 2 cm wide in fruit; tepals ca 1.7 mm high and 2 mm wide in flower, the fruiting tepals to 4 mm long and 5 mm wide at base, tapered upward, the apex narrow and truncate. Berries of irregular shape, broader than long, ca 5 mm long, 5–7 mm wide, pale yellow-orange, truncate at apex with a central depression, borne on 4 slender filaments; seeds (1)3–4(5), ± ovate, to 2.7 mm long, greenish or yellowish (darker on one end), embedded in fleshy clear matrix, bearing a slender, mucilaginous, sticky appendage. *Croat 6614, 6980.*

Common in the forest, from near the ground to more than 30 m high, usually pendent from tree branches. Flowers mostly in the dry season (January to April), rarely later in the rainy season. The fruits develop slowly, requiring possibly several months, maturing mostly from June to October.

Recognized by the thick, linear, bicolorous, punctate leaves. Juvenile plants have short, elliptic leaves.

Guatemala to Colombia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Coclé, Panamá, and Darién; known also from premontane wet forest in Colón and from tropical wet forest in Colón and Chiriquí.

Anthurium gracile (Rudge) Lindl., Edward's Bot. Reg. 19:1635. 1833

A. scolopendrinum (Ham.) Kunth

Epiphyte, usually erect; caudex 1.5–30 cm long, 7–10 cm wide; internodes moderately close together; roots fleshy, often whitish, 4–6 mm thick; cataphylls 2–9.5 cm long, reddish or brown, the uppermost persisting and remaining intact, ultimately deciduous. Leaves moderately thin, held ± erect; petioles distinctly broadened at base and sheathed to 4.5 cm from base, rounded but with flat rib to 2 mm wide on upper surface, 1–20 cm long, to 3 mm wide, slightly to moderately geniculate and nodose at apex, the geniculum not extending onto blade; blades broadest above middle, gradually acuminate at apex, gradually tapered to long-cuneate base, 11–32 cm long, 0.7–8.5 cm wide, essentially concolorous, glabrous, epunctate; midrib prominent above, the lateral veins and collecting vein indistinct (moderately distinct on drying). Peduncles very slender, ± erect, 21–40 cm long in flower, to 60 cm long in fruit; spathe maroon, 13–25 mm long (to 5 cm in South American material), mostly to 6 mm wide and often joining on opposite side of peduncle, ± pendent; spadix sessile, mostly less than 3 cm long and 4 mm wide in flower, often ± curved, to 10 cm long and 1.5 cm wide in fruit. Berries ± globose, ca 7 mm diam, bright red; seeds 2(4), white, embedded in a very sticky, gelatinous matrix. *Croat 5392, 7957a.*

Occasional, in the forest and on trees in the lake. Ap-

parently lacking any distinct seasonal behavior. Flowers and fruits may be seen at all times of the year.

Distinguished by its thin, oblanceolate, epunctate leaves and persistent, intact cataphylls. The species has been confused with *A. friedrichsthalii,* which has thick, linear, bicolorous, punctate leaves. It may also be confused with *A. bakeri,* which has linear-lanceolate, punctate leaves. The mass of roots is sometimes infested with black stinging ants.

Guatemala to Ecuador and southern Brazil. In Panama, known only from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién.

Anthurium littorale Engler, Bot. Jahrb. Syst. 25:405. 1898

Epiphyte; caudex to 1.5 cm diam, very short or to 30 cm long; leaf scars prominent; internodes short, especially near apex; cataphylls brown, usually nonfibrous, soon deciduous, to 9 cm long and 1 cm wide. Petioles 3–14 cm long (even on a single plant!), conical and to 12 mm thick at base, canaliculate above, weakly to strongly geniculate at apex, the geniculum 1.5–2 cm long, the sheath 1–6 cm long; blades oblong-lanceolate to oblanceolate-oblong, obtuse to acute at apex and often with downturned apiculum, acute at base, the margins continuous with the margins of petiole, the blades 10–38 cm long, 3–11 cm wide, coriaceous, sparsely to moderately punctate on both surfaces, often turned somewhat upward along midrib; midrib often arched, the lateral veins forming 1 or 2 faint collecting veins. Inflorescences 1 or 2 from upper axils; peduncles melon-colored to reddish in flower, 9–25 cm long; spathe whitish, oblong, acuminate, 3–7 cm long, to 1.4 cm wide; spadix (7)9–22 cm long, ca 5 mm wide in flower, melon-colored when young, becoming violet-purple in age; tepals much broader than long, thickened, flat and triangular at apex; ovary depressed-globose, the apex square or rectangular; stigma sessile. Fruits ± globose, 4–5 mm diam, yellowish, orange, or white tinged with orange, the stigma small, buttonlike. *Croat 8821, 13989.*

Frequent at the margin of the lake and in the forest, usually rather high in trees. Flowers primarily from February to April, sometimes as early as January elsewhere in Panama.

The species has been confused with several other undescribed species of *Anthurium* in Panama.

Costa Rica and Panama. In Panama, known from tropical moist forest on BCI and in Bocas del Toro, Colón, San Blas, and Darién, from premontane wet forest in the Canal Zone and Panamá, and from tropical wet forest in Colón, San Blas, and Panamá.

See Fig. 85.

Anthurium ochranthum C. Koch, Ind. Sem. Hort. Berol. App. 16. 1853

A. lapathifolium Schott; *A. triangulum* Engler; *A. baileyi* Standl.

Terrestrial, rarely more than 1.3 m tall; caudex short-creeping over ground, then erect, to 45 cm high (usually shorter), to 3–4 cm thick (rarely thicker); cataphylls short. Petioles slender, round to canaliculate on upper surface (conspicuously canaliculate on drying), 30–70(90) cm long, the very base vaginate; blades ± ovate-cordate to triangular, abruptly acuminate at apex, cordate at base, the basal lobes to 25 cm long, narrow, directed downward or outward with sinus narrow to open, mostly ca 50 cm long, 33–60 cm long above the sinus, 29–33 cm wide, ± thin, the lower surface much lighter than the upper; major veins above sinus 7–11 pairs, at least the uppermost forming a collecting vein near margin, the basal lobes each with usually 4 veins. Peduncles terete, about as long as petioles; spathe usually less than 15 cm long (but occasionally to 32 cm) and 3.5–5 cm wide, tapered to an attenuate apex, as long as or shorter than spadix, decurrent on peduncle; spadix sessile or on a stipe to 13 mm long, tapering to blunt end, in flower yellow, 13–19 cm long and 10–13 cm wide at base, in fruit violet-purple, to 37 cm long and 2.5 cm wide; ovules ovate, ca 3 mm high; style sessile; sepals yellow, becoming green then violet-purple in fruit, irregular in shape, much thicker and truncate at apex, covering ovule, to 7 mm long in fruit. Fruits obovoid, 7–9 mm long, beaked, violet-purple at apex, white at base, extruded at maturity and suspended on 2 slender white strands; seeds usually 1, greenish, 4–5 mm long, immersed in a fleshy, whitish matrix. *Croat 10219.*

Moderately common in some areas of the forest, especially on steeper slopes. Flowers with successive inflorescences being produced mostly from late March to July, rarely in August and September. The fruits develop within about a month or 6 weeks, maturing mostly from May to September.

The only species of *Anthurium* on BCI that is consistently terrestrial (though *Kenoyer 191* was recorded as epiphytic). In commenting on *A. baileyi* both in his type description and in the *Flora of Panama,* Standley obviously confused sterile plants of *Homalomena wendlandii* with this species. The two often occupy the same habitat, but in *H. wendlandii* the petioles are aculeate and the lower leaf surface is puberulent; *A. ochranthum* never has these characteristics.

Honduras to Panama; probably also Colombia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, Panamá, and Darién, from premontane moist forest in Panamá, from premontane wet forest in Colón, and from tropical wet forest in Bocas del Toro, Colón, and Panamá.

See Fig. 86.

Anthurium scandens (Aubl.) Engler in Mart., Fl. Brasil. 3(2):78. 1878

A. rigidulum Schott

Creeping epiphyte; caudex elongate, occasionally branching, usually less than 1 m long, with extensive long roots at lower nodes, the internodes usually short but distinct, the leaves not clustered at apex; cataphylls brown, tightly appressed, persistent and often weathering into fine fibers on the leafy part. Petioles usually 2–7.5(10.5) cm long, to two-thirds as long as blade, canaliculate on upper side, nodose at base and apex, geniculate at apex; blades narrowly to broadly elliptic, tapered evenly to both ends,

Fig. 85.
Anthurium littorale

Fig. 87. *Anthurium scandens*

Fig. 86. *Anthurium ochranthum*

Fig. 88. *Anthurium tetragonum*

acute to acuminate and downturned at apex, usually acute at base, 4.5–14 cm long, 2–7 cm wide, subcoriaceous, obscurely to prominently punctate on lower surface; collecting and lateral veins obscure (distinct on dried specimens). Peduncles 2.5–5 cm long, usually exceeding petiole of subtending leaf; spathe lanceolate to oblong-lanceolate, decurrent on peduncle; persisting but becoming dried, (0.4)2–3 cm long, to 12 mm wide at base, acuminate at apex; spadix sessile, usually to 3 cm long and lavender at anthesis, 4–10.5 cm long in fruit, to 17 mm wide; tepals at first lavender becoming whitish, 1 mm high and 2.3 mm broad in flower, to 4 mm high and 6.7 mm broad in fruit; anthers emerging beneath margin of tepal when spadix is quite small. Fruits white, very fleshy and weakly exserted at maturity, ovoid, minutely beaked, ca 7 mm long; seeds usually 5–9, ca 2.5 mm long, ± elliptic, embedded in a thick, clear jelly. *Croat 6292, 14969.*

Infrequent, in the forest, usually high in trees. Though flowers and fruits may be present throughout much of the year, BCI plants flower mostly in the dry season and fruits develop mostly in the rainy season.

Though not so great on BCI, the variability throughout the range of this species is immense. This variability is generally exhibited in the size of plant parts.

Mexico throughout Central America to the Guianas and southern Brazil; Trinidad, Greater Antilles. In Panama, ecologically variable and widespread; known from tropical moist forest in the Canal Zone, Bocas del Toro, Veraguas, Panamá, and Darién, from premontane wet forest in Bocas del Toro, Chiriquí, Coclé, and Panamá, from tropical wet forest in San Blas, Colón, Chiriquí, Coclé (both slopes), Panamá, and Darién, and from premontane rain and lower montane rain forests in Chiriquí.

See Fig. 87.

Anthurium tetragonum Hook. ex Schott, Prodr. Aroid. 1860

Moderate to large, rosulate epiphyte; caudex short, 6–8 cm thick, usually very densely covered with an irregular mass of fleshy roots, the roots often extending above the short petioles. Leaves crowded; petioles 10–20 cm long, 1–2 cm wide, ± flattened on upper surface above geniculum, ± rounded below, becoming carinate on underside after drying, geniculate at base of blade or 5–6 cm below blade, the geniculum about as long as broad; blades broadly obovate to oblanceolate, acute to shortly acuminate at apex, gradually tapered to the usually cuneate base (rarely rounded or subcordate), 60–153 cm long, 25–50 cm wide (rarely smaller when fertile), coriaceous when dried; midrib and veins prominently raised on both surfaces, the major veins mostly 9–14 pairs, arcuate-ascending to margin, not forming a collecting vein. Inflorescences ± pendent below leaves; peduncles terete, 30–64 cm long; spathe green, 15–30 cm long, 2–4 cm wide and decurrent at base, tapered to long-cuspidate point; spadix dull green, to 34 cm long in flower, becoming magenta, to 50 cm long and 3 cm diam at base in fruit, the apex often withered; sepals pale magenta, obovoid, accrescent. Berries ± oblong, 1–1.5 cm long, red, exserted at maturity; seeds 2, oblong, to 3.3 mm long, flattened, embedded in a clear, jellylike matrix. *Croat 7920, 8512, 10195, 11325.*

Common in the forest, growing from near the ground to ca 20 m high. Quite variable in size, and may be fertile while plants are still fairly small. Flowers mostly in the dry season during February and March. Most fruits mature during the rainy season, July to September. Inflorescences usually begin to develop again by December or earlier.

This species is not confused with any other on the island. The names *A. crassinervium* (Jacq.) Schott, *A. maximum* (Desf.) Engler, and *A. schlechtendalii* Kunth, all reported by Standley for BCI, were apparently based on misdeterminations of *A. tetragonum.* Most determinations were based on the shape of the petiole, a character that is of little value, since drying affects each plant somewhat differently.

Mexico to Panama, probably also Colombia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, Panamá, and Darién; known also from premontane moist forest in the Canal Zone (Ancón), from premontane wet forest in Panamá, and from tropical wet forest in Colón and Chiriquí.

See Fig. 88.

CALADIUM Vent.

Caladium bicolor (Ait.) Vent., Descr. Cels. pl. 30. 1801

Terrestrial, acaulescent. Leaves from a depressed-globose rhizome; petioles fleshy, 30–80 cm long, sheathed at base; blades ovate-cordate to ovate-sagittate, acute to acuminate, 10–60 cm long, to 40 cm wide, thin, peltate far above base, glaucescent, usually reddish near center and spotted on upper surface with white, red, or yellow, the basal lobes rounded, directed downward or outward. Inflorescences shorter than leaves; peduncles slender and fleshy; spathe 7–15 cm long, the tube ovoid, greenish, the blade 2–3 times longer than tube, cuspidate, white, weathering away with upper staminate part of spadix after anthesis; sterile staminate part of spadix to 1.5 cm long, ending abruptly at base, its cells longer than broad, continuous with fertile staminate part but discontinuous with pistillate part; pistillate part of spadix ovoid-cylindrical, to 2 cm long; flowers unisexual, naked; staminate flowers with 3–5 connate stamens, the connective flat, angulate marginally; ovary with 2 or 3 cells, several ovules in each locule. Fruits baccate, bearing several to many-seeds; seeds ovoid. *Croat 10184.*

Cultivated at the Laboratory Clearing; seen once on Shannon Trail. Flowers and fruits chiefly throughout the rainy season.

Native to the Amazon region; widely cultivated. In Panama, known from tropical moist forest in the Canal Zone (doubtlessly cultivated elsewhere).

DIEFFENBACHIA Schott

Members of the genus may be distinguished by their naked unisexual flowers, which have four stamens and

KEY TO THE SPECIES OF DIEFFENBACHIA

Stems usually more than 5 cm thick; plants usually well over 1 m tall when fertile; spathes 27–48 cm long; leaf blades more than 40 cm long; both leaf blades and petioles solid green in color (petioles sometimes with lighter streaks but never splotched) .... *D. longispatha* Engler & Krause

Stems usually less than 3 cm thick; plants usually less than 1 m tall when fertile; spathes usually less than 25 cm long; leaf blades usually less than 30 cm long; leaf blades often with light streak on midrib or the petioles speckled:

Leaves narrow, less than 8 cm wide, the base usually acute, sometimes obtuse, never cordate; midribs and petioles mottled with whitish spots ..... *D. pittieri* Engler & Krause

Leaves mostly more than 10 cm wide, often cordate at base; midribs and petioles solid green, not speckled, the midrib often with a white streak ..... *D. oerstedii* Schott

are enclosed after anthesis by the spathe. The stamens are fused together to form a synandrium with four or five sides, truncate at the apex; pistillate flowers have four or five club-shaped staminodia; ovaries have one to three locules with a single ovule per locule. The sap contains relatively high amounts of oxalic acid, which gives the plant a characteristic odor and may burn the skin.

Dieffenbachia longispatha Engler & Krause, Pflanzenr. IV. 23DC(Heft 64):44. 1915

Terrestrial, 1.2–3.5 m tall; caudex 4–12 cm diam at maturity, at first prostrate, then erect; leaf scars prominent. Petioles thick and succulent, 27–50 cm long, ± terete at apex or with faint flat rib on upper surface, prominently sheathed to about middle; blades thick, oblong-elliptic, short-acuminate, acute to rounded at base, 46–71 cm long, 24–35 cm wide, the edges usually turned upward near base; midrib flat on upper surface, 1–2 cm wide at base, prominently raised on lower surface, the major lateral veins in 2–26 pairs, impressed above, raised below, the smaller veins indistinct; juvenile blades with acute base and solid green midrib. Inflorescences usually 1–3; peduncles 7–25 cm long; spathe green, broadly curved, long-acuminate, 27–48 cm long, to ca 4 cm broad when closed, the distal inner surface white when open and 5–6 cm broad; free staminate part of spadix 13–19 cm long, 12–14 mm wide; pistillate part of spadix (except sometimes the uppermost part) fused to spathe; pistillate flowers 10–25, widely spaced, in a single row or scattered, round or barely bilobed; stigmas 6 mm broad, yellow; staminodia white, irregular, 2–3 mm long. Fruits 1.5–2 cm diam, often deeply emarginate at both ends appearing to be a double fruit, yellow to orange; mesocarp ca 2 mm thick, soft, sweet and tasty at maturity; seeds oblong, 7–8 mm diam, brown, smooth. *Croat 6276, 11321.*

Common throughout the forest, in streams or on sediment deposits in standing water at the edge of the lake; usually not highly colonized. Juvenile plants are much more abundant than adults. Flowers from May to September, although individuals apparently do not flower every year. The fruits develop from September to December.

The species may not be separable from *D. sequine* (Jacq.) Schott of Central America and the West Indies, which has the pistillate flowers closely congested and all parts much smaller. Until more thorough studies can be made, it is best to consider *D. longispatha* distinct from *D. sequine.* Another related but apparently undescribed species occurring in tropical wet forest in Panamá (Cerro Campana), Coclé (El Valle), and Colón (Portobelo) has flowers very closely congested, but its petiole is vaginate its entire length. (See *Croat 12710, 13403, 14175.*) *Croat 5709,* a sterile collection from BCI, is similar and might also be this undescribed taxon, but it is in some ways intermediate between *D. longispatha* and *D. oerstedii.* This is the largest of all Central American *Dieffenbachia* species.

Costa Rica, Honduras, and Panama; possibly to Colombia and Venezuela. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, and Panamá, from premontane moist forest in Panamá, from premontane wet forest in Colón, Chiriquí, Coclé, and Panamá, and from tropical wet forest in Colón.

See Figs. 89, 90, and 91.

Dieffenbachia oerstedii Schott, Oesterr. Bot. Z. 8:179. 1858

Terrestrial, glabrous, usually no more than 1 m tall; stem 2–2.5(3.5) cm diam; caudex long or short, usually creeping over surface of ground; internodes short. Petioles 12–22 cm long, vaginate to near middle or slightly above, flattened on upper surface at apex; blades oblong-ovate, abruptly acuminate at apex, cuneate to cordate with the sides often ± unequal below, 12–30 cm long, 6–15 cm wide, thin, deep green above, often with light green streak on midrib in distal half of blade; midrib flat above, 5–8 mm broad, the major veins 7–12 pairs, ± impressed above, the smaller veins obscurely visible below. Inflorescences usually 3–5, straight to slightly curved; peduncles 7–12 cm long; spathe green (inner part white at top of blade when open), 15–23 cm long at anthesis (elongating somewhat after closing of spathe), 2.5–3 cm broad at top when open, less than 2 cm broad when closed, often becoming ± orange at maturity; free staminate part 7–13 cm long, 6–8 mm broad; pistillate flowers minute, 30–45, closely spaced; staminodia flattened below, the tips globular. Fruits ellipsoid, 7–8 mm long, orange to red, the stigmatic area round, ca 2 mm wide. *Croat 5896, 7712.*

Common throughout the forest; often locally abundant in moist areas. Flowers chiefly in the early rainy season, May to August. The fruits develop mostly during the

Fig. 89. *Dieffenbachia longispatha*

Fig. 90. *Dieffenbachia longispatha*

Fig. 91. *Dieffenbachia longispatha*

Fig. 93. *Dieffenbachia oerstedii*

Fig. 92. *Dieffenbachia oerstedii*

dry and early rainy seasons of the following year, February to May.

Distinguished by its small size and somewhat cordate leaves, often with a white streak on distal half of midrib.

Guatemala to Panama. In Panama, known chiefly from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, Los Santos, Panamá, and Darién; known also from premontane wet forest in Colón and Panamá.

See Figs. 92 and 93.

Dieffenbachia pittieri Engler & Krause, Pflanzenr. IV.23Dc(Heft 64):42. 1915

Terrestrial, 0.8–1.5 m tall; caudex to 3 cm diam (usually less than 2 cm), weakly rooted, decumbent then erect, covered with thin brown epidermis with reticulate pattern; leaf scars inconspicuous. Petioles 8–12 cm long, dark green with whitish maculations, the spots extending along most of midrib below; sheaths prominent, extending halfway or almost to blade; blades narrowly elliptic, gradually acuminate, often somewhat falcate, cuneate to obtuse (elsewhere subcordate) and often slightly inequilateral at base, 20–30 cm long, 5–8 cm wide; midrib rounded and slightly raised on upper surface, the veins many, obscure above, weak but all more or less equally distinct below. Inflorescences 1–3, 14–20 cm long; peduncles about 4 cm long, somewhat flattened; spathe 12–20 cm long, colored like petioles in basal half, pale green at apex at anthesis, caudate-acuminate, sometimes sharply bent backward below apex; spadix 10–18 cm long, the pistillate and sterile parts united to spathe; staminate part 5–9 cm long, the staminate flowers nearest pistillate ones widely spaced and probably sterile; pistillate flowers usually 20–40, moderately close together, not in obvious rows but scattered, their staminodia white, usually 3, flattened, oblong to clavate, slightly longer than stigmas; stigmas orange, depressed-globose, ca 1.5 mm high; fruiting spadices broadly arched, the spathe mostly deciduous, exposing fruits. Fruits broadly ellipsoid, to ca 1.5 cm long, less than 1 cm wide, orange. *Croat 5759, 6775.*

Occasional, in older forest, possibly most common in the vicinity of Drayton and Armour Trails. Seasonal behavior is uncertain. Believed to flower from May to December and to fruit from October to May.

Easily distinguished by its leaves, which are acute at the base with spotted petioles. BCI populations of the species differ somewhat from others in having slightly narrower leaves, in being acute to obtuse at the base (usually subcordate elsewhere), and in being consistently maculate on the petioles (rare elsewhere). It is possible that additional work will show that the BCI plants, which match others found along the Atlantic slope of Panama, are a distinct species.

When the spathe first opens, the stigmas appear receptive, but the white staminate flowers are so closely compacted that the pollen cannot be shed. Later the staminate flowers become cream-colored and shrink somewhat to expose the thecae of the anthers around the margin. By the time the staminate flowers reach anthesis, the spathe has closed somewhat, all but blocking the opening to the pistillate flowers. This is a general phenomenon for all *Dieffenbachia* (at least those species on BCI) and no doubt helps promote cross-pollination.

Known only from the lowland forest on the Atlantic slope of Panama.

See Figs. 94 and 95.

DRACONTIUM L.

Dracontium dressleri Croat, Selbeyana 1:168. 1975

Terrestrial, consisting of a single large leaf arising from an underground tuber; tuber ovoid, ca 9 cm long and 7 cm wide, the upper part rounded. Leaf 2–4-pinnate to sub-5-pinnate, glabrous; petiole fleshy, to 6.5 cm diam near base, to 3 cm diam at apex, 1–1.8 m long, green blotched with dark brown and pale green in a reptilian pattern, the protuberances irregular, short, especially close together in proximal half; blade thin, with 3 principal divisions, these each leafy mostly in distal two-thirds, the middle section 40–100 cm long, the lateral sections somewhat shorter, the rachises smooth or bearing protuberances, faintly patterned like the petiole; leaflets 3.5–20 cm long, 1–7.5 cm wide, gradually acuminate at apex or bilobed, the lobes acuminate, acute at base and decurrent along the rachis, the decurrent part ± erect on upper side of petiole and irregularly lobed; lateral veins of ultimate segments arcuate-ascending, loop-connected, occasionally interconnected with an equally prominent cross-vein, all major veins impressed on upper surface, raised on lower surface. Inflorescence arising from the apex of the tuber before the leaf is produced; peduncle ca 2 cm long and 1 cm thick, subtended on the outside by a lanceolate sheath, the sheath ca 5 cm long and 2 cm wide, acuminate at apex, with an obscure medial vein, at first violet-purple, soon drying and turning brown; peduncle subtended on the inside by a prophyll ca 2 cm long, this bearing 2 prominent ribs on its outer surface; spathe ± oblong in face view, ca 10 cm long, arcuate in side view, convolute in lower third and to 2.5 cm wide, broadened above and to 4 cm wide, becoming tapered at apex and curving forward to form a portico over the mouth of the spathe, the tip cuspidate-acuminate, the outer surface of spathe dull, violet-purple, tinged with green, bearing 15, ± equidistant veins, the inner surface of spathe shiny, smooth, dark violet-purple except for a weakly transparent area around the spadix, this ca 4 mm wide at any point, the tube of the spathe roomy within; spadix dark violet-purple, short-stipitate, the stipe ca 7 mm long and 6 mm diam, the fertile part ca 2 cm long, 7–9 mm diam, bearing 10 slender appendages at the apex ca 5 mm long; flowers bisexual, closely spiraled in ca 10–12 rows; tepals 4–8 (usually 5 or 6), biseriate, ca 2 mm long, broadened and arched inward at apex, the upper edge truncate, irregularly shaped, mostly triangular to diamond-shaped, ca 1.5–2.5 mm wide, thickened except along the irregular distal margin; stamens usually free, 5–9, to 2.2 mm long, opposite the tepals and emerging slightly above them at anthesis, crowded together by the tepals to form a single locus of pollen; filaments fleshy and swollen toward apex, broader than the anthers, the

Fig. 94. *Dieffenbachia pittieri*

Fig. 95. *Dieffenbachia pittieri*

Fig. 96. *Homalomena wendlandii*

Fig. 97. *Homalomena wendlandii*

inner whorl sometimes fused laterally forming a tube around the pistil, the tube white, streaked with violet-purple; anthers linear-elliptic, ca 4 mm long, vertically dehiscent, the thecae touching at apex, separated at base; pollen light-brown, the grains clinging together in a mass but the mass of pollen not tacky; pistil violet-purple, ca 1.6 mm long; ovary ± oblong, pale-colored, incompletely 2–5-locular (for the genus); ovules solitary; style eccentric, darkly colored, tapered to a slender apex. Fruits unknown, those of the genus surrounded by perianth as in *Anthurium;* seeds rounded to reniform, somewhat compressed. *Dressler s.n.*

Rare, in the forest; collected near the end of Zetek Trail by Dressler. Flowers in the early rainy season before the leaf emerges. The fruits probably also mature in the rainy season. The plant is leafless in the dry season.

The inflorescence presents a typical fly-pollination syndrome (sapromyophily), with a foul aroma, purplish spathe, and easy access to the flowers (Faegri & van der Pijl, 1966). The species also has a transparent window around the spadix at the base of the spathe tube, which is not apparent from the outside but can be seen easily from within if the front of the spathe is closed off. The inner surface of the spathe is very smooth, perhaps making it difficult for an insect visitor to crawl out.

Known from tropical moist forest on BCI and from premontane wet forest in Colón (Achiote).

HOMALOMENA Schott

Homalomena wendlandii Schott, Prodr. Aroid. 308. 1860

Terrestrial, acaulescent. Petioles to 1.3 m long, usually shorter, terete, sheathed in lower third, densely puberulent and armed with short, sharp prickles usually below middle; blades ovate-cordate to ovate-sagittate, abruptly short-acuminate and turned downward at apex, cordate at base, 37–78 cm long, 23–53 cm wide, glabrous above, puberulent below, the basal sinus 13–24 cm deep and 2–10 cm broad at open end with its apex acute; major veins 7–10 pairs above sinus, 3–5 joining in basal lobes, impressed above, markedly raised below. Inflorescences arising from ground; peduncles 5–20 cm long, puberulent; spathe convolute, pale green with white spots, often pure white at apex at anthesis, 19–30 cm long, enveloping spadix, caudate-acuminate at apex, only slightly bulbous at base, becoming purplish in age (especially base), white within (at least when open); spadix white, 17–26 cm long, the area between staminate and pistillate flowers often pink, its flowers sterile; pistillate part 3.5–7 cm long, to 1.8 cm wide (3 cm in fruit), mostly adnate to spathe; staminate flowers with 2–4 (6) stamens; fruiting inflorescences 10 cm long or more and 5 cm wide. Mature fruits obovoid to oblong, to ca 6 mm long, incompletely 2–5-celled, truncate at apex; stigmas persistent, rounded, and depressed with 4 or 5 lobes; seeds many in each cell, ± ellipsoid, to ca 0.7 mm long, longitudinally striate, attached by a long funicle, immersed in a clear, gelatinous matrix. *Croat 14853.*

Very common, preferring steep, moist slopes and creek banks. Flowers from late March to May. Mature fruiting inflorescences have never been seen on BCI but apparently develop soon after flowering.

Recognized by its terrestrial habit, prickly petioles, and puberulent parts (an uncommon feature in the Araceae). The flowering inflorescence has a pungent, sweet aroma resembling anise (also uncommon in the Araceae, which often have rather foul odors). Standley (1944) in the *Flora of Panama* misspelled the genus as *Homalonema.*

The entire inflorescence is often missing above the peduncle (apparently eaten by animals), and this perhaps constitutes the plant's method of dispersal.

Costa Rica and Panama, and southeastern Colombia, along the Río Putomayo (*Schultes & Cabrera 19054, GH*); probably more widespread. In Panama, known from tropical moist forest on the Atlantic slope in the Canal Zone, San Blas, and Chiriquí Provinces, from premontane wet forest in the Canal Zone, Chiriquí, and Panamá, and from tropical wet forest in Colón.

See Figs. 96 and 97.

MONSTERA Adans.

Members of the genus are recognized by the bisexual flowers, which are naked with four stamens, and by the uniform spadix, from which the spathe generally falls free after anthesis. The ovary has two cells, each with two ovules.

Monstera adansonii Schott var. **laniata** (Schott) Mad., Contr. Gray Herb. 207:38. 1977

Epiphytic vine; caudex minutely speckled, smooth, 1–2.5 cm diam, closely appressed to tree or more often free,

KEY TO THE SPECIES OF MONSTERA

Adult blades deeply pinnatifid, not perforate ..... *M. dilacerata* C. Koch
Adult blades perforate to irregularly pinnatifid (the result of a large perforation reaching the margin), not regularly and deeply pinnatifid:
  Caudex and base of petioles densely and conspicuously tuberculate, the adult caudex often flattened, to 2.5 cm diam; reticulate venation on leaves about as prominent as major lateral veins when dried; spathe coriaceous, rounded at apex ..... *M. dubia* (H.B.K.) Engler & Krause
  Caudex and base of petiole usually smooth, the adult caudex terete, less than 1.5 cm diam; reticulate venation on leaves not at all prominulous, much less prominent than major lateral veins; spathe thin, narrowly acuminate at apex .....
  ..... *M. adansonii* Schott var. *laniata* (Schott) Mad.

Fig. 98. *Monstera dilacerata*

Fig. 100. *Monstera dubia* (see also Figs. 101, 102)

Fig. 99. *Monstera dilacerata*

scandent; internodes 6–10 cm long. Petioles minutely speckled, 10–33 cm long, sheathed to near the apex, canaliculate above the sheath, the sheaths to ca 1 cm high on the sides, tapered somewhat toward apex, the sides rounded and free at apex; blades ovate, rarely elliptic, inequilateral, abruptly acuminate, downturned, and weakly inequilateral at apex, obtuse to truncate or subcordate at base, 15–35 cm long, 9–28 cm wide, semiglossy, the lower surface slightly paler; midrib and major lateral veins sunken, slightly paler, the secondary lateral veins visible, dark; preadult leaves much like adult but smaller. Inflorescences solitary or up to 6 per node, each subtended by a bracteole to 12–16 cm long; peduncles flattened somewhat laterally, minutely speckled, 6–9 cm long, to 1 cm diam, to 16 cm long in fruit; spathe creamy-white at anthesis, caducous, acuminate, ca 11 cm long; spadix white at anthesis, soon becoming pale greenish-white, 6–9 cm long, to ca 1 cm wide; fruiting spadices white, to 16 cm long and 2 cm wide. Fruits not coalesced at maturity, to ca 10 mm long and 4 mm wide. *Croat 6225.*

Apparently rare on the island, though common elsewhere in adjacent areas of the Canal Zone; collected once between the dock and Fairchild Point. Flowers and fruits throughout the rainy season, mostly from April to August, less frequently as early as February and as late as October. Fruiting occurs mostly from September to December, less frequently as early as July.

Honduras to Colombia, Venezuela, and the Guianas. In Panama, known principally from tropical moist forest in Bocas del Toro, Colón, Canal Zone, Chiriquí, and Darién, but also from premontane wet forest in Bocas del Toro and from tropical wet forest in Colón and Coclé.

Monstera dilacerata C. Koch, Ind. Sem. Hort. Berol. App. 5. 1855

Ceriman, Anona piña

Epiphytic climber; caudex usually short and thick at maturity (usually less than 1.5 m long), terete with prominent leaf scars; juvenile plants at first terrestrial, often with few leaves. Petioles to 36 cm long, shorter than blade, the sheaths often extending to base of geniculum, the remainder of petiole canaliculate with thin, raised, minutely undulate margins; blades regularly and deeply pinnatifid, rounded to cordate at base, 35–46 cm long, 28–35 cm wide, the apical segment acuminate; lobes 3–9 on each side, 1.5–4.5 cm wide, acute and falcate at apex, dark green and glossy above, paler and drying very darkened below; lateral veins in 1–3 pairs, whitish and raised on underside; juvenile blades thick, ovate-lanceolate, oblique and falcate, acute to acuminate at apex, to about 20 cm long and 9 cm wide, bicolorous (drying black), the major veins in 2–5 pairs; immature plants later forming runners that ascend tree trunks, the leaves then distichously arranged, the blades entire or less frequently perforate to pinnatifid, 7–26 cm long, 7–14 cm wide, the larger with petioles to 18 cm and spreading. Inflorescences several, from upper axils; peduncles 15–23 cm long, subterete with a broad spathe scar at apex; spathe acute to acuminate at apex, white at anthesis, to 24 cm long, soon deciduous; spadix narrowly oblong, narrowly rounded at apex, mostly 13–16 cm long at anthesis (to 19 cm long in fruit); pistils ca 5 mm long at anthesis (more than 1 cm long in fruit), the sides angulate, the apex truncate, to ca 5 mm diam at anthesis; stigmas linear. Fruits not coalesced at maturity, whitish, to 12 mm long and 5 mm wide. *Croat 7251.*

Juvenile plants common; adults apparently infrequent, occurring at least sometimes within 4 m of the ground on the smooth face of tree trunks in the forest. Flowers in the late rainy season through the dry season (December to March), with the fruits maturing by the early rainy season.

In general the species may be distinguished from other *Monstera* in Panama by having adult blades that are deeply pinnatifid and lacking perforations.

Nicaraqua to Venezuela and Peru. In Panama, known from tropical moist forest in the Canal Zone and Darién, from premontane wet forest in Panamá (Cerro Azul), from tropical wet forest in Panamá, and from lower montane rain forest in Chiriquí.

See Figs. 98 and 99.

Monstera dubia (H.B.K.) Engler & Krause, Pflanzenr. IV.23B(Heft 37):117. 1908

Epiphytic vine; caudex mostly 2–2.5 cm thick, usually with many short roots, strongly tuberculate the tuberculae extending onto lower part of petiole; juvenile plants creeping over rocks or up tree trunks, the caudex flattened, to 2.5 cm diam. Petioles stiff and narrow, 20–47 cm long, often twisted at base, broadly canaliculate to near blade; blades mostly ovate-oblong, acute and often somewhat cuspidate at apex, rounded to subcordate at base, 27–83 cm long, 18–52 cm wide, often somewhat falcate and oblique, one side considerably larger, drying ± green, usually with small and large perforations, the latter often reaching margin, the leaf thus irregularly pinnatifid; major veins in 11–14 pairs, the reticulate veins prominent; juvenile leaves at first appressed to their support, ovate-cordate, oblique, shortly acuminate at apex, with basal lobes usually overlapping, 1.5–15 cm long, the petioles very short, flattened; leaves increasing in size with age, becoming more petiolate and distant from tree. Inflorescences several at apex, overtopped by leaves in fruit; peduncles 5–8 cm long, tuberculate, the spathe scar prominent; spathe coriaceous, oblong, rounded on both ends, white to pinkish at anthesis or becoming pale green, 8–12 cm long, 4–8 cm wide when open, remaining open after anthesis, ultimately deciduous, often removed by the growing spadix; spadix 7–11 cm long, 1.5–2.3 cm thick, and white in flower, to 14 cm long and 4–5 cm thick with mature fruit, rupturing to expose seeds; pistils ca 5 mm high in flower (to 1.5 cm in fruit), the sides angulate, the apex truncate, pithy, angulate, 6–7 mm diam, deciduous individually or in sheets (evidence on the ground that plant is in fruit); stigma linear. Seeds broadly oblong, ± flattened, ca 8 mm long and 5 mm wide, surrounded by a sweet, fleshy layer. *Croat 5476, 6225, 6254.*

Fig. 101. *Monstera dubia*

Fig. 102. *Monstera dubia*

Fig. 103.
Montrichardia arborescens

Juvenile plants are very common and adults common, usually tightly appressed high in trees, but occasionally loosely attached in trees at the margin of the lake. Flowering season uncertain. Since individuals continue to produce inflorescences, a plant may bear a flowering inflorescence at a time when its first inflorescences carry nearly mature fruit. Most flowering, however, appears to begin with the rainy season, and most fruits are mature between August and October. A second and apparently smaller flowering season is in the early dry season, with fruits maturing during March and April.

Distinguished from most *Monstera* in Panama by its warty stems and petioles, its short peduncles, and its short blunt spathe. *Kenoyer 183* was cited in the *Flora of Panama* as *M. deliciosa* Liebm.; the specimen is sterile but is surely *M. dubia.* This species was reported as *M. pertusa* (L.) DeVr. by Standley, but that name cannot be used, since it is a later homonym of *M. pertusa* (Roxb.) Schott, an Indian species.

Southern Costa Rica to Bolivia and western Brazil, and eastward along the Caribbean to Trinidad. In Panama, known from tropical moist forest chiefly on the Atlantic slope, but also on the Pacific slope in Chiriquí.

See Figs. 100, 101, and 102.

MONTRICHARDIA Crueger

Montrichardia arborescens (L.) Schott, Arac. Betreff. 1:4. 1854

Aquatic; caudex 1–3 m high, to 4.5 cm thick near base, mostly 1.5–2 cm thick above, all but occasionally upper internodes armed with short prickles. Petioles 20–45 cm long; sheaths extending to ca middle or beyond, the remainder of the petiole convex below, triangulate above; blades very deeply sagittate, 15–40 cm long or more, often cuspidate at apex, the basal lobes usually acuminate, spreading, often as long as or longer than upper lobe; primary lateral veins in 3 or 4 pairs above sinus, a single basal vein directed into each basal lobe and submarginal at apex of narrow sinus. Peduncles ca one-third as long as spathe or less; spathe ± oblong, 10–18 cm long, convolute basally even at anthesis, opening in upper half with a distinct constriction above spadix, the apex cuspidate (often twisted forward before anthesis), the tube green at base, the blade white (at least within) at anthesis, the entire spathe ultimately deciduous; spadix mostly 2–4 cm shorter than spathe; staminate part more than 1.5 cm wide, deciduous with spathe, the flowers with 3–6 stamens; lower pistillate part slender, to 4 cm long, usually ca 1 cm wide or less; pistils 1-celled; ovules 1 or 2; stigma sessile, orbicular. Fruit clusters usually broadly oblong, to 11 cm long and 8 cm wide; berries green except for roughened stigmatic area, irregularly developed (some aborted), subglobose and 2.5–3 cm wide when mature, irregularly dehiscent; seeds broad at apex, narrowed below, to 2.5 cm long. *Croat 4961.*

Restricted on BCI to shallow water at the edge of the lake, commonly in somewhat protected areas. Flowers and fruits throughout most of the year.

Distinguished by its aquatic habitat, armed caudices, and large fruits. Seeds float to shore and germinate.

Guatemala and Belize to the Guianas; the Antilles. In Panama, known chiefly from freshwater swamps and river banks all along the Atlantic coast and in Darién.

See Fig. 103.

PHILODENDRON Schott

The genus *Philodendron* can be recognized by an inflorescence that is usually enlarged at the base, with the spadix completely enveloped by the spathe, except for a brief period when the spathe opens to allow entrance of the beetle pollinators. The spadix has unisexual flowers, the short, basal, pistillate part and the longer, upper, staminate part. The ovary has two to several locules with numerous ovules per locule. Stamens number two to six. At maturity the spathe bursts irregularly or at least at the base and falls free to expose the large cluster of closely aggregated fruits. The tannins in the sap of this genus often cause the sap to turn reddish; this is particularly pronounced in *P. sagittifolium* and *panamense.*

Plants of the genus are of three types on BCI: (1) Scandent vines, often hemiephiphytic, especially the juvenile forms: *P. tripartitum, scandens, inconcinnum, hederaceum, guttiferum, nervosum,* and *inaequilaterum.* The internodes are elongate at maturity (when forming an inflorescence)

KEY TO THE SPECIES OF PHILODENDRON

Blades tripartite or pinnatifid:
- Blades tripartite, the center lobe symmetrical, the lateral lobes asymmetrical ..... *P. tripartitum* (Jacq.) Schott
- Blades pinnatifid, deeply divided ..... *P. radiatum* Schott

Blades entire:
- Basal lobes well developed and separated by a deep sinus:
  - Mature blades usually broadest at about middle, mostly 15–25 cm long (some to 30 cm or, if more, then pubescent on veins); mature leaves widely spaced; caudex 1–2 cm diam near ends, not appressed to its support maturity:
    - Blades ± oblong, more than 2 times longer than wide ..... *P. inconcinnum* Schott
    - Blades broadly ovate-cordate, usually less than 1.5 times longer than wide:
      - Leaf veins, petioles, and stems shortly pubescent; blades thin, the veins prominently raised on underside ..... *P. hederaceum* (Jacq.) Schott
      - Leaves, petioles, and stems glabrous; blades thick at maturity, the veins not raised on underside ..... *P. scandens* C. Koch & Sell.

Mature blades broadest below middle, usually more than 35 cm long; mature leaves clustered at ends of thick caudex 3–12 cm diam; caudex tightly appressed to its support:
Blades usually more than 80 cm long, the basal sinus often closed by overlapping lobes; petioles more than 90 cm long and 2.5 cm wide, the upper side flattened with an erect membranaceous wing 4–5 mm high on margin ..... *P. pterotum* C. Koch & Aug.
Blades usually less than 65 cm long, the basal sinus open; petioles less than 75 cm long and 2 cm wide, rounded or flat on top without membranaceous wing:
Plants terrestrial; major lateral veins in 11–17 pairs, markedly impressed above; petioles usually less than 1 cm wide, flat on upper surface; spathe to 11 cm long ..... *P. grandipes* Krause
Plants epiphytic or hemiepiphytic, usually at 2 m or more; major lateral veins in usually fewer than 10 pairs, not impressed above; petioles usually more than 1 cm wide, terete or flattened on upper surface; spathe larger, at least at anthesis:
Petioles flat to concave on upper surface; cataphylls red at maturity, persistent as brown fibers; peduncles less than 8 cm long, straight; spathe tube bright red on outside; caudex usually with a slender, ± leafless branch near apex ..... *P. fragrantissimum* (Hook.) Kunth
Petioles terete; cataphylls reddish or green, caducous; peduncles 6–23 cm long, straight or curved at apex; spathe tube green on outside; caudex lacking slender stem near apex:
Blades thin, the smaller veins readily visible (on both fresh and dry specimens), the midrib and primary lateral veins not noticeably lighter in color than rest of blade; peduncles usually more than 11 cm long (at least at anthesis), often markedly bent just below spathe and prominently white-lineate at apex of peduncle and base of spathe ..... *P. panamense* Krause
Blades thick, the smaller veins obscure, the midrib and primary lateral veins noticeably lighter in color than rest of blade; peduncles less than 11 cm long, straight, not white-lineate near apex nor on tube of spathe ..... *P. sagittifolium* Liebm.

• Basal lobes not well developed:
Blades cordate at base, broadest above middle ..... *P. inconcinnum* Schott
Blades truncate to acute at base, broadest at or below middle:
Petiole sheaths ending far below base of blade (on BCI) ..... *P. nervosum* (Schult. & Schult.) Kunth
Petiole sheaths extending to or almost to base of blade:
Leaf sheaths with margins only slightly raised, very narrowly rounded at apex, ending decidedly below base of blade; primary lateral veins much more prominent than secondary ones, the secondaries all ± distinguishable ..... *P. inaequilaterum* Liebm.
Leaf sheaths with margins prominently raised or spreading, usually broadly rounded at apex, ending very near or extending slightly beyond base of blade; primary lateral veins scarcely more prominent than secondary ones, the secondaries usually obscure ..... *P. guttiferum* Kunth

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and the degree of plant attachment varies from complete to loose, the plants sometimes hanging pendent from the trees. *Philodendron guttiferum, nervosum,* and *inaequilaterum* lack cataphylls except at the inflorescences; new leaves are protected by the vaginate sheath of the next lower petiole. (2) Epiphytic or hemiepiphytic, thick-stemmed climbers: *P. radiatum, sagittifolium, fragrantissimum, panamense,* and *pterotum.* The caudex is usually short (less than a few meters) and 4 cm or more in diameter, with adult leaves closely clustered near the apex of the caudex. (3) Terrestrial: *P. grandipes* is always terrestrial on BCI and everywhere else I have seen it, though Standley reported it as an epiphyte.

Philodendron fragrantissimum (Hook.) Kunth, Enum. Pl. 3:49. 1841

Thick-stemmed, closely appressed, epiphytic or hemiepiphytic climber at maturity, usually forming a slender, leafless, dangling stem at apex; caudex 3–6 cm diam; cataphylls 11–25 cm long, reddish at maturity, persisting among leaf bases as brown weathered fibers; cut parts with red sap (especially spathe). Adult leaves clustered near apex; petioles 32–73 cm long, flat to slightly concave on upper surface with rigid, marginal rib; blades triangular, short-acuminate at apex, cordate at base, 33–52 cm long, 26–39 cm wide, the short broad lobes forming a sinus 4–10 cm deep and widely broadened to 8–16 cm; major veins in 6–9 pairs, not very prominent, the smaller veins all distinct; juvenile leaves narrowly ovate, acute to rounded or truncate at base, sheathed half or more of their length, spaced 3 cm apart or less, becoming slightly cordate with the petioles only slightly sheathed, the internodes longer. Inflorescences several to numerous, clustered amid weathered cataphylls; peduncles short, 4–8 cm long; spathe 14–19 cm long, the blade white to greenish, abruptly long-acuminate, the tube red, to 4.5 cm broad; spadix 13–16 cm long, the pistillate part 4–5 cm long, red with white flowers, utlimately with abundant red sap when cut. Fruits broadly oblong, 7–10 mm long, truncate at apex; seeds many, narrowly oblong, ca 1.5 mm long. *Croat 9410, 11007.*

Fig. 105. *Philodendron fragrantissimum*

Fig. 104.
Philodendron fragrantissimum

Fig. 106. *Philodendron fragrantissimum*

Fig. 107. *Philodendron grandipes*

Fig. 108. *Philodendron grandipes*

Fig. 109. *Philodendron guttiferum*

Fairly common in some areas of the island, particularly the older forest. Flowers chiefly in the early rainy season (June to August), less frequently in the late dry season. The fruits develop in October or later.

This species is most easily confused with *P. sagittifolium* or *P. panamense.* It differs from both in having the petioles flattened on the upper surface, in bearing persistent cataphylls, and in forming a slender, usually unbranched stem at the apex, which usually dangles back to the ground, creeps across the forest floor, and climbs another tree. This method of vegetative reproduction appears to be absent in the other thick-stemmed, appressed species on BCI. *P. fragrantissimum* is similar also to *P. clementis* (C. Wright) Griseb. of Cuba, which may prove to be synonymous. A sterile collection from Nicaragua (*Molino 15043*) may also be this species.

Panama to Amazonian Peru, Venezuela, and the Guianas. In Panama, known from tropical moist forest in the Canal Zone and Bocas del Toro, from premontane wet forest in Colón and Panamá, and from tropical wet forest in Colón and Panamá.

See Figs. 104, 105, and 106.

Philodendron grandipes Krause, Pflanzenr. IV.23Db(Heft 60):48. 1913

Terrestrial; stems 2–3 cm thick, usually less than 1 m long, creeping along the ground, leafy the last 15–30 cm, the leaves mostly clustered toward apex; internodes very short; cataphylls 12–25 cm long, green to pinkish, 2-ribbed, persisting as brown fibers. Petioles 20–70 cm long (mostly more than 40 cm), flattened on upper side, with the lateral margins sharply raised; mature blades ovate-cordate, acute and falcate-cuspidate at apex with the tip downturned, 20–43 cm long, 13–30 cm wide, bicolorous, shiny above, the basal sinus 3–11 cm deep, broader than deep on small leaves, usually 8–11 cm deep and closed by overlapping basal lobes on larger leaves; major veins in 11–17 pairs above sinus, much impressed above, dark and prominently raised below, the smaller parallel veins distinct; juvenile blades narrowly elliptic to ovate, acute to rounded at base, soon truncate to cordate, usually less than 15 cm long. Peduncles 8–11 cm long, white-lineate; spathe green inside and out (except limb white at anthesis), enveloping spadix, 9–11 cm long, 2.5–3.8 cm wide at base, ca 1.5 cm at apex (when closed), sometimes with long-acuminate tip; spadix very short-stipitate, 7–8 cm long, the pistillate part 2 cm long, ca 1 cm wide, to ca 2 cm wide in fruit. Fruits obovoid, truncate at apex, the stigma rounded, with 3–5 minute punctations. *Croat 11886.*

Apparently rare, restricted to steep creek banks. Flowers in the early rainy season (May to August), rarely earlier or later (April to October). Most of the fruits mature from August to October.

Distinguished from other species in Panama by being terrestrial and by having the upper petiole surface flat.

Known only from Panama, from tropical moist forest on the Atlantic slope of the Canal Zone and in Bocas del Toro and San Blas, from premontane wet forest in Colón and Coclé, and from tropical wet forest in Colón, Chiriquí, and Coclé.

See Figs. 107 and 108.

Philodendron guttiferum Kunth, Enum. Pl. 3:51. 1841
P. rigidifolium Krause

Hemiepiphytic vine, frequently branched; stems gray to brown, 1 cm or less diam, only loosely attached to trees, frequently pendent. Petioles 8–18 cm long, the sheath broad, extending almost to or slightly beyond base of blade, the sides of sheath 5–10 mm high on mature leaves, one side clearly exceeding the other; leaf blades ovate to ovate-elliptic, those of climbing stems mostly 15–26 cm long and 9–15 cm wide, spaced 2–16 cm apart, those of terrestrial creeping stems smaller, mostly less than 14 cm long and 7 cm wide, the dangling stems often with leafless portions 2–4 m long, the internodes to 30 cm long; major veins of all leaves 5–8 per side, scarcely more prominent than the obscure smaller veins. Peduncles stout, 1–3 cm long; spathe green or yellow-green, red-lineolate inside base of tube, 8–26 cm long, spadix sessile, 10–23 cm long, the staminate part white, the pistillate part green, to 5.5 cm long. Fruits white, to ca 6 mm long and 3 mm wide. *Croat 10912, 11776.*

Abundant. Flowers chiefly from the late dry season to the early rainy season (February to September) but mostly during the early rainy season (June to July). The fruits apparently develop within the rainy season of the same year.

Distinguished by its scandent habit and broadly winged petiole. Cut parts are usually quite aromatic. Most easily confused with *P. inaequilaterum,* which has a similar habit but has the petioles winged nearly to the leaf base.

Southern Mexico to Panama, French Guiana, and Peru. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Bocas del Toro, and Darién, from premontane wet forest in Colón, Chiriquí, and Panamá, and from premontane rain and lower montane rain forests in Chiriquí.

See Fig. 109.

Philodendron hederaceum (Jacq.) Schott, Wiener Z. Kunst 3:780. 1829
P. jacquinii Schott; *P. erlansonii* Johnston

Hemiepiphytic vine; stems, petioles, and veins of lower leaf surface shortly setose-pubescent; internodes 6–15 cm apart and usually ca 1.5 cm diam (to 3.5 cm); periderm paper-thin, sometimes peeling from larger stems. Petioles to 40 cm long, round in cross section, those subtending the inflorescence winged-vaginate; blades ovate, acute to short-acuminate and mucronate at apex, cordate at base with narrow sinus, 14–46 cm long, 11–35 cm wide, papyraceous; veins in 4–6 pairs, prominently impressed above and raised below; juvenile leaves similar to adult, though narrower and with the petioles vaginate-winged almost half their length. Peduncles glabrous, to 14 cm long in fruit; spathe glabrous, 13–19 cm long, oblique and inflated-bulbous at base (much of the space empty

in flower), to 7 cm wide in fruit, green outside, red inside, the tube green or white inside, falling free in fruit; spadix sessile, ca 8 cm long, the staminate part to 12 cm long, the pistillate part to 3 cm long and 3.5 cm diam; styles to 5 mm long; stigmas 3. Immature fruits greenish, irregular, filling entire cavity; mature fruiting spadix naked with fruit cluster 8–9 cm long and to 5 cm wide; mature fruits pale orange, ca 1 cm long, 5 mm wide; seeds usually 4–6 per fruit, ovoid, white, ca 4 mm long, only moderately sticky. *Croat 9259.*

Apparently rare on BCI, though common elsewhere in the Canal Zone. Flowers in the middle of the rainy season (July to September). The fruits mature by early in the rainy season of the following year (May to August). Inflorescences hang on leafless caudices during most of the dry season.

Distinguished by the cordate blade, the puberulence on the leaf veins, petioles, and caudices, and by the bulbous-based spathe and long-styled ovaries. The species was for many years confused nomenclaturally with *P. scandens* C. Koch & Sell.; for a discussion of this, see papers by Dugand (1945) and Bunting (1963).

Mexico (Veracruz) to Colombia, Venezuela, and the Guianas. In Panama, known from tropical moist forest in the Canal Zone, Herrera, Panamá, and Darién, from tropical dry forest in Los Santos, from premontane moist forest in Los Santos, and from premontane wet forest in Panamá.

See Fig. 110.

Philodendron inaequilaterum Liebm., Vidensk. Meddel. 16. 1850

P. coerulescens Engler

Hemiepiphytic vine, slender, branched many times, the main axis loosely attached; branches widespread, some very long and almost leafless, usually less than 1.5 cm diam, usually green when fresh and almost the same color as petioles (drying brown, sharply contrasting with the green petioles); internodes 5–22 cm (short near ends of branches). Petioles 5–24 cm long, canaliculate, narrowly sheathed almost to base of blade, the sheath margins usually 5 mm high, held erect (those subtending the branches of inflorescences larger); blades broadly ovate or elliptic-ovate, frequently oblique, abruptly acuminate at apex, rounded or truncate at base (slightly subcordate on largest leaves), usually 15–30 cm long but to 40 cm long and 20 cm wide on climbing, appressed stems, thin, usually drying dark; major veins 9–13 per side (to 20 on largest blades), upstanding and more prominent than the minor veins, the minor veins obscure but distinguishable on fresh leaves; juvenile leaves like adults except usually narrower in relation to length. Inflorescences few; peduncles short and stout, 2–4 cm long; spathe usually whitish or green and minutely white-lineate, 12–20 cm long, cuspidate, often recurved below apex at anthesis, usually not reclosing tightly after anthesis, the slender staminate part of spadix remaining protruded; spadix with short stipe, the staminate part narrowly tapered, broadly curved forward, long-persistent after anthesis, the pistillate part 2.5–6 cm long, the fruiting spadix to 9 cm long and 2.5 cm wide. Fruits orange, angulate, to 4 mm long and 2 mm wide; seeds 6–20, usually ca 14, narrowly oblong, to 1 mm wide, immersed in a clear, sweet, watery matrix at maturity. *Croat 5831, 15570.*

Abundant in the forest, sometimes climbing to the top of the canopy; the most abundant *Philodendron* on BCI. Flowers mostly from April to May, occasionally as early as March or as late as September. The fruits mature mostly during June and July.

This species is most easily confused with *P. guttiferum,* a species of similar habit, but is distinguished by having a narrow sheath ending well below the base of the blade; *P. guttiferum* has a broad sheath ending nearly at or beyond the base of the blade. Blades of *P. inaequilaterum* may also be confused with those of *Rhodospatha wendlandii,* but they lack the prominently geniculate petioles toward the apex of the plant that are so characteristic of *R. wendlandii.*

Mexico, Panama, Colombia, Venezuela, Ecuador, and Peru, and no doubt elsewhere in Central America. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién, from premontane wet forest in Coclé and Chiriquí, and from premontane rain forest in Darién.

Philodendron inconcinnum Schott, Syn. Aroid. 81. 1856

Narrow-stemmed, hemiepiphytic vine, loosely attached at maturity; stems brown at maturity; internodes 4–15 cm long (closer at apex), about 1–2 cm thick, usually with 1–3 roots at nodes, the roots 20 cm or more long; periderm crisply and longitudinally folded when dried, often peeling off; cataphylls pale green, 6–12 cm long, with 1 or 2 faint ribs. Petioles 7–15 cm long, sheathed 1.5–2.5 cm at base (those subtending branches or inflorescences more completely sheathed); blades oblong or oblong-ovate, acute to rounded and cuspidate at apex, shallowly cordate at base, 16–30 cm long, 7–10 cm wide; the lobes rounded at base, the sinus generally shallow, square at apex; major veins in 4–6 pairs, impressed above, scarcely more prominent than smaller veins below, the secondary veins somewhat obscure; juvenile blades constricted above petiole, the basal lobes hastate. Peduncles 5–11 cm long; spathe 10–18 cm long, only slightly broader at base, green outside, the inside pale green but reddish at base of tube; spadix subsessile, only slightly shorter than spathe, the pistillate part 3–4 cm long in flower, 8 cm or more in fruit. Fruits white, to ca 6 mm long and 3.5 mm wide. *Croat 5064.*

Apparently uncommon, seen only a few times along the shore of Orchid Island. Known to flower at the beginning of the rainy season (late April to July). The fruits develop within a few months, probably mostly in July and August.

Distinguished from all other species by its small, oblong, shallowly cordate blade. The species was confused

Fig. 110. *Philodendron hederaceum*

Fig. 111. *Philodendron nervosum*

Fig. 112. *Philodendron panamense*

with *P. wendlandii* Schott by Standley and was called by that name in the *Flora of Panama.* However, *P. wendlandii* has rosulate leaves and thick stems with much larger, more or less oblanceolate-obovate leaves; it also occurs in Panama.

Costa Rica, Panama, and Venezuela. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Darién and from premontane wet forest in Colón.

Philodendron nervosum (Schult. & Schult.) Kunth, Enum. Pl. 3:51. 1841
P. karstenianum Schott

Narrow-stemmed, hemiepiphytic climber, with mature stems tightly appressed or more frequently scandent; stems green when fresh (becoming tan and longitudinally wrinkled on drying, contrasting sharply with green petioles); internodes 3–10 cm, becoming even shorter at flowering apex; cataphylls lacking except beneath inflorescences. Petioles 11–34 cm long, broadly sheathed at least half of their length, the sheath 5–10 mm high, the remainder of the petiole flattened or canaliculate on upper surface; blades mostly ovate to oblong-elliptic, frequently somewhat oblique, rounded to acute and abruptly long-acuminate at apex, broadly rounded to short-cuneate at base, 17–37(46) cm long, 8–16(22) cm wide (much smaller on trailing stems); major veins mostly in 6–11 pairs, scarcely more prominent than the smaller veins, the secondary veins obscure (at least when fresh); juvenile leaves similar to mature leaves but smaller. Inflorescences few, emerging from leaf sheaths of uppermost nodes; prophylls green, to 12 cm long, with 2 narrow, longitudinal ribs on outer surface; peduncles about 10 cm long at maturity; spathe 12–16 cm long, green, caudate-acuminate at apex, scarcely widened at base; spadix stipitate or nearly sessile, slightly shorter than spathe, the pistillate part 2.5–4 cm long, the pistils slender; stigma doughnut-shaped in fruit. Fruits white, to 7 mm long and 4 mm wide. *Croat 6500.*

Occasional, in the forest. Flowers principally in the dry season and early rainy season (February to May), but also collected in flower in the late rainy season.

Recognized by its elongate, obscurely veined leaves with petioles winged much of their length. Plants on Cerro Campana (Panamá Province) often have petioles winged all the way to the blade.

Guatemala to Venezuela, Ecuador, and Peru. In Panama, known from tropical moist forest in the Canal Zone and Bocas del Toro, from premontane wet forest in the Canal Zone, Coclé, and Panamá, and from tropical wet forest in Colón, Chiriquí, Coclé, and Panamá.

See Fig. 111.

Philodendron panamense Krause, Pflanzenr. IV.23Db(Heft 60):65. 1913

Large-stemmed, epiphytic or hemiepiphytic climber, growing at all heights; stems of medium length, 4–6 cm diam; internodes to 15 cm long, becoming much shorter near apex; cataphylls deciduous. Petioles 60–70 cm long, solid green, minutely grooved, ± terete with narrow flattened rib on upper surface, scarcely vaginate at base; mature blades broadly triangulate, short-acuminate, thin, rounded at apex, deeply cordate at base, 40–65 cm long, 30–47 cm wide, the lobes broadly rounded, the sinus 10–18 cm deep and 6–11 cm broad; major veins in 7–9 pairs above sinus, the veins into basal lobes united, the smaller veins easily distinguished; juvenile leaves at first acute to rounded at base, broadest at middle, soon becoming weakly to strongly cordate, the petioles terete, winged, broadly sheathed half to three-fourths their length. Inflorescences few, long-pedunculate, the peduncles 7–23 cm long (mostly more than 15 cm), slightly to moderately bent just below spathe; peduncle and spathe both strongly white-lineate; spathe 11–18 cm long, pale green on inside, the outside with blade whitish and tube green; spadix sessile, slightly shorter than spathe, the pistillate part to 6.5 cm long. Berries white, ca 6 mm long; seeds many, white, narrowly cylindrical, 1.3 mm long, sticky. *Croat 10264, 10867.*

Common in the forest. One of the more abundant species, growing closely appressed to trees at 2–12 m from the ground, often with several large caudices in the same tree. Flowering from late March to July. The fruits develop mostly from June to August.

Most easily confused with *P. fragrantissimum,* which has much-flattened petioles, and with *P. sagittifolium,* which has much thicker, more narrowly triangulate leaves and dark-green petioles with light-green specks.

Honduras, Costa Rica, Panama, and Ecuador, no doubt in Nicaragua as well. In Panama, known from tropical moist forest on both slopes of the Canal Zone, from premontane wet and tropical wet forests in Panamá and from lower montane wet forest in Chiriquí.

See Fig. 112.

Philodendron pterotum C. Koch & Aug., Ind. Sem. Hort. Berol. App. 6. 1854

Large-stemmed, epiphytic or hemiepiphytic climber; stems usually short, 5–12 cm diam. Leaves closely clustered near apex; petioles 90–120 cm long, rounded below, flattened above (the basal 15–20 cm vaginate), the upper margins with a narrow, erect, wavy, membranaceous wing 4–5 mm high on margin; blades ovate, short-acuminate, cordate at base, 65–130 cm long, 46–100 cm wide, the lobes sometimes overlapping, the sinus narrow and acute at apex; major veins in about 10 pairs above sinus, the veins extending into basal lobes about 7, the smaller veins obscure; juvenile stems loosely attached to tree, the internodes long, the leaves broadly ovate, glistening on upper surface, the youngest rounded at base, becoming increasingly cordate with size, the smaller veins easily distinguished, the petioles flattened, 2-edged. Inflorescences in leaf axils, 6–22 or more near apex of single stem; peduncles 6–12 cm long, white-lineate; spathe 20–25 cm long, long-acuminate at apex, the tube purple outside, red within at base, the limb green outside, white within; spadix sessile, ca 20 cm long, the pistillate part 5 cm long, to 6 cm long in fruit. Fruits obovoid, to ca 1 cm long,

with a buttonlike style bearing 5 or 6 minute depressions. *Croat 6581, 6640.*

Occasional, in the forest on trees at 2–8 m. Flowers on BCI from May to July. The fruits mature usually before the end of the rainy season in December. At Summit Garden in the Canal Zone populations begin to flower in the early dry season, continuing until the middle of the rainy season, with the fruits mostly gone by the end of the rainy season.

Distinguished by its very large leaves with a flattened petiole bearing thin marginal ribs.

Costa Rica and Panama. In Panama, known from tropical moist forest in the Canal Zone (BCI and Summit Garden) and Chiriquí and from tropical wet forest in Colón.

See Figs. 113 and 114.

Philodendron radiatum Schott, Oesterr. Bot. Wochenbl. 3:378. 1853

P. augustinum C. Koch; *P. polytomum* Schott

Thick-stemmed, epiphytic or hemiepiphytic climber; stems closely attached, 5–12 cm thick; cataphylls green to pale pink, linear-lanceolate, to ca 30 cm long, weathering and persistent; sap sticky, clear. Leaves clustered near end of stem; petioles to 1 m or more, often ± dark-speckled, the sheath usually 8–10 cm long or less; blades broadly ovate-cordate in outline, 35–80 cm long and 30–65 cm wide or larger, often ± dark-speckled along major veins, pinnately dissected once or twice nearly to midrib into 5–10 linear-lanceolate segments on each side, the segments 2–4 cm wide, acuminate, thin except for very stout midrib on lower surface, the secondary veins obscure, closely parallel, the uppermost segments undivided, the middle segments becoming pinnately lobed or lobulate, the basal segments shorter and coherent, their major veins joining to form a stout trunk vein; juvenile leaves ovate-oblong, cordate and subentire, becoming shallowly or deeply incised-lobed. Inflorescences several (usually 4 or 5 or more), closely congested in upper axils; peduncles 5–9 cm long; spathe 20–25 cm long, apiculate at apex, the tube green, the blade whitish, often with sparse dark punctations; spadix slightly shorter than spathe, the pistillate part 6–8 cm long; style round; fruiting spadices exposed by rupture of the deciduous spathes, ca 5 cm diam. Fruits whitish, many-seeded; seeds oblong, sticky. *Croat 6060, 6124, 7178.*

Abundant in the forest, usually very high in trees on stout limbs or in the crotches of branches, often nearer the ground along the shore. Seasonal behavior uncertain. Probably flowers from the middle to late rainy season, with the fruits maturing during the rainy season of the following year.

Juvenile plants are wholly epiphytic, eventually sending long roots to the ground. The roots are generally 5–20 mm thick, mostly unbranched, and densely warty throughout their length, with aborted rootlets. When the end nears the ground, it branches profusely and roots. Thus, plants become hemiepiphytic in age, though such roots probably provide only a part of the plant's nutrients.

Blades of the species are variable (Bunting, 1965), and while the type description and drawing of *P. radiatum* do not closely match most of our material, it is probable that this taxon is represented in Central America by a single, very variable species. Should separate entities be segregated, our material matches most closely *P. augustinum* C. Koch and *P. polytonum* Schott, which are clearly synonymous with each ohter.

Seeds of this species have been observed being carried by leaf-cutter ants; however, since ants rarely ascend another tree in their return to their nest, this method of dispersal is of dubious value.

Range uncertain; Mexico to Panama and no doubt in South America as well. In Panama, apparently restricted to the Atlantic slope, where it is known from tropical moist forest in the Canal Zone and Bocas del Toro and from premontane wet forest in Colón.

See Fig. 115.

Philodendron sagittifolium Liebm., Vidensk. Meddel. 17. 1850

Closely appressed, epiphytic or hemiepiphytic climber; stems 4–6 cm diam; internodes to 15 cm long, but 1–3 cm long near apex; nodes often with thick, very long, brownish roots, the roots with thin periderm, longitudinally folded on drying, often peeling off; periderm of caudex similar to that of roots but lighter in color on drying and with numerous horizontal cracks; cataphylls ca 30 cm long, dark red at maturity (sometimes green), with 2 prominent ribs on outer surface, deciduous. Petioles 30–60 cm long, round in cross section, dark green with light-green specks, with an obscure, flattened sheath about 6 cm long at base; blades narrowly triangular-ovate, short-acuminate at apex, cordate at base, about 35–65 cm long, usually narrower than 40 cm, thick, with broadly revolute margins, the basal sinus 8–13 cm long, 3–6 cm wide, obtuse to acute at apex; major veins light green on upper surface, prominent against dark-green leaf color, in 7–9 pairs above sinus, the veins into the basal lobes united, the smaller veins obscurely visible on lower surface; juvenile leaves thick, oblanceolate, acuminate at apex, acute to rounded at the narrow base, sheathed three-fourths the length of petiole, the blades becoming elliptic, then increasingly broadened and cordate to nearly hastate at base. Inflorescences few to several; peduncles 6–11 cm long; spathe 12–22 cm long, the blade reddish (at least on margin) on outside, white (at anthesis) or yellowish-green within, the tube usually greenish on outside, usually red within at base; spadix slightly shorter than spathe, the pistillate part 5–8.5 cm long, to 10.5 cm long in fruit. Fruits ca 7 mm long at maturity; stigma round, weakly raised, with 10–12 minute, round depressions around periphery; seeds numerous, narrowly ellipsoid, ca 1.5 mm long, weakly striate longitudinally when dried, with a weak constriction near one end. *Croat 5052, 6334, 10901.*

Occasional, on trees at usually less than 4 m above the ground; juvenile plants may be epiphytic on rocks. Apparently flowering later than most *Philodendron* on BCI,

Fig. 113. *Philodendron pterotum*

Fig. 114. *Philodendron pterotum*

Fig. 115. *Philodendron radiatum*

Fig. 117.
Philodendron sagittifolium

Fig. 116. *Philodendron sagittifolium*

often not until August or September. At Summit Garden in the Canal Zone plants may begin to develop inflorescences by the early dry season and flower from March through July. The fruits probably do not mature before the middle of the dry season.

Most easily distinguished by its elongate blade, which is longer in relation to its width than any other large-leaved ovate-cordate *Philodendron;* distinguished also by its large red leaf sheath and by its thick leaves with prominent whitish midrib and veins on the upper surface, and speckled, round petiole.

Mexico to Colombia, possibly throughout northern South America as well. In Panama, common all along the Atlantic slope, and known at higher elevations on the Pacific slope; collected from tropical moist forest in the Canal Zone and San Blas (Puerto Obaldia), from premontane wet forest in Panamá (Cerro Azul and Cerro Campana), and from tropical wet forest in Colón (Miguel de la Borda).

See Figs. 116 and 117.

Philodendron scandens C. Koch & Sell., Ind. Sem. Hort. Berol. App. 14. 1853

P. oxycardium Schott; *P. harlowii* Johnston

Narrow-stemmed vine, glabrous, occasionally branching, widely spreading and dangling from trees at maturity; stems green, with clusters of brown roots to 10 cm long and prominent cataphyll scars; cataphylls ca 10 cm long, pale green, caducous. Petioles 9–25 cm long or more, to 1 cm broad at base, terete, without invagination at base or invaginate to about middle; blades broadly ovate-cordate, 15–36 cm long, 10–27 cm wide, thick, the lobes directed outward or inward and overlapped, the sinus usually 3–7 cm deep, usually deeper than broad; primary veins in 4 or 5 pairs, the veins extending into the basal lobes united; juvenile plants usually hemiepiphytic and closely appressed, the blades ovate, caudate-acuminate, the upper surface dark green (sometimes reddish-green), glistening with minute, close papillations, the lower surface somewhat maroon. Peduncles 8–10 cm long; spathe green, cuspidate at apex, only slightly broader at base, 14–16 cm long, red inside especially at base of tube; spadix short-stipitate, the pistillate part ca 6 cm long; stigmas with thin margins. Fruits with numerous seeds, the seeds oblong-ellipsoid, slightly constricted at one end, ca 1 mm long. *Croat 7129, 10383.*

Common, especially along the shore, where it may festoon trees or hang long-pendent from tree branches. Probably flowers and fruits all year.

Not confused with any other species on the island. The Panamanian material of this species has been assigned to subsp. *scandens* f. *scandens* by Bunting (1968).

Throughout Mexico and Central America and much of tropical lowland South America; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién, from premontane moist forest in Panamá (Tocumen), from premontane wet forest in Coclé, and from tropical wet forest in Colón, San Blas, and Chiriquí.

See Fig. 118.

Philodendron tripartitum (Jacq.) Schott, Melet. 1:19. 1832

Branched, narrow-stemmed vine; stems brown except near apex; internodes 3–12 cm long; nodes 1–1.5 cm thick, drying with a ± loose, paper-thin periderm; cataphylls elongate-lanceolate, 18–33 cm long, greenish, thin, unribbed, caducous; sap, especially in the inflorescence, very aromatic. Petioles mostly 20–60 cm long; blades 3-parted, thin, the segments oblong-lanceolate, 15–30 cm long, to 13 cm wide, the lateral segments conspicuously oblique; veins close, subequal, ascending, even the smaller veins conspicuous; juvenile plants hemiepiphytic, the terminal lobe of blade elliptic to oblanceolate, the basal lobes small, slender and spreading, the lower blade surface green. Peduncles 3–13 cm long; spathe 14–21 cm long (only slightly broadened in lower half), the tube greenish, white on upper margins of blade and inside when open, maroon inside base in fruit; spadix sessile or borne on short stipe, the pistillate part 3–11 cm long, green at anthesis, the staminate part white. Fruits white, ca 4 mm long, irregularly angulate, 2–2.7 mm wide; seeds usually 6–8, cylindrical, ca 1.5 mm long, sticky. *Croat 10741.*

Occasional, climbing over trees. Flowers to some extent throughout the rainy season but especially during the early part (May to July); elsewhere flowers rarely in the dry season. The fruits develop chiefly in the middle to late rainy season.

Because of similar shape, juvenile leaves of this species are confused with juvenile leaves of *Syngonium erythrophyllum,* in which the underside of the blade is violet-purple and the venation is markedly different.

Mexico to Colombia, Venezuela, and Brazil; Jamaica. In Panama, known from tropical moist forest in the Canal Zone and Bocas del Toro, from premontane moist forest in Panamá, and from tropical wet forest in Coclé.

PISTIA L.

Pistia stratiotes L., Sp. Pl. 963. 1753

Water lettuce, Lechuga de agua

Floating aquatic, nearly acaulescent; caudex sometimes producing stolons with new rosettes of leaves at apex. Leaves forming dense rosette; petioles very short; blades ± obovate, rounded or emarginate at apex, cuneate at base, mostly 5–17 cm long, 2–7 cm wide, thick and spongy, pubescent on both surfaces with short, few-celled trichomes; veins in 5–15 pairs, parallel, prominent beneath. Inflorescences small and inconspicuous, subsessile, borne among leaves; spathe white, constricted at middle, the lateral margins connate to middle; spadix shorter than spathe and adnate to it for two-thirds of its length, with a single naked pistillate flower and 2–8 naked staminate flowers arranged in verticils; stamens 2, connate to form a synandrium; ovary obliquely attached to spadix, 1-celled; ovules numerous with basal placentation. Seeds cylindrical, minute. *Croat 8431.*

Occasional, at the lake margin, usually in quiet waters. Flowering period unknown.

Throughout the tropics of the world. Probably throughout Panama at lower elevations; known from tropical moist forest on both slopes in the Canal Zone and in Panamá and Darién.

RHODOSPATHA Poepp.

Anepsias, previously considered a distinct genus, is included with *Rhodospatha.* See the discussion following *Rhodospatha moritziana.*

Rhodospatha moritziana (Schott), comb. nov.
Anepsias moritzianus Schott, Gen. Aroid. pl. 73. 1858

Terrestrial; caudex thick, mostly or entirely creeping over the ground, usually less than 1 m long, to 5 cm diam below leaves, tapering to a narrow end entering the soil, secured by smaller roots along its length. Leaves closely spaced, imbricate; petioles minutely speckled with light green, on adult plants usually 30–50 cm long, vaginate-winged about three-fourths its length, one side higher, to 2.5 cm wide at base, ± nodose and geniculate just below blade; blades broadest in middle and tapering evenly to both ends, short-acuminate at apex, cuneate to obtuse at base, usually 50–76 cm long, 20–42 cm wide, glabrous or minutely papillate, dark green and glossy above, light brownish-green below, densely covered with minute reddish-brown spots, midrib sunken and light green above, raised below; major lateral veins in 24–34 pairs, somewhat impressed above, 10–25 mm apart. Inflorescences solitary in leaf axils; peduncles to 40 cm long; spathe boat-shaped, white, 15–26 cm long, with cuspidate apiculum ca 2.5 cm long, decurrent on and tightly enveloping spadix, to 12 cm broad when open, 5–6 cm deep, soon deciduous, the margins revolute; spadix uniform, salmon-pink, slightly shorter than spathe, densely many-flowered, short-stipitate, cylindrical, blunt on end, 16–20 mm wide, becoming covered with a sticky thick solution shortly after anthesis; flowers perfect, naked; stamens 4; anthers narrowly pointed; ovary ca 3 mm long, the sides angulate, 1-locular but with a partial division suggesting 2 locules, each division containing 1 placenta with numerous ovules; style as broad as ovary; stigma linear. Berries small (mature berries not seen), prismatic, truncate; seeds minute (probably less than 0.5 mm), elbow-shaped, very numerous, embedded in a sticky matrix. *Croat 11275, 12297.*

Uncommon; locally abundant, occurring on steep, moist creek banks in the vicinity of the laboratory. Flowers principally throughout the middle to late rainy season (August to November). Fruiting inflorescences have never been seen, but fruits probably develop in a short time.

Possibly confused with *R. wendlandii,* which is, however, always epiphytic as an adult. Simmonds's report (1950) of this species from Trinidad was possibly an error, because he described it as a high-climbing epiphyte, a habit I have never encountered among the exclusively terrestrial Panamanian specimens. Standley reported the species from Chiriquí (Burica Peninsula) on the basis of *Woodson & Schery 929,* but that specimen may be of another species of *Rhodospatha.*

Traditionally *Anepsias* has been separated from *Rhodospatha* by having two to six cells in the ovary, compared to two in *Rhodospatha.* The ovules of those *Rhodospatha* investigated on BCI were indeed bilocular, but all of the *Anepsias* specimens investigated were found to have an incomplete septum and thus were unilocular. Therefore, it appears likely that the divisions of the ovary are variable and cannot be used as a character of generic separation; the genus *Anepsias* is here reduced to synonymy under *Rhodospatha.*

Costa Rica to Colombia and Venezuela. In Panama, probably restricted to the Atlantic slope and known from tropical moist forest in the Canal Zone and San Blas and from tropical wet forest in Colón.

See Figs. 119 and 120.

Rhodospatha wendlandii Schott, J. Bot. 2:52. 1864
R. forgetii N. E. Brown

Epiphytic climber; caudex usually unbranched, 1–2(7) m long, to 4 cm thick, tightly appressed to its support; juvenile plants terrestrial, the stems creeping, rooting at nodes. Leaves closely spaced near apex of stem, well spaced below; petioles 25–72 cm long, canaliculate on upper surface to base of blade, vaginate-winged most of length (the wing weathering away), prominently swollen and geniculate below blade; blades oblong-lanceolate, cuspidate-acuminate at apex, usually rounded to truncate at base; midrib much raised and narrow below, the veins branching from midrib at nearly 90°, the major lateral veins 6–20 mm apart; leaves of juveniles gray-green, ovate to elliptic, acuminate, rounded to acute at base, mostly 4–10 cm long; juvenile leaves on climbing stems lanceolate-elliptic, dark green, mostly 18–35 cm long, acuminate at apex, acute to narrowly acute at base. Flowering inflorescences from upper axils; peduncles 12–23 cm long; spathe 20–44 cm long, 9–18 cm wide when expanded, white to somewhat pinkish, deciduous; spadix rose-pink, short-stipitate (the stipe to 2 cm long), slightly shorter than spathe, cylindrical, blunt at apex, ca 1.5 cm

KEY TO THE SPECIES OF RHODOSPATHA

Plants epiphytic at maturity; blades drying blackened, rounded to truncate at base, the major lateral veins often less than 10 mm apart ..... *R. wendlandii* Schott
Plants terrestrial at maturity; blades drying bronze-colored beneath (the result of numerous minute reddish-brown spots), attenuate at base, the major lateral veins usually more than 10 mm apart ..... *R. moritziana* (Schott) Croat

Fig. 118. *Philodendron scandens*

Fig. 119. *Rhodospatha moritziana*

Fig. 120. *Rhodospatha moritziana*

wide, sometimes recurved in fruit; flowers mostly perfect, naked; stamens 4, ca 3 mm long, tightly compressed in small cavity between adjoining pistils; ovary 3–4 mm long, the stigma round or ellipsoid; fruiting spadices usually moderately short, ca 3 cm wide. Berries less than 1 cm long, obovoid, prismatic and truncate, 2-celled, the septum broad; ovules numerous, elbow-shaped, sticking together in a gelantinous mass; seeds round, flattened, ca 1 mm long. *Croat 11406.*

Very common in trees, to 10 m high; even more abundant as juvenile plants, occasionally carpeting the forest floor. The adults usually lose their connection with the ground. Flowers mostly throughout the rainy season, from July to December. The fruits probably develop within about 1 month after flowering. Fruiting inflorescences are seldom seen, and mature fruiting spadices seldom last long. They are apparently removed by arboreal animals, including to some extent birds.

The species is possibly confused with *Philodendron inaequilaterum* with its large oblong leaves, but *Rhodospatha* may also be distinguished by having the uppermost petioles very strongly geniculate, with the blade hanging downward. Reported by Standley in the *Flora of Panama* as *R. forgetii* N. E. Brown, but the Panamanian material matches very well the type of *R. wendlandii.* The inflorescence on the type specimen is smaller than those in Panama, but size is quite variable even in central Panama, where the spathe varies from 20 to 40 cm in length. It is also likely that *R. costaricensis* Engler & Krause, *R. nervosa* Lundell, and *R. roseospadix* Mat. are synonymous with *R. wendlandii.*

It is uncertain how the plants prevent predation on the fruit, since the fruits are much like those of *Philodendron* at maturity but do not have the benefit of the protective spathe before maturity.

Costa Rica and Panama, probably also along all of the lowland Atlantic slope of Mexico and Central America to Colombia. In Panama, known from tropical moist forest on the Atlantic slope in the Canal Zone, from premontane wet forest in Coclé, and from tropical wet forest in Coclé and Darién.

See Fig. 121.

SPATHIPHYLLUM Schott

The genus *Spathiphyllum* is distinguished by its terrestrial habit, its uniform inflorescence of bisexual flowers, and its persistent spathe. Flowers are bisexual with three (rarely two or four) tepals and stamens equal in number to the tepals.

KEY TO THE SPECIES OF SPATHIPHYLLUM

Plants usually growing in water at the lake margin; spathe white at anthesis; leaf blade and spathe usually acute to narrowly acute at base; pistils with 5–8 ovules per locule ..... *S. friedrichsthalii* Schott

Plants growing in moist areas in the forest; spathe usually green at anthesis; leaf blade and spathe usually obtuse to rounded at base (acute on smaller plants); pistils with 1 or 2 ovules per locule ..... *S. phryniifolium* Schott

Spathiphyllum friedrichsthalii Schott, Aroid. 2, pl. 4. 1853

Acaulescent plants, robust, often more than 1 m tall, usually growing in large clones in shallow water. Petioles 30–60 cm long, sheathed to about middle or more, otherwise terete, weakly geniculate at apex; blades narrowly elliptic, narrowed to both ends, gradually long-acuminate to abruptly short-acuminate, attenuate to acute and somewhat decurrent at base, 28–70 cm long, 7–22 cm wide; primary lateral veins many, the smaller veins ± distinct. Inflorescences about as high as leaves; spathe boat-shaped, ± elliptic, oblique, cuspidate and somewhat asymmetrical at apex, long-decurrent at base, (10)13–32 cm long, (4)5–11 cm wide, white in flower except for green midrib, green in fruit; spadix cylindrical, blunt, sessile or short-stipitate, white, 3–7 cm long, less than 2 cm wide in flower; tepals ca 2.3 mm long and 1.7 mm wide; pistils 3-locular, greatly exceeding perianth, to 6 mm long in flower, to more than 1 cm long in fruit, the apex green; ovules (3)5–8 per locule; fruiting spadices green, somewhat longer but chiefly broader, to 3 cm wide (including protruding styles). Fruits obovoid; seeds usually 2–11 per fruit, warty and very irregular, brown at maturity, to 4 mm long. *Croat 11766, 11802.*

Locally common in secluded coves in shallow water. Flowering plants may be seen throughout most of the year, especially during the rainy season.

Distinguished from *S. phryniifolium* by its aquatic habit and white spathe. The species is exceedingly variable in the size of parts, possibly reflecting the age of the clone. It is confused with *S. blandum* Schott in parts of Central America.

The sweet aroma of the flowers is very characteristic and can be detected from a considerable distance. In flower the inflorescences are often visited by *Trigona* bees.

Nicaragua to Colombia on the Atlantic slope and along the Pacific slope from lower Panama to southern Colombia. In Panama, known from tropical moist forest on both slopes of the Canal Zone and in Bocas del Toro, Colón, and Darién, from premontane wet forest in Colón, Chiriquí, and Coclé, from tropical wet forest in Bocas del Toro, Colón, and Darién, and from lower montane wet forest in Chiriquí.

See Fig. 122.

Spathiphyllum phryniifolium Schott, Oesterr. Bot. Wochenbl. 7:59. 1857

S. zetekianum Standl.

Acaulescent herb, quite variable, to more than 1 m tall. Petioles 9–100 cm long, the sheath to middle or, less

Fig. 121. *Rhodospatha wendlandii*

Fig. 122. *Spathiphyllum friedrichsthalii*

Fig. 123. *Spathiphyllum phryniifolium*

frequently, to just beneath geniculum; blades lanceolate to oblong-elliptic, gradually to abruptly acuminate, obtuse to subtruncate or acute on smaller plants at base, 12–60 cm long, 4–22 cm wide; veins many and close together, the major ones impressed above, raised below. Inflorescences held well above leaves; spathe boat-shaped, about shape of leaf blades, attenuate at apex, oblique and rounded to acute at base, green at anthesis, 7–26(33) cm long; spadix cylindrical, white at anthesis, 2–8 cm long, 8–15 mm wide, to 13 cm long and 15 mm wide in fruit, borne on stipe ca 1 cm long; perianth segments truncate, their outer margins thin; pistil (2)3-locular; style conic, greatly exceeding perianth, persisting in fruit; ovules 1 or 2 per locule. Fruits obovoid; seeds usually irregular, smooth or foveolate. *Croat 10930, 17050.*

Occasional, in the forest along trails or streams. Flowers mostly from the middle of the dry season to the middle of the rainy season (March to September), especially in the early rainy season. The fruits develop mostly within 2 months and mature chiefly in the rainy season.

The species has been confused with *S. floribundum* N. E. Brown and *S. patinii* (Hogg) N. E. Brown, both Colombian species; *S. patinii* is known only from cultivation. Further work needs to be done on the species throughout the range. Bunting (1960) wrote that plants from the Perlas Islands (Panamá Province) and Guanacaste most clearly match the type.

Costa Rica (Guanacaste) and Panama. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Veraguas, Los Santos, and Panamá, from premontane wet forest in Coclé and Panamá, from tropical wet forest in Colón, and from lower montane rain forest in Chiriquí.

See Fig. 123.

STENOSPERMATION Schott

Stenospermation angustifolium Hemsl., Biol. Centr.-Amer. Bot. 3:425. 1885

Epiphytic vine; stems 4–8 mm diam, weakly rooting at lower nodes; internodes mostly 1–5 cm long. Petioles 1.5–8.5 cm long, the sheath thick, extending almost to blade, the upper edge free; blades lanceolate to narrowly elliptic, sharply acuminate, cuneate to rounded and often unequal at base, 4–18 cm long, 1–7 cm wide, entire, the lower leaves deciduous; midrib distinguishable almost to apex, all lateral veins equally indistinct, ± parallel to midrib. Peduncles 6–8 cm long, frequently recurved near apex before anthesis; spathe acuminate, 4–6 cm long, soon deciduous; spadix 2–4 cm long in flower, ca 4 mm diam, the stipe obsolete or to 3.3 mm long; flowers bisexual, naked; stamens 4; pistils ca 4 mm diam, 2-locular; style raised, cylindrical; fruiting spadices white, fleshy. Seeds obovate, to 1.8 mm long, tan, with many vertical greenish lines, constricted slightly below base. *Croat 14038.*

Occasional, growing high in trees. Flowers and fruits throughout the year, perhaps chiefly in the dry season.

Seeds are probably dispersed by birds.

Costa Rica and Panama. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, and Veraguas, from premontane wet forest in Colón, Coclé, and Panamá, from tropical wet forest in Chiriquí, and from premontane rain forest in Panamá.

SYNGONIUM Schott

The genus *Syngonium* is distinguished by its epiphytic habit, syncarpous fruits, and unisexual flowers borne on separate parts of the spadix and separated by sterile staminate flowers. Its leaves have two or three collecting veins, and tertiary veins regularly interconnect the major laterals. The genus is closest to *Xanthosoma.*

Syngonium sp.

Herbaceous vine, probably becoming hemiepiphytic in its natural habitat; stems slender, densely short-puberulent, the caudices puberulent, the underside of leaf veins and the petioles papillate-puberulent, the plant otherwise glabrous. Petioles to 17 cm long, sheathed one-fourth to one-half their length, the lower side ribbed, the ribs close together, weakly raised, papillate-puberulent; blades thin, tripartite, the lobes distinct, the terminal lobe ± elliptic, acuminate on both ends, to 17 cm long and 5.5 cm wide, the lateral lobes distinctly inequilateral, the outer half rounded to cordate, the inner edge diminishing before base, the slender base to ca 1 cm long; reticulate veins distinct, at least below, the midrib green or slightly achlorophyllous; juvenile blades ovate to ovate-elliptic, acuminate, cordate or hastate at base, solid green or ± achlorophyllous along midrib. Fertile parts unknown. *Croat 17016.*

Cultivated in the Laboratory Clearing.

KEY TO THE SPECIES OF SYNGONIUM

Petiole and veins of lower blade surface papillate-puberulent; plants cultivated in the Laboratory Clearing ..... *S.* sp.

Petiole and blades glabrous; plants occurring in the forest or at the lake margin:

Adult leaf blades 5-lobed or 3-lobed with conspicuous auricles, thus appearing 5-lobed; juvenile blades with terminal and basal lobes narrowly acuminate, never violet-purple beneath .... *S. podophyllum* Schott

Adult leaf blades 3-lobed; juvenile blades acute or very narrowly rounded and apiculate at apex, the basal lobes usually very blunt, violet-purple beneath when young .... *S. erythrophyllum* Bunt.

The species is similar to *S. mauroanum* Birds. ex Bunt. of northwestern Panama, but can be distinguished by the puberulent caudices and the papillate-puberulent petioles and underside of veins.

The BCI plants perhaps represent a new species, but since they are never fertile it is not possible to provide the species with a name. The plants may be some aberrant cultivar. No similar plants have been found elsewhere in Panama.

Syngonium erythrophyllum Birds. ex Bunt., Baileya 14:17. 1966

Hemiepiphytic vine; caudex usually less than 1 cm diam, covered with thin, minutely papillate, flaky periderm, branched, usually well attached high on tree trunks; sap milky; juvenile plants at first terrestrial, frequently as single plants, some branching with slender, leafy, somewhat scandent shoots, later climbing trees. Petioles 11–20 cm long, vaginate-winged to near apex; blades deeply tripartite, dark green above, paler beneath, acuminate to rounded at apex, ending abruptly with minute apiculum, to 21 cm long and 8.5 cm wide, the lobes distinct, the median lobe elliptic to lanceolate-elliptic, the lateral lobes asymmetrical, lanceolate-oblong, to 16 cm long and 6 cm wide, blunt at apex, oblique at base, cuneate on upper side, the lower side broader and rounded or subcordate; major lateral veins usually in 3 pairs, the smaller veins distinct below; juvenile blades simple, lanceolate-ovate and cordate, the lobes rounded and short, the apex acute to rounded, the blades 3–9 cm long, blackish-green above, at first green below, soon becoming violet-purple, the major lateral veins mostly near base, the intercostals weaker, anastomosing; juvenile blades on climbing stems larger, entire, hastate to trilobate, dark green above, deep violet-purple beneath, 9–17 cm long, becoming indistinctly 3-lobed. Inflorescences axillary, commonly 2 or 3; peduncles 4–11 cm long, recurved in fruit; spathe as long as or longer than spadix, the tube green, 4–6 cm long, the blade white, 6–11 cm long, ca 5.5 cm wide, turning brown, withering or deciduous; spadix to 9.5 cm long, the fertile staminate part 6–7 cm long, the pistillate part 1.7 cm long; pollen white, in arachnoid clusters. Fruits ovoid, usually ca 3.5 cm long, soft at maturity, the fruiting blade of the spathe opening when fruit matures; seeds white, ± oblong, rounded on one side, apiculate and angled on the other, 6–7 mm long. *Croat 6253, 14955.*

Juvenile plants are very abundant in the forest, both creeping on the ground and climbing on trees; adults, not commonly seen, are usually high in trees in the forest and occasionally along the shore. Appears to flower in the dry season and the early rainy season (March to July). The fruits mature in the rainy season (mostly May to September).

Leaf coloration of juvenile plants distinguishes the species from juveniles of *S. podophyllum.* Though resembling juvenile leaves of *Syngonium* in shape and habit, those of *Philodendron tripartitum* can be distinguished by having many, closely spaced, parallel veins; the smaller veins of *Syngonium* are always reticulate.

Known only from Panama in tropical moist forest on BCI and in Chiriquí and from premontane wet forest in Chiriquí and Panamá.

Syngonium podophyllum Schott, Bot. Zeitung (Berlin) 9:85. 1851

Hemiepiphytic climbing vine; caudex ca 1 cm diam, branching; adult plants with milky sap; juvenile plants at first terrestrial as single individuals or more often with trailing stems, rooting at nodes. Petioles to 50 cm long, sheathed one-half to two-thirds their length (the sheath free above), rounded above sheath; blades usually 3-lobed, dark green above, pale below, 12–27 cm long, the lobes connected or free, the lowermost variously auriculate below, the blades sometimes becoming 5-lobed, the ear free, the middle segment of blade ± ovate to elliptic, to 32 cm long and 16 cm wide; major lateral veins in 3–5 pairs, impressed above, raised below, the collecting veins 2 or 3, irregular, the smaller veins all distinct; juvenile leaves simple, cordate, 7–14 cm long, becoming sagittate, acuminate, the terminal lobe somewhat constricted and with margin broadly undulate at base, the basal lobes usually ± triangulate, acuminate, directed toward stem or prominently outward. Inflorescences axillary, mostly 4–9 per axil; peduncles usually less than 9 cm long at anthesis (to 13 cm) and usually ± twisted and pendent in fruit; spathe 9–11 cm long, the blade 6–7 cm long, ca 5 cm wide and white when open, soon deciduous; spadix short-stipitate, ca 8 cm long, the staminate part 4.5–6 cm long; stigmas sessile, white, raised and rounded in flower, flattened and brown in fruit, the tube eventually turning yellow to yellow-orange at maturity and opening to expose the brown compound fruit. Fruits ovoid, ca 4 cm long, 2.5 cm wide, the outer surface scurfy; seeds numerous, ovoid, 7–8 mm long, 5–6 mm wide, brown, enveloped in a grayish tissue, embedded in a sweet, soft, white pulp. *Croat 16218.*

Abundant in the forest, commonly rather high in trees. The species may be seen in flower from November to August and perhaps all year, but chiefly throughout the dry season. Individuals flower over a long period, with inflorescences appearing sequentially, and thus bear fruits in successive stages. The fruits mature mostly in the rainy season, beginning to mature shortly after the season starts.

Range is uncertain, but probably throughout Central America. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, Veraguas, Panamá, and Darién, and from tropical wet forest in Bocas del Toro and Panamá.

See Figs. 124 and 125.

XANTHOSOMA Schott

The genus *Xanthosoma* is distinguished by its terrestrial habit and unisexual flowers borne on separate parts of the spadix and separated by sterile staminate flowers. It is in many respects like the epiphytic genus *Syngonium,* but lacks the syncarpous fruit and milky sap (may have milky sap elsewhere). The flowers are naked, with four to

KEY TO THE SPECIES OF XANTHOSOMA

Leaf blades deeply pedately lobed ..... *X. helleborifolium* (Jacq.) Schott
Leaf blades entire:
  Underside of blades glabrous, usually pruinose ..... *X. nigrum* (Vell.) Stellf.
  Underside of blades conspicuously pubescent and not pruinose ..... *X. pilosum* C. Koch & Aug.

six stamens; the ovaries have two to four locules, and each locule has few to many ovules.

Xanthosoma helleborifolium (Jacq.) Schott, Oesterr. Bot. Z. 15:33. 1865

Terrestrial, occasionally more than 1 m tall, glabrous; caudex tuberous, the leaves and peduncles arising from the ground. Petioles thick and succulent, the lower part broadly vaginate-winged; petioles and parts of leaf rachis with characteristic textured pattern of maroon and white but predominantly maroon; blades reniform in outline, deeply dissected, the central lobe to 30 cm long and 7 cm wide; rachis branching, curving to both sides; leaflets 5–18, thin, sessile and diminishing markedly in size toward either end, oblong or lanceolate, acuminate, cuneate at base; veins prominent, the collecting vein within 5 mm of margin. Peduncles 40 cm long or more, textured like petiole and rachis; spathe to 19 cm long, enveloping spadix, the blade white or greenish at anthesis, soon withering, the tube green, persisting, broad in fruit; spadix white, to 17 cm long, with a broad short stipe, the staminate part ca 10 cm long, the sterile staminate part constricted apically, much broadened basally, the pistillate part ca 2.5 cm long. Fruits not seen. *Croat 10892, 11483.*

A common species of clearings and very open trails in the forest. The plant dies back after the beginning of the dry season and reappears shortly after the rains begin, flowering mostly from May to September, with inflorescences repeatedly produced. The fruits develop within about 1 month.

El Salvador to the Guianas and Amazonian Peru; the Antilles. In Panama, known from tropical moist forest in the Canal Zone and in San Blas and Panamá and from premontane wet forest in Coclé (El Valle).

See Fig. 126.

Xanthosoma nigrum (Vell.) Stellf., Tribuna Farm. 12:20. 1944

X. violaceum Schott

Acaulescent, plant robust, glabrous, with large tuberous rhizome, often more than 1 m tall. Petioles 30–85 cm long, fleshy, rounded except for vaginate basal part; blades sagittate-ovate, short-acuminate at apex, 20–70 cm long, 15–45 cm wide, pruinose beneath at least when young, the basal lobes ± triangular, obtuse, directed outward, to 36 cm long, the sinus open, acute; costae 3; midrib plus large veins extending almost to tip of either lobe, the major lateral veins in ca 6 pairs above sinus, all veins merging with a prominent collecting vein near the margin. Peduncles to 30 cm long; spathe to 21 cm long, green on basal bulbous part, white apically, to 8 cm broad when open; spadix to 17 cm long, emitting sweet odor when open, the fertile staminate part white, 10 cm long, the sterile staminate part bulbous at base, 4.5 cm long, the pistillate part yellowish, to 2.5 cm long. Fruits not seen.

The species has never been collected on the island, but has been seen cultivated near the dock in the Laboratory Clearing. Flowering and fruiting during much of the rainy season in the Canal Zone.

A native of unknown parts of tropical America; cultivated and naturalized throughout much of tropical America, Africa, and Asia. In Panama, known from tropical moist forest in the Canal Zone and Panamá and from tropical dry forest in Panamá (Taboga Island).

Xanthosoma pilosum C. Koch & Aug., Ind. Sem. Hort. Berol. App. 2. 1855

Primrose malanga, Badu, Coro, Otó

Essentially acaulescent plant, most parts densely short-villous (upper leaf surface only moderately so); roots shallow, with many fine smaller roots, to 3 cm broad; cataphylls to about 20 cm long, prominently 2-ribbed. Petioles fleshy, 15–40 cm long, vaginate-winged to near middle or beyond, then terete; blades mostly cordate-ovate, cuspidate-acuminate at apex, thin, sometimes mottled with white spots, the basal sinus open to closed with the basal lobes often overlapping, the medial vein of lobes marginal at apex of sinus; major veins impressed above, 4 or 5 pairs above sinus, the collecting vein prominent. Peduncles usually shorter than leaves, to 33 cm long; spathe to 17 cm long, the tube green, the blade white, ca 10 cm long, to 4.5 cm wide when open, usually purplish within near mouth of tube; spadix 13 cm long, the fertile staminate part 5–7 cm long, the sterile staminate part purple-violet, the pistillate part ca 3 cm long; fruiting inflorescences nearly globular. Fruits ± obovoid, to ca 7 mm diam, whitish, the blade opening or weathering away by the time the fruits mature; seeds many, irregular, ± elliptic, white, ca 1 mm long. *Croat 11256.*

Apparently restricted to open areas in the vicinity of the laboratory, often locally abundant. Plants usually disappear during the dry season and reappear with the onset of the rains. Flowers chiefly from May to October, the fruits developing within about 1 month.

Standley reported both *X. pilosum* and *X. mexicanum* Liebm. in the *Flora of Panama.* Engler reported *X. mexicanum* only from Mexico and *X. pilosum* from Panama and Costa Rica. In my opinion Panamanian material is not separable into two species and the two will prove, in all probability, to be synonymous. If so, the name *X. mexicanum* would have precedence.

Costa Rica to Colombia. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone,

Fig. 124. *Syngonium podophyllum*

Fig. 125. *Syngonium podophyllum*

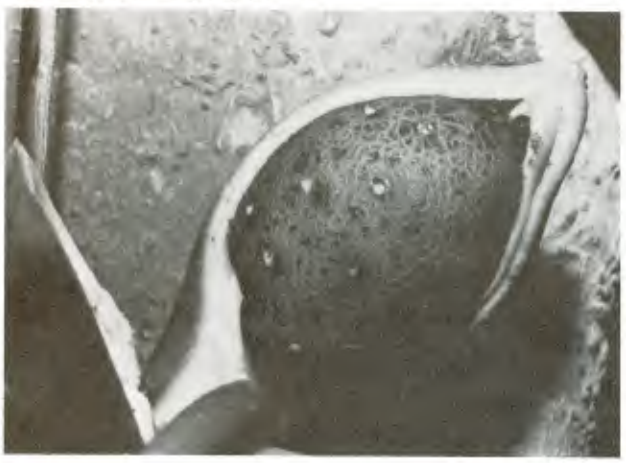

Fig. 126. *Xanthosoma helleborifolium*

Fig. 127. *Xanthosoma pilosum*

Chiriquí, Veraguas, Panamá, and Darién, from tropical dry forest in Panamá, from premontane moist forest in Los Santos and Panamá, from premontane wet forest in Chiriquí, Coclé, and Panamá, and from premontane rain forest in Darién.

See Fig. 127.

22. BROMELIACEAE

Epiphytic or rarely terrestrial (*Aechmea, Ananas*) herbs. Leaves spirally arranged in a basal rosette, often forming a watertight tank; blades acicular to ligulate, simple, entire or spiny-serrate, lacking hairlike trichomes but often with peltate scales; venation parallel; stipules lacking. Flowers bisexual or functionally unisexual (dioecious), actinomorphic, in terminal, usually conspicuously bracteate panicles, racemes, or spikes; sepals 3, free or connate; petals 3, free or connate, showy; stamens 6, free or connate, epipetalous or not; anthers 2-celled, versatile, dehiscing introrsely by vertical slits; ovary superior (partly superior in *Pitcairnia*) or inferior, 3-locular, 3-carpellate; placentation axile; ovules numerous, anatropous; style 1; stigmas 3. Fruits berries (*Aechmea, Ananas*) or capsules; seeds naked, winged or plumose, with mealy endosperm.

Bromeliaceae are not confused with members of any other family and may be recognized by their rosulate, acicular or sword-shaped leaves and usually colorfully bracteated inflorescences.

The flowers are usually colorful and often produce copious nectar. Nectaries are usually well protected by floral bracts, and the plants require specialized pollinators with adaptations for reaching the nectar. Though flowers may be green, yellow, white, or blue, the floral and scape bracts of the larger-flowered species are usually red and attract hummingbirds. Some, especially *Vriesia,* which has a more open throat, may also be visited by long-tongued bees.

Diaspore strategy has diverged in two directions in the family, those with superior ovaries having capsular fruits with plumose, wind-dispersed seeds, and those with inferior ovaries having fleshy fruits dispersed by animals, chiefly birds. Among the latter, *Aechmea magdalenae* is eaten by coatis (Kaufmann, 1962), and *A. tillandsioides,* often associated with ant nests, is partly dispersed by ants, I believe.

About 45 genera and over 1,000 species; almost exclusively in the tropics and subtropics of the New World.

AECHMEA R. & P.

Aechmea magdalenae (André) André ex Baker, Handb. Bromel. 65. 1889

Pita, Pingwing

Terrestrial. Leaves in a somewhat spreading rosette, sessile or from a short, stout trunk, linear, acuminate, to 2.5 m long and 5–10 cm wide, pale-lepidote between veins below, the midrib broadly sunken, the margins

KEY TO THE TAXA OF BROMELIACEAE

Plants terrestrial:
- Plants cultivated, seldom more than 1 m tall; fruits usually more than 15 cm long ..... *Ananas comosus* (L.) Merr.
- Plants native, most more than 1.5 m tall; fruits 5–6 cm long .... *Aechmea magdalenae* (André) Baker

Plants epiphytic:
- Blades at least in part with margins toothed:
  - Blades dimorphic, the outer ones reduced to spinose-serrate, brownish spines, the largest blades less than 1.5 cm wide; ovaries superior or only partly inferior; flowering plants less than 25 cm tall ..... *Pitcairnia heterophylla* (Lindl.) Beer
  - Blades all ± alike, the largest more than 2 cm wide; ovaries inferior:
    - Leaves blotched with silver, usually less than 3 cm wide, often very long and pendent; inflorescence simple, pendulous; scape bracts not red ..... *Billbergia macrolepis* L. B. Smith
    - Leaves solid green, often more than 3 cm wide, usually erect (occasionally pendent in *A. tillandsioides*); inflorescence branched, often erect; scape bracts red ..... *Aechmea* (in part)
- Blades with margins entire:
  - Leaves broad below but quickly tapered to a very long, narrow tip; most of blade very narrow, less than 1 cm wide throughout much of its length; petals lacking scales within ..... *Tillandsia*
  - Leaves with apex blunt or abruptly acuminate; most of blade not very narrow in relation to base; petals each bearing 2 scales on inner surface:
    - Leaves usually less than 20 cm long; scape and floral bracts less than 1 cm long, shorter than sepals; scape bracts shorter than internodes ..... *Catopsis sessiliflora* (R. & P.) Mez
    - Leaves usually more than 20 cm long; scape and floral bracts usually much more than 1 cm long, longer than sepals; scape bracts usually longer than internodes:
      - Flowers polystichous, the flowers and bracts arranged in a whorl or spiral, not in 1 or 2 planes ..... *Guzmania*
      - Flowers distichous or secund, the bracts and flowers arranged along either 1 or 2 sides of scape, not in spirals or whorls ..... *Vriesia*

Fig. 128. *Aechmea magdalenae*

Fig. 129. *Aechmea pubescens*

KEY TO THE SPECIES OF AECHMEA

Plants terrestrial ..... *A. magdalenae* (André) Baker
Plants epiphytic:
  Scape bracts below inflorescence entire; leaves dull (especially beneath), their appressed scales conspicuous ..... *A. pubescens* Baker
  Scape bracts below inflorescence prominently toothed; leaves ± shiny, their appressed scales inconspicuous:
    Branches of inflorescence bearing dark, needlelike spines; floral bracts forming tubular sheaths around flowers ..... *A. setigera* Schult.
    Branches of inflorescence lacking spines; floral bracts boat-shaped, merely subtending flower ..... *A. tillandsioides* (Mart.) Baker var. *kienastii* (Mez) L. B. Smith

sparsely armed with stout, uncinate spines, the spines near the apex antrorse, those toward middle and base retrorse. Inflorescences simple or compound, on stout terete stalk to ca 4 cm diam, if compound, the heads closely clustered, subequal; heads sessile, hemispherical or globose, rarely more elongate, 10–15 cm diam; floral bracts red, recurved, spinose-serrate, to 6.5 cm long, cinerous-lepidote beneath; flowers sessile, yellow, to 5 cm long, few exserted at a time; calyx lobes sharply pointed, persisting in fruit; petals acute, to 4 cm long, bearing 2 minute truncate scales well above base; ovary inferior. Berries elliptic to ovate, 5–6 cm long, to ca 2 cm diam, fleshy, irregular, angulate, yellow, becoming orange and soft at maturity; mesocarp orange, fibrous, sweet and very tasty; seeds 6–12 or more, very irregular, ca 6 mm long, dark brown, shiny, weakly striate. *Croat 6473, 11341.*

Abundant throughout the forest, often forming dense stands, as along Zetek Trail near 1300. Probably the most objectionable plant on the island because of its fierce spines. Apparently flowering and fruiting chiefly in the rainy season.

Fruits are both colorful and very tasty and are frequently torn open, apparently by coatis or other animals.

Mexico to Ecuador. In Panama, apparently restricted to tropical moist forest on the Atlantic slope and in Darién.

See Fig. 128.

Aechmea pubescens Baker, J. Bot. 17:135. 1879

Epiphyte, to about 1 m tall (usually less than 60 cm tall). Leaves forming a rosette, ligulate, strongly narrowed below middle, acuminate or acute at apex, moderately lepidote to glabrous above, dull and densely lepidote below, to 1.2 m long and 2–4 cm wide, drying moderately thin except for somewhat thickened midrib, the margins prominently armed with straight to recurved spines, the basal sheath unarmed, often purplish at least within. Scapes ± equaling leaves, white-lanate, soon glabrous; scape bracts acuminate, well spaced, bright red, those subtending the branches of the inflorescence spreading; inflorescence usually bipinnate (the lower branches sometimes divided), 10–40 cm long (usually short on BCI), most parts at least at first white-woolly-pubescent; spikes narrow, 8- to 16-flowered; floral bracts ovate, acuminate, 10–13 mm long; flowers sessile; sepals asymmetrical; petals obtuse, ca 1 cm long; ovary inferior. Berries ca 1 cm long and 6 mm wide, fleshy, dark bluish-green, contrasting sharply with the lighter green floral bracts; seeds many, narrowly oblong, to 3.5 mm long, white, immersed in a sweet, white, watery matrix, the funiculus slender, sticky. *Croat 5826, 10905.*

Occasional, in the forest, much less abundant than *A. tillandsioides* and preferring lower areas out of full sunlight. Flowers principally from January to March. The fruits mature mostly from May to July.

Honduras to Colombia. In Panama, known chiefly from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Panamá, and Darién; known also from tropical wet forest in Colón and Coclé and from premontane moist forest in Panamá (Juan Diaz).

See Fig. 129.

Aechmea setigera Mart. ex Schult. in R. & S., Syst. Veg. 7(2):1273. 1830

Epiphyte, usually to 1.5 m tall. Leaves ligulate, acute to rounded with a triangular apiculum, to 1 m long, 3.5–7 cm wide, glabrous above, densely lepidote below, the margins with black spines to 1 cm long, the spines antrorse at apex of blade, otherwise spreading, the sheath of blade suborbicular, to 10 cm long, brown at base. Scapes usually arched in flower; scape bracts linear-lanceolate, acuminate, to 20 cm long, bright red; inflorescences densely flowered, bipinnate, cylindrical, often more than 1 m long, the spikes with 2–4 fertile flowers, the uppermost reduced; floral bracts forming a tubular sheath around calyx, the outermost bracts with a slender dark spine at apex to 2.5 cm long; sepals coriaceous, tapered to apex, ca 2 cm long, tightly enveloping lower part of corolla, persistent in fruit; petals pale yellow or greenish-yellow, to 3.5 cm long, spreading above the sepals, each subtended within by 2 fimbriate scales; stamens exserted; style with 3 branches; stigmas oblique, twisted together in bud, their margins and apex pubescent; ovary inferior; nectar copious, accumulating in flower tube. Berries fleshy, 8-seeded; seeds narrowly ovoid, ca 5 mm long and 2 mm wide, reddish. *Croat 8033.*

Occasional, in the forest, usually high in trees. Flowers from February to May. The fruits mature in the rainy season.

A variety of creatures, including ants, lives at the base

Fig. 130. *Aechmea setigera*

Fig. 131. *Aechmea tillandsioides* var. *kienastii*

of the leaves. The fruits are no doubt chiefly dispersed by birds though they are apparently neither colorful nor very well exposed at maturity.

Panama, Colombia, the Guianas, and Amazonian Brazil. In Panama, known from tropical moist forest in the Canal Zone, Colón, Panamá, and Darién, most abundantly in wettest areas such as the Atlantic coast.

See Fig. 130.

Aechmea tillandsioides (Mart.) Baker var. **kienastii** (E. Morr. ex Mez) L. B. Smith, Caldasia 1(5):5. 1942

Epiphyte. Leaf blades linear, sharply tapered and acuminate at apex, 50–120 cm long, slightly to greatly exceeding inflorescence, 1–7 cm wide, minutely appressed-lepidote, the margins with dark spinelike teeth to 4 mm long, those near apex antrorse, those near base retrorse. Scapes slender or to ca 1 cm thick, white-woolly-pubescent at first; scape bracts widely spaced, lanceolate, 3–10 cm long, bright red, sharply toothed like the leaves; inflorescences digitately or pinnately compound to simple, densely white-woolly when young; primary bracts like scape bracts, suberect, longer or shorter than spikes; spikes spreading to erect, oblong, to 12 cm long and 2 cm wide, distichously 6–30-flowered; rachis square, the wings angled, adnate to base of floral bracts; floral bracts red, imbricate at anthesis, spreading and persistent in fruit, broadly elliptic, acute, mucronulate, 7–15 mm long; sepals asymmetrical, elliptic, mucronulate, 7–10 mm long, ± free; petals acute, mucronulate, 13–16 mm long, bearing 2 fimbriate scales; ovary inferior. Berries oblong-ovoid with a prominent beak, to 2.5 cm long, at first red at apex, white at base, becoming blue overall, the exocarp thin; seeds ca 20–40, ± oblong, to 3.4 mm long, brown, minutely longitudinally striate, surrounded by a sweet watery matrix, each seed bearing a slender, sticky, mucilaginous appendage on one end to 1 cm long. *Croat 6655, 8267, 13806.*

Common in the tops of trees in the full sunlight; less common on exposed branches over the edge of the lake. Inflorescences usually begin to open in the early dry season, but individual plants may flower over a long period, perhaps for the full flowering season. Flowering from at least January to August. Mature fruits have been seen from May to December.

Fruits are no doubt chiefly dispersed by birds. The seeds ooze from the base when the fruit is pressed in the midsection, in the manner of *Anthurium* (21. Araceae). Part of the seeds may stick to the bird's beak, owing to the slender mucilaginous funicles.

The species *A. tillandsioides* ranges from Mexico throughout Central America and much of South America. The variety *kienastii* is known from Mexico, Central America, Colombia, and the Amazon basin. The typical variety is in Colombia, the Amazon basin, and the Guianas. In Panama, apparently restricted to the Atlantic slope; known from tropical moist forest in the Canal Zone and Bocas del Toro and from tropical moist forest, premontane wet forest, and tropical wet forest in Colón.

See Fig. 131.

ANANAS Mill.

Ananas comosus (L.) Merr., Interpr. Rumph. Amb. 133. 1917

Pineapple, Piña

Terrestrial, to ca 1 m tall. Leaves forming a basal rosette; blades sword-shaped, heavily armed on margin. Inflorescences globular or ellipsoid, headlike, borne on a stout stem much shorter than leaves; flowers bisexual, sterile, sessile, spirally arranged and sunken into dense, swollen, pulpy rachis; calyx very short; petals with 2 ligules at base; ovary inferior; style filiform, 3-branched. Fruits syncarps formed of the spiny-toothed floral bracts, the aborted ovaries, and the thickened, fleshy, sweet, edible rachis.

Cultivated at the Laboratory Clearing.

Native to Brazil; widely cultivated in the tropics.

BILLBERGIA Thunb.

Billbergia macrolepis L. B. Smith, Contr. Gray Herb. 114:3, pl. I, f. 6. 1936

Slender epiphyte, often pendent. Leaves linear, acuminate, usually 1–1.8 m long, 1–4 cm wide, densely pale-lepidote, the lower surface marked with small to large, whitish spots, the margins sparsely spinose-serrate below middle, the spines 2–3 mm long, mostly antrorse, sometimes retrorse. Scapes pendent, less than 5 mm thick; scape bracts imbricate near base, more widely spaced higher on scape, lanceolate, acuminate, to 2.8 cm long, membranaceous; inflorescences simple, cylindrical, to 40 cm long, densely covered with a meallike pubescence of tiny trichomes in minute clusters; floral bracts spreading-oblong, the lower ones exceeding flower, the upper ones ovate and shorter than ovary; flowers sessile, suberect, broadly acute and apiculate, to 10 mm long, borne on an epigynous tube ca 3 mm long; petals linear, acute, to 4 cm long and 4 mm wide, bronze-green, spirally recurved at anthesis (*fide* Smith (1944) in *Flora of Panama*), bearing 2 scales at base; ovary inferior, subglobose, ca 15 mm long, coarsely sulcate, densely covered with pubescence similar to that of rachis. Fruits 1.5–1.8 mm long, fleshy; seeds numerous. *Croat 9255.*

Infrequent in the forest, usually moderately high in the canopy, rarely near the ground. Flowers in the dry season. The fruits probably mature in the late dry and early rainy seasons.

Fruits are probably dispersed by mammals or birds.

Costa Rica and Panama. In Panama, known only from tropical moist forest in the Canal Zone and Panamá.

CATOPSIS Griseb.

Catopsis sessiliflora (R. & P.) Mez in DC., Monogr. Phan. 9:625. 1896

C. sessiliflora var. *dioica* L. B. Smith

Dioecious (rarely monoecious) epiphyte; glabrous. Leaves ligulate, arching, divergent, rounded or obtuse and apiculate at apex, to 22 cm long, 1.2–2.5 cm wide, obscurely lepidote, moderately thin, the outermost markedly re-

KEY TO THE SPECIES OF CATOPSIS

Sepals less than 4.5 mm long ..... *C. sessiliflora* (R. & P.) Mez (staminate)
Sepals more than 6 mm long ..... *C. sessiliflora* (R. & P.) Mez (pistillate)

duced, acute at apex, becoming bractlike, often strongly recurved. Scapes generally much longer than leaves, erect, slender; scape bracts broadly elliptic, apiculate, erect, green, to ca 1 cm long, much shorter than internodes; staminate inflorescences widely spaced, bipinnate, pyramidal, the axis flexuous to geniculate; branches ascending, bearing many widely spaced flowers; rachis very slender; floral bracts ovate, 3–4 mm long, equaling or shorter than sepals; flowers spreading or subspreading; sepals asymmetrical, to 4.5 mm long; petals elliptic, obtuse, 4–6 mm long, greenish-yellow; stamens 6, in 2 unequal whorls, the filaments flattened; anthers slightly longer than broad; ovary ovoid, ca 1.5 mm long; style short; stigmas 3, slender, nonfunctional. Pistillate inflorescences usually simple, sometimes branched, 2.5–11 cm long; floral bracts broadly ovate, obtuse, much shorter than sepals, 3–7 mm long; sepals asymmetrical, suborbicular, 7–8 mm long, the apical edge discolored in age; petals free, lance-ovate, only slightly exserted, not appendaged, white; style very short; ovary superior, broadly ovate. Capsules ovoid, short-beaked, 10–13 mm long; seeds ca 1.5 mm long, slender, with an apical coma, the coma to 3.5 cm long, pale brown, folded 2 or 3 times in the capsule. *Croat 5230, 8263, Shattuck 604.*

Occasional, in the forest; perhaps at one time more abundant on the island. Seasonal behavior uncertain, apparently flowers mostly in the rainy season. Fruits mature in the dry season.

Because of the dimorphic nature of the inflorescences, both sexes of this species have been described as distinct species and were regarded as separate taxa in the *Flora of Panama* (Smith, 1944). Dr. Smith (pers. comm.) concurs in the reduction of the variety *dioica*, the name given the staminate form of the plant.

Southern Mexico to southern Brazil; West Indies. In Panama, known only from tropical moist forest in the Canal Zone and Bocas del Toro.

GUZMANIA R. & P.

Guzmania lingulata (L.) Mez var. **minor** (Mez) L. B. Smith & Pittend., Phytologia 7:105. 1960
G. minor Mez

Glabrous epiphyte. Leaves thin, ascending then spreading, the plant thus often broader than long; sheaths ovate; blades ligulate, acute or acuminate, caudate at apex, mostly 20–35 cm long and 1–2.5 cm wide, the inner leaves held well above scape. Inflorescences simple, flat-topped and cup-shaped, few-flowered, 15–25 cm long, the outer scape bracts leaflike, the inner ones orange-red, grading to red-orange tipped with yellow-orange, the innermost ones yellow-orange tipped with white, all becoming green in fruit; floral bracts white tinged with yellow, ca 4.5 cm long, scarcely longer than flowers; sepals slender, white; petals linear, ± fused for most of their length, ca 3.5 cm long, yellow tipped with white; stamens 6, about as long as petals; filaments ± flattened, adnate to petals much of their length; anthers ca 6.5 mm long; pollen white, sticky, amassing in large clusters; ovary superior. Capsules ± 3-sided, ca 3 cm long and 5 mm wide, brown, acute at apex, smooth or rugose, the 3 valves splitting at maturity; seeds numerous, 1.5–2 mm long, the seminiferous areas brown, 3–4 mm long, bearing a folded tuft (coma) of brownish trichomes from base, the trichomes fused together at the fold in the middle, the distal part fused to the seminiferous area of the seed. *Croat 10897.*

Common to locally abundant in the forest, especially in moist ravines, usually growing rather close to the ground on small trees or branches. Flowers mostly in the early rainy season, less often from late in the dry season to the middle of the rainy season. The fruits mature from the latter half of the rainy season through the dry season.

The seeds of *G. lingulata* differ in their construction from those of *G. monostachya.* Although both species have the coma refolded at the middle, the distal end in *G. lingulata* is folded to the seed body, whereas it is not in *G. monostachya.* Upon drying, the coma of *G. lingulata* opens to form an airy and globular mass.

Belize to Panama, Colombia, Venezuela, the Guianas, Brazil, and Bolivia; West Indies. In Panama, known from wetter regions of tropical moist forest in the Canal Zone, Bocas del Toro, and Darién, as well as from premontane wet forest in Bocas del Toro, Coclé, Panamá, and Darién and from tropical wet forest in Coclé (La Mesa), Panamá (Cerro Jefe), and Darién (Cerro Pirre).

See Figs. 132 and 133.

Guzmania monostachya (L.) Rusby ex Mez in DC., Monogr. Phan. 9:905. 1896

Epiphyte, to 44 cm high, often with several plants in dense clusters. Leaves ligulate, acute to acuminate, 15–41

KEY TO THE SPECIES OF GUZMANIA

Inflorescences flat-topped (cup-shaped), the flowers closely clustered at apex; scape bracts merging imperceptibly with leaves; floral bracts lacking stripes ..... *G. lingulata* (L.) Mez var. *minor* (Mez) L. B. Smith & Pittend.
Inflorescences cylindrial (cone-shaped), the flowers spirally arranged along its length; scape bracts distinct from leaves; floral bracts striped with purple ..... *G. monostachya* (L.) Mez

Fig. 132. *Guzmania lingulata* var. *minor*

Fig. 133. *Guzmania lingulata* var. *minor*

Fig. 134. *Guzmania monostachya*

cm long, 2–3 cm wide except at the broadly ovate base, glabrous at least in age. Scapes about as long as leaves; scape bracts imbricate, ovate, acuminate, the lower ones green and leaflike, the upper ones increasingly striped with purple, ultimately merging imperceptibly with floral bracts; inflorescences simple, oblong, the lower floral bracts to 4 cm long, those intermediate shorter and becoming tinged with dark violet, the uppermost bright red to orange-red, slightly exserted, all floral bracts soon fading and withering; flowers spirally arranged in upper half of scape; sepals lanceolate, ca 1.5 cm long, brown, indurate; petals white, ca 3 cm long, connate to near apex, rounded and concave at apex, sharply constricted at apex of sepals; stamens 6, included (held well below apex of tube); filaments flattened, adnate to petals, broader than anthers; anthers narrowly tapered to both ends, ca 5 mm long; ovary superior; style shorter than anthers, 3-branched, the branches ca 6 mm long. Capsules to 3.5 cm long, narrowly pointed at apex; valves rough and brown outside, shiny and black within; seeds 1.5–2 cm long, the seminiferous area ca 3.5 mm long, dark reddish-brown, the coma fused midway and reflexed back to seed, the refolded part not fused to the seminiferous area. *Croat 6715, 15058.*

Infrequently encountered in the forest, possibly more common at higher levels of the forest. Flowers in the late dry and early rainy seasons, mostly June and July. The fruits mature during the following dry season, mostly from December to March.

Southern Florida, and Nicaragua to Panama, Colombia, Venezuela, Ecuador, Peru, and Bolivia; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, and Panamá and from premontane wet forest in Bocas del Toro and Panamá.

See Fig. 134.

PITCAIRNIA L'Hér.

Pitcairnia heterophylla (Lindl.) Beer, Bromel. 68. 1857

Epiphyte, the flowering plants 8–12(20) cm tall. Leaves of flowering plants numerous, closely imbricate; blades dimorphic, the outermost reduced to awnlike, spinose-serrate spines, blackened at least at base, the bases ovate to rounded, sheathed, the inner leaves usually to 20 cm long and 15 mm wide, sometimes to 70 cm long and narrower, shorter than inflorescence, becoming decreasingly narrowed and spinose-serrate, softly woolly-pubescent, the innermost glabrous; vegetative stems like those of flowering plants but the inner leaves 50–100 cm long. Scapes scarcely exceeding leaves; scape bracts ovate, acuminate to spinose (especially the lowermost) at apex; inflorescences 3–12-flowered, simple, capitate or subspicate; floral bracts like upper scape bracts, entire, shorter than sepals; pedicels ca 3 mm long; flowers erect; sepals narrowly triangular, ca 3 cm long; petals linear, white (sometimes red), to 5.5 cm long, bearing a saccate, retuse scale well above base; stamens 6, slightly shorter than petals; anthers linear, ca 9 mm long; ovary superior for most of its length. Capsules narrowly ovoid, acute, shorter than sepals; seeds brown, caudate on both ends, the tails white, flattened, twisted, ca 3 mm long, both directed at 45° angle to the seed, parallel to each other. *Aviles 61.*

Collected once by Aviles, but not seen in recent years. The plant is an inconspicuous one, not common at such low elevations. Flowers and fruits during the dry season.

The seeds are probably wind dispersed though not well adapted for it. The capsules do not open wide, but the tails of the seeds are no doubt hygroscopically active, which could cause them to be slowly loosened from the capsule.

Southern Mexico to Venezuela and Ecuador; probably more prevalent in the Canal Zone before original deforestation. In Panama, mostly at elevations from 500–1,500 m in premontane wet, tropical wet, and premontane rain forests in Chiriquí, Coclé, and Panamá (Cerro Campana).

TILLANDSIA L.

Tillandsia anceps Lodd., Bot. Cab. 8, pl. 771. 1823

Cogollos

Epiphyte. Leaves many, equaling or exceeding inflorescences in length, very narrowly triangular, acuminate, 15–40 cm long, 7–12 mm wide, densely and minutely appressed-lepidote, recurving; sheaths triangular-ovate, with purple stripes. Scapes erect, very short; scape bracts imbricate, mostly ovate and acute; inflorescences simple, elliptic, strongly flattened, 10–15 cm long, to 5.5 cm wide; floral bracts densely imbricate, boat-shaped, acute, to 4 cm long, as many as 20 of them fertile, each subtending a flower; flowers appearing one at a time, soon withering; sepals narrowly lanceolate, acute, ca 3 cm long, keeled; petals more than twice as long as sepals, the claw linear, white, the blade lanceolate-elliptic, blue, recurved at anthesis; stamens deeply included, exceeding the style; ovary superior. Capsules cylindrical, to 2.5 cm long, rugose outside; seeds ca 1.7 cm long, comose, the seminiferous area ca 3 mm long, the coma fused and refolded at middle. *Croat 8503, Shattuck 560.*

Apparently rare, though the number of earlier collections indicates possibly greater abundance. Flowers in the middle to late rainy season. The fruits mature in the dry season.

Guatemala to Colombia, Venezuela, and the Guianas; Trinidad. In Panama, known only from tropical moist forest in the Canal Zone and Darién.

Tillandsia bulbosa Hook., Exot. Fl. pl. 173. 1826

Epiphyte; usually growing in dense clusters. Leaves often exceeding inflorescences in length, covered with fine, appressed-cinerous scales; sheaths orbicular, 2–5 cm long, inflated and sometimes housing ants, abruptly contracted into blade; blades involute-subulate, acuminate, to 30 cm long, 2–7 mm wide, contorted and spreading. Scapes erect; scape bracts often exceeding inflorescence; inflorescences simple to subdigitate, distichous, red or green; spikes spreading, lanceolate, acute, flattened, 2–5 cm long, 2–8-flowered; floral bracts erect, imbricate, ovate, acute,

KEY TO THE SPECIES OF TILLANDSIA

Spikes more than 5 cm long *and* floral bracts conspicuously imbricate:
- Spikes ± elliptic, always solitary; scape usually inconspicuous, often hidden by leaves, less than 10 cm long; sheath of leaf often with purplish stripes; stamens included ..... *T. anceps* Lodd.
- Spikes ± oblong, frequently digitate (sometimes simple); scape usually conspicuous, more than 10 cm long; sheath of leaf not with purple stripes; stamens excluded:
  - Spikes markedly flattened ..... *T. fasciculata* Sw. var. *fasciculata*
  - Spikes only slightly flattened ..... *T. fasciculata* Sw. var. *convexispica* Mez

Spikes less than 5 cm long *or* floral bracts not conspicuously imbricate:
- Leaf sheath orbicular and inflated; blades widely spreading, contorted; spikes 2- to 8-flowered .. .. *T. bulbosa* Hook.
- Leaf sheath not orbicular and inflated; blades ± erect, not contorted; spikes with less than 7 or more than 10 flowers:
  - Leaves thick, the sheaths about half as long as blades; outer leaves greatly reduced; spikes 4- to 6-flowered; plants rare or absent ..... *T. subulifera* Mez
  - Leaves thin, the sheaths less than one-fourth the length of blade; outer leaves (except for some withered ones) not greatly reduced; spikes with more than 10 flowers when fully open; plants common ..... *T. monadelpha* (E. Morr.) Baker

ca 15 mm long, exceeding sepals, keeled, densely lepidote; flowers sessile; sepals oblong, apiculate, ca 13 mm long; petals violet-blue, 3–4 cm long; stamens exserted; ovary superior. Capsules narrowly cylindrical, 3–4 cm long, the valves 3, roughened outside, brown and shiny inside; seeds ca 2.5 cm long, comose, the coma white, very fine, fused and refolded midway. *Croat 6098, 7048.*

Occasional, in the forest, usually rather high in trees. Flowering time uncertain. Apparently flowering most of the year, but most mature fruits seen in the dry season.

Southern Mexico to Colombia, Venezuela, the Guianas, and Brazil; West Indies. In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, and Darién, but known also from tropical wet forest in Colón (Guásimo).

See Fig. 135.

Tillandsia fasciculata Sw. var. **fasciculata,** Prodr. Veg. Ind. Occ. 56. 1788

Epiphyte, 20–100 cm tall (usually less than 60 cm), with 1 to several stems. Leaves rosulate, 2–3 cm broad above the ovate sheath, narrowed to 1 cm or less for most of its length, often red to purple near base, sometimes also apically, gradually narrowed to a sharp point, mostly less than 40 cm long, finely lepidote, the lower ones spreading, the upper ones ± erect, narrower, and merging with scape bracts. Scape bracts gradually tapered to acicular apex; inflorescences simple or digitate; spikes flattened, reddish- to greenish-yellow, mostly 12–18 cm long, to 3.5 cm broad; floral bracts acute, strongly keeled near apex, coriaceous; sepals linear-lanceolate, ca 3.5 cm long, shorter than bracts; petals ca 7 cm long, slender, violet above middle; stamens 6, exserted, violet above middle, 3 of them long and equaling style, the other 3 somewhat shorter; style to ca 8 cm long with the 3 bristly stigmas somewhat twisted together; ovary superior. Capsules 3.5–4 cm long, the 3 valves twisting and spreading widely at maturity, one remaining in the bract, the inner valve surface shiny and black; seeds very numerous, ca 2 cm long, comose, the seminiferous area slender, 2–3 mm long, brown, the coma weakly fused and strongly folded back near middle, the lower half of the strands held together in 3 or more clusters at apex, the outer half of the strands of each cluster spreading widely. *Croat 6171, 9523.*

Uncommon; seen only along the southeast shore, but no doubt occurring on upper branches of trees in the forest as well. Seasonal behavior uncertain. Possibly flowering and fruiting throughout the year, but most flowering collections have been made in January and July at the beginning of the dry and rainy seasons, respectively. Mature fruits have been seen chiefly in the dry season.

Mexico to Colombia; Florida, West Indies, Trinidad, and the Guianas. In Panama, known from drier parts of tropical moist forest in the Canal Zone and Darién.

See Fig. 136.

Tillandsia fasciculata Sw. var. **convexispica** Mez in DC., Monogr. Phan. 9:683. 1896

Like the typical variety, except the spikes to 20 cm long, only slightly flattened. *Chickering 63.*

Collected once on BCI, but not seen in recent years. Seasonality unknown, but probably like that of the typical variety.

Mexico, Guatemala, Belize, and Panama; Jamaica. In Panama, known only from tropical moist forest on BCI.

Tillandsia monadelpha (E. Morr.) Baker, J. Bot. 25:281. 1887

Epiphyte. Leaves very narrowly triangular, gradually tapered to the ovate sheath, mostly 10–30 cm long, ca 1 cm wide, thin, often purplish in age. Scapes erect, slender, 20–33 cm long, shorter or longer than leaves; scape bracts lanceolate-elliptic; inflorescences simple, oblong, distichous, 4–10 cm long, ca 22-flowered, compressed; rachis flexuous; floral bracts ovate, acute, ca 17 mm long, equaling sepals, at first erect, soon spreading; flowers sessile, ca 3 cm long; sepals equal, short-connate, lanceolate-elliptic, keeled; petals white, rarely seen, the

Fig. 135. *Tillandsia bulbosa*

Fig. 136. *Tillandsia fasciculata* var. *fasciculata*

Fig. 137. *Vriesia sanguinolenta*

blade ± oblong, spreading at anthesis, soon withering; stamens deeply included, exceeding style; ovary superior. Capsules narrowly cylindrical, 4–7 cm long, the 3 valves dark brown and shiny inside, spreading widely and twisting to release the comose seeds; seeds 2.5–3 cm long, the seminiferous part ca 3 mm long, the coma fused and refolded midway. *Croat 8233.*

Common in the forest; epiphytic at various levels. Flowers chiefly in the late dry and early rainy seasons. Buds appear during the early part of the dry season, but open flowers are rarely seen. The fruits mature chiefly in the dry season of the following year, but some may open during the rainy season as they are of mature size long before the end of the rainy season.

Guatemala to Colombia, Ecuador, and the Guianas; Trinidad. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Panamá, and Darién and from premontane wet and tropical wet forests in Colón (Santa Rita Ridge) and Panamá (Cerro Campana and Cerro Jefe).

Tillandsia subulifera Mez, Feddes Repert. 16:74. 1919

Epiphyte, 15–19 cm tall. Leaves few, stiffly erect, thick, sheathed about half their length, narrowly tapered and folded together toward apex, appressed-lepidote, sometimes with faint white cross-bands, the inner blades to 18 cm long and ca 5 mm wide above sheath, the outer ones greatly reduced. Scapes erect, mostly concealed by leaves; scape bracts imbricate; inflorescences simple, oblong, distichous, 5–7 cm long, 4–6-flowered; axis geniculate, mostly exposed; floral bracts erect, elliptic, broadly acute, ca 2 cm long, shorter than sepals, incurved and ± keeled at apex; flowers short-pedicellate; sepals free, elliptic, narrowly obtuse, ca 2 cm long; petals tubular-erect, ca 3 cm long, yellowish; stamens exserted; ovary superior. Capsules narrowly cylindrical, ca 6 cm long. *Chickering 62, Shattuck 1166.*

Collected twice on the island, but not seen in recent years; rare if still present. Seasonality unknown.

Panama and Trinidad (further collecting will no doubt show a wider range). In Panama, known only from tropical moist forest in the Canal Zone.

VRIESIA Lindl.

Vriesia gladioliflora (Wendl.) Ant., Wiener Ill. Gart.-Zeitung 5:97. 1880

Epiphyte, but apparently also terrestrial (perhaps accidentally), to 1 m tall. Leaves ligulate, broadly acute or obtuse and apiculate at apex, ca 60 cm long, 6–8 cm wide, purplish when young, becoming deep green, glabrous above, obscurely punctulate-lepidote beneath. Scapes erect, very stout; scape bracts imbricate, elliptic, abruptly acute; inflorescences simple, of many dense flowers, subcylindrical, 20–40 cm long, ca 5 cm wide; floral bracts distichous, coriaceous, erect, imbricate, broadly ovate, obtuse, 4.5–5.5 cm long, equaling or exceeding sepals, green, purplish toward apex; pedicels very short, stout; sepals broadly elliptic, obtuse at apex; petals ligulate, greenish-white, with suborbicular blade, 4–7 cm long, bearing 2 subincised scales at base; stamens included; ovary superior. Capsules to 3.5 cm long, 3-valved, brown, each valve consisting of an outer oblong part and an inner, ± ellipsoid part, the inner black and shiny within; seeds ca 2 cm long, comose, the seminiferous area ca 4 mm long and brown, the coma refolded at its middle, the distal part not fused to the seminiferous area. *Shattuck 524.*

Collected once on the island, but not seen in recent years; apparently rare elsewhere in Panama. Flowering time uncertain, probably mostly in the late rainy season. The fruits mature in the dry season.

Mexico, Guatemala, Belize, Costa Rica, Panama, and Colombia (probably from Mexico to Colombia). In Panama, known only from tropical moist forest in the Canal Zone.

Vriesia heliconioides (H.B.K.) Hook. ex Walp., Ann. Bot. Syst. 3:623. 1852

Epiphyte, rarely more than 40 cm tall (mostly to 30 cm) including inflorescence. Leaves ligulate, acuminate at apex, mostly 12–30 cm long and 3 cm wide, subglabrous, often recurled. Scapes erect, exceeding leaves when fully mature; scape bracts imbricate, the lower ones foliaceous,

KEY TO THE SPECIES OF VRIESIA

Flowers secund (borne along 1 side of inflorescence):
- Floral bracts acuminate ..... *V. ringens* (Griseb.) Harms
- Floral bracts obtuse to abruptly acute at apex:
  - Floral bracts smooth when dried, not closely imbricate, directed to one side with the flowers; much of the rachis exposed; uncommon but locally abundant ..... *V. sanguinolenta* Cogn. & Marchal
  - Floral bracts rugulose when dried, closely imbricate, not directed to one side with the flowers; most of the rachis hidden; plants rare or no longer present on the island ..... *V. gladioliflora* (Wendl.) Ant.

Flowers distichous (borne along 2 sides of inflorescence):
- Inflorescence long and narrow, subcylindrical at anthesis; floral bracts not red; petals with suborbicular blade ..... *V. gladioliflora* (Wendl.) Ant.
- Inflorescence flattened, not at all cylindrical; floral bracts red with white margins; petals long and slender ..... *V. heliconioides* (H.B.K.) Walp.

the upper ones reddish; inflorescences flattened; floral bracts very colorful, distichous, ovate, broadly spreading (much as for *Heliconia*, 31. Musaceae), cuspidate and turned upward at apex, red except white on the upper margins; flowers white, generally appearing one at a time; sepals rigid, keeled, acuminate, to 3.5 cm long, green sometimes tinged with red; corollas to 6.5 cm long, curved outward, fused to calyx near base, bearing 2 slender scales on inner surface above base; stamens 6, included; anthers dark, ca 3.3 cm long; pollen oblong, white, tacky; style ± equaling stamens, the 3 branches ca 4 mm long; ovary superior. Capsules to ca 6 cm long and 7 mm wide, narrowly acuminate at apex, fully exposed by weathered bracts at maturity, the valves spreading but not markedly twisting, black and shiny inside; seeds ca 3 cm long, the seminiferous area brown, the coma white, refolded, the folded area obscurely fused and the distal part free. *Croat 11130.*

Locally abundant in the vicinity of the coves on the eastern side of Burrunga Peninsula; not known elsewhere. Flowers from late May to August. The fruits mature during the dry season of the following year.

Guatemala to Bolivia and southwestern Brazil. In Panama, known only from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién.

Vriesia ringens (Griseb.) Harms, Notizbl. Bot. Gart. Berlin-Dahlem 10:801. 1929

Epiphyte, variable in size, to ca 1 m tall. Leaves ligulate, acute to acuminate, mostly 30–90 cm long, 3–6 cm wide, obscurely punctate-lepidote on underside. Scapes stout, erect, held above leaves; scape bracts lanceolate-elliptic, pale green, closely imbricate; inflorescences laxly compound, rarely simple, to 50 cm long; branches suberect, bearing few secund flowers and several imbricate sterile bracts at base; floral bracts broadly ovate, acuminate, 3–6.5 cm long, enfolding flowers and exceeding sepals of at least the lowest flowers, green or brownish, weakly keeled toward apex; sepals elliptic, acuminate, 2.5–3.5 cm long, ca 1.3 cm wide, subcoriaceous; petals white or yellowish, coiling and recurved, bearing 2 spatulate, acute scales at base; stamens exserted; ovary superior. Capsules oblong, ca 4 cm long, black; seeds nearly 2 cm long, basally comose, the seminiferous area brown, ca 3 mm long, the coma refolded and fused at middle, the distal part free. *Shattuck 337.*

Collected once on the island, but not seen in recent years. Flowers in the rainy season. The fruits mature in the dry season.

Costa Rica, Panama, and Colombia; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Colón, and Darién and from tropical wet forest in Colón (Guásimo).

Vriesia sanguinolenta Cogn. & Marchal, Pl. Ornem. 2:52. 1874

Epiphyte, to ca 1 m tall. Leaves ligulate, mostly gradually acuminate, sometimes rounded and long-apiculate, to 1 m or more long, (4.5)8–10 cm wide, obscurely punctate-lepidote. Scapes erect, much longer than leaves, mostly 1.2–2 m long; scape bracts closely imbricate, long-acuminate, coriaceous; inflorescences simple or having few branches, 25–100 cm long; branches suberect, bearing 11 to 19 secund flowers; rachis to 1 cm thick, strongly angled on drying; floral bracts broad, elliptic to suborbicular, abruptly acute, to 5 cm long, directed to one side like the flowers; pedicels stout, ca 1 cm long; sepals ± ovate, mostly obtuse, 2–4.5 cm long, rigid; petals greenish-white, bearing 2 scales at base; ovary superior. Capsules oblong-ellipsoid, pointed at apex, 3.5–6 cm long, dark brown and shiny, tightly enveloped by persistent sepals; seeds 2–2.5 cm long, comose, the seminiferous area ca 4 mm long, brown, the coma white, fused midway and refolded, the distal end free to spread. *Croat 12879.*

Uncommon, but locally abundant in some areas along the shore, usually in trees fairly low over the water; probably also occurring in upper branches of canopy trees. Seasonal behavior uncertain. Flowering probably occurs in the rainy season on BCI; in upland regions of Chiriquí flowers have been seen in February. The fruits mature during the dry season.

Costa Rica, Panama, Colombia; Cuba and Jamaica. In Panama, common along the Atlantic slope in tropical moist and tropical wet forests, but also abundant at higher elevations in lower montane wet forest in Chiriquí.

See Fig. 137.

23. COMMELINACEAE

Erect to sprawling, succulent herbs; stems with enlarged, often rooting nodes. Leaves alternate; petioles sheathing; blades sessile or not, simple, entire. Flowers withering rapidly, bisexual, actinomorphic or zygomorphic, solitary or on simple or paniculate, often umbelliform, helicoid cymes; sepals 3, free, imbricate, equal or 1 much reduced; petals 3, showy, free, equal or the anterior reduced; stamens 3 (*Callisia*), or 6 with 3 frequently longer, showy, and sterile; anthers 2-celled, the cells parallel or divergent, dehiscing longitudinally or by a terminal pore (*Dichorisandra*); ovary superior, 3-locular, 3-carpellate; placentation axile, the ovules 1–6, orthotropous; style 1; stigma 1, capitate or simple. Fruits loculicidal capsules; seeds 1 to several, with copious, mealy endosperm.

Members of the family are most easily recognized by being herbaceous and by having sheathing stipules and usually small, blue, white, or pink, ephemeral flowers sometimes subtended by spathaceous bracts.

Flowers are mostly open and are probably pollinated by small insects. In species with six stamens, the three longer, sterile stamens bear colored trichomes, an adaptation probably acting as an attractant. Many are zygomorphic, with obvious adaptations toward a specialized pollinator.

Several taxa (*Phaeosphaerion, Campelia, Dichorisandra*) have colorful fruits well suited for bird dispersal. The remainder have tiny seeds in small, thin-shelled capsules. Many seeds are no doubt merely spilled.

About 45 genera and 550 species; warm regions of the world.

KEY TO THE SPECIES OF COMMELINACEAE

Ultimate cymes subtended by conspicuous foliaceous bracts, large compared to the cyme:
- Spathe united at base; flowers usually blue or lavender ..... *Commelina erecta* L.
- Spathe open to base; flowers white:
  - Spathe solitary; inflorescence essentially sessile; capsules white at maturity, pearllike, with a thin, hard, outer shell; leaf blades ending abruptly at petiole, less than 3.5 cm wide ..... *Phaeosphaerion persicariifolium* (DC.) C. B. Clarke
  - Spathes paired; inflorescences on long, often branched peduncles; fruits purple, fleshy; leaf blades tapering onto petiole, often more than 4 cm wide ..... *Campelia zanonia* (L.) H.B.K.

Ultimate cymes with inconspicuous bracts, small compared to inflorescence:
- Flowers blue; sepals more than 7 mm long; plants usually more than 1 m tall, growing in the forest ..... *Dichorisandra hexandra* (Aubl.) Standl.
- Flowers white to pale lavender; sepals less than 4 mm long; plants less than 1 m tall, growing in the forest or in clearings:
  - Leaf sheaths pilose all over; leaf margins pilose ..... *Gibasis geniculata* (Jacq.) Rohw.
  - Leaf sheaths pubescent only on margins; leaf margins scabrid:
    - Stamens 3, equal; sepals and pedicels eglandular; inflorescences usually with 3 or fewer umbelliform clusters per axil, on long peduncles; flowers pink; leaves glabrous, equilateral at base ..... *Callisia ciliata* H.B.K.
    - Stamens 6, unequal, the 3 longer ones sterile and bearded; sepals and pedicels often glandular; inflorescences often with more than 3 umbelliform clusters per axil; flowers usually white; leaves usually pubescent, at least on underside, inequilateral at base with one side rounded, the other obtuse ..... *Tripogandra serrulata* (Vahl) Handl.

CALLISIA Loefl.

Callisia ciliata H.B.K., Nov. Gen. & Sp. 1:261. 1816

Decumbent to erect herb, usually less than 30 cm long. Leaves sheathed and sessile, the sheaths glabrous but with pilose margins, sometimes red-striate; blades oblong-lanceolate to lanceolate, acuminate, obtuse to acute at base, 1.8–8 cm long, 5–17 mm wide, glabrous except the margins scabrid or (rarely) the midrib pubescent on upper surface. Flowers in pedunculate, terminal or subterminal, umbelliform clusters, the clusters 1–3 (4) per axil, often solitary; peduncles mostly 1.5–3.5 cm long, hispidulous; pedicels and sepals glabrous, eglandular; pedicels ca 3.5 mm long; sepals 3, oblong-ovate, 3.5–4 mm long, bluntly acute at apex, thin, prominently keeled especially at apex; petals 3, pink, ± oblong, ± equaling sepals; stamens 3, ± equaling petals; filaments thin, flattened, broader at base; anther 7–8 mm long, widely separated by an expanded connective, the thecae unequal; ovary ovoid; style simple, ca 0.7 mm long, persisting in fruit. Capsules subglobose, 3-sulcate, 2.5 mm long; seeds 6, 2 per carpel, ca 1 mm long, irregularly trigonous, white, foveolate with a depression on the side opposite the point of attachment. *Croat 6081.*

Infrequent, in the Laboratory Clearing. Flowers and fruits throughout the rainy season and in the early dry season, mostly from August to January.

The species may be confused with *Tripogandra serrulata,* but is distinguished by having flowers with pink petals and three stamens.

The capsule possibly never dehisces; it may be dispersed by birds because of the fleshy, colorful calyx enclosing it at maturity.

Panama and Colombia. In Panama, known from tropical moist forest in the Canal Zone and Panamá and from premontane moist forest in Panamá.

CAMPELIA L. C. Rich.

Campelia zanonia (L.) H.B.K., Nov. Gen. & Sp. 1:264. 1816

Coyontura

Somewhat succulent herb, mostly 1.5 m tall or less; stems mostly 1 cm thick except at enlarged nodes, sometimes with few, widely arching branches. Leaves sessile or obscurely petiolate, usually broadest in middle, gradually tapered to both ends, narrowly acuminate at apex, mostly 25–35 cm long and 4–8 cm wide, widely spaced at base of plant, becoming closely spaced near apex, usually glabrous but the margins pilose near base. Inflorescences lateral, 8–30 cm long, often extending above apex of stem, simple or branched, bracteate at base of branches; peduncles usually branched, glabrous or velutinous, slender, bearing 2 or 4 paired foliaceous bracts at apex, the bracts 1.5–5 cm long; flowers umbellate above bracts; sepals 3, somewhat zygomorphic, fleshy, becoming enlarged, crosier-shaped, and purple, to 9 mm long, enclosing fruit at maturity; petals 3, white, broadly acute or rounded, ca 6 mm long, spreading at anthesis; stamens 6, weakly exserted, 8–9 mm long, often clustered to one side of the flower opposite the style; style bent to one side near apex, sometimes merged with anthers. Capsules fleshy, white to purplish, to 2.3 mm long, enclosed within an attractive, fruitlike calyx, 3-carpellate but usually forming 1 or 2 seeds; seeds black, minutely reticulate, ellipsoid and ± flattened on one side. *Croat 8610.*

Uncommon, throughout the forest, though locally very abundant in the swampy area extending northward from Armour Trail 900. Flowers and fruits throughout the rainy season. The fruits are especially abundant near the end of the rainy season.

The capsules possibly never dehisce. Because they are wholly enveloped by the fleshy colorful calyx at maturity,

they are probably dispersed intact by the birds that feed on them.

Mexico to Bolivia and Brazil; Greater Antilles. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, Darién, from premontane moist forest in Coclé, from premontane wet forest in Coclé and Panamá, and from lower montane wet forest in Chiriquí.

COMMELINA L.

Commelina erecta L., Sp. Pl. 41. 1753

C. elegans H.B.K.

Cadillo

Trailing or suberect herb; stems branching, glabrous or sparsely pubescent with maroon lines. Leaves mostly widely spaced, sessile or nearly so, the sheaths 8–20 mm long, usually pubescent; blades ± elliptic to lanceolate, gradually acuminate at apex, cuneate to rounded at base, mostly 3–14 cm long, 2–3.5 cm wide, moderately pubescent with longer trichomes above, densely short-pubescent below. Inflorescences terminal or subterminal; spathes ovate, truncate and united on one side, usually puberulent and with longer trichomes at base, usually filled with a watery or gelatinous fluid; peduncles short, each with several short-pedicellate flowers; flowers usually emerging one at a time, protruding above spathe at anthesis, later withdrawing, white to blue or very pale lavender; sepals 3, transparent, one much reduced, the others obovate; petals 3, the anterior one reduced, the posterior ones prominently clawed, the blade mostly 6 mm long and 10 mm wide, often overlapping; stamens 6, 3 reduced, the other 3 unequal in size, the shortest 1 medial with an enlarged anther, the lateral 2 ± equal; style curved, longer than lateral stamens, the stigma held just in front of the anthers of the lateral stamens. Capsules fleshy, dehiscent, 2-valved, to 4 mm long. *Croat 11697.*

The species is common in clearings, where it may form dense stands. Flowers and fruits throughout the year.

Throughout the American tropics and subtropics. In Panama, known from tropical moist forest in the Canal Zone, San Blas, and Panamá, from tropical dry forest in Coclé and Panamá, and from premontane moist forest in the Canal Zone.

DICHORISANDRA Mikan

Dichorisandra hexandra (Aubl.) Standl. in Standl. & Cald., Lista Prelim. Pl. El Salvador 48. 1925

Plant erect or clambering, 1–3 m tall (usually 1.5 m and erect); stems slender, glabrous to minutely puberulent, the lower part with conspicuous green-and-white striations. Leaves sessile or short-petiolate, the sheaths ca 2 cm long, often maroon and somewhat ciliate at apex; blades ovate to ovate-elliptic, abruptly long-acuminate, tapering to base, often ± oblique at base, mostly 10–20 cm long, 2.5–5 cm wide, thin, glabrous to indefinitely puberulous beneath, the margins ± undulate. Inflorescences terminal, paniculate, 3–15 cm long, the branches subtended by narrow bracts 0.5–3 cm long; flowers few to many; pedicels to 5 mm long; sepals 3, ca 12 mm long; petals 3, blue or white with bluish edges, lanceolate, 7–17 mm long; stamens 6, all fertile, the filaments fused to petals at base, the anthers blue, 4–8 mm long. Capsules obovoid, 1–1.5 cm long; seeds 3–5, orange-arillate. *Croat 11666.*

Frequent in the forest. Flowers in the rainy season (July to November), with the fruits maturing from September to December.

Seeds are probably dispersed by birds.

Guatemala to Brazil and Paraguay. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, Los Santos, Panamá, and Darién; known also from premontane moist forest in the Canal Zone and Panamá and from premontane wet forest in Colón, Chiriquí, Coclé, and Panamá.

GIBASIS Raf.

Gibasis geniculata (Jacq.) Rohw., Farinosae Veg. El. Salv. 143. 1956

Tradescantia geniculata Jacq.; *Aneilema geniculata* (Jacq.) Woods.

Sparsely villous herb, to ca 60 cm tall; stems ± succulent, creeping at base, rooting at lower nodes, with a single row of trichomes on internodes. Leaves ± sessile; sheaths pilose all over; blades ovate to ovate-lanceolate, 3–7 cm long, sparsely pilose on both surfaces. Inflorescences terminal, slender, to 7 cm long, dichotomously branched; flowers 3-parted; petals ovate, to 3 mm long, white, broader than sepals; sepals ovate-lanceolate, to 3 mm long and 1 mm wide; stamens 6, somewhat shorter than petals, interspersed with and slightly exceeding numerous moniliform trichomes; style ± equaling stamens; stigma minutely bristly. Capsules dry, 3-valved, 3-loculed, to 2 mm long, each locule with 1 or 2 seeds; seeds 1–1.5 mm long, each bearing a prominent funicular scar. *Croat 12799.*

Rare, in isolated, partially open areas along forest trails; often very abundant locally. Flowering and fruiting to some extent throughout the year, but mostly in the late rainy season and in the dry season.

Capsules do not appear to be always dehiscent; some may merely weather open. Seeds are possibly carried away by small insects.

Mexico to Bolivia and Brazil; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, and Darién; doubtlessly elsewhere in tropical moist forest.

PHAEOSPHAERION Hassk.

Phaeosphaerion persicariifolium (DC.) C. B. Clarke in DC., Monogr. Phan. 3:137. 1881

Erect or ± reclining herb, 30–60 cm tall; stems usually unbranched, rooting at nodes, glabrous or sparsely pubescent. Leaf sheaths with ferruginous trichomes; blades elliptic-lanceolate, narrowly acuminate, inequilateral at

base (one side acute, the other rounded), 6–12 cm long, 1.5–3.5 cm wide, pilose on both surfaces, the upper margins long-ciliate. Inflorescences on short, subterminal branches; flowers scorpioid, pedicellate, usually in clusters of 3 or 4, subtended by a broadly ovate spathe 2–3 cm long; sepals 3, free, hyaline; petals 3, white, the anterior petal reduced; stamens 6, the upper 3 sterile with sagittate anthers, the lower 3 fertile. Capsules ovoid, ca 5 mm long, pearly white, the exocarp thin, fragile; seeds 4–6, very small, black. *Croat 14070.*

Rare, along trails in the older forest. Probably flowers in the early dry season, with the fruits maturing later in the dry season or in the early rainy season (February to June).

The shiny, white, fragile fruits are probably attractive to birds, but apparently would not provide anything of food value. Crushing the thin-shelled capsule (possibly even while in flight), birds would scatter the tiny seeds.

Guatemala to Peru. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién, from tropical dry forest in Coclé, and from premontane moist forest in the Canal Zone.

TRIPOGANDRA Raf.

Tripogandra serrulata (Vahl) Handl., Baileya 17:33. 1970

Decumbent to erect herb, rooting at nodes, usually 30–100 cm long, often with red striations on stems and sheaths. Leaves sheathed and sessile, the sheaths glabrous except the margins pilose; blades oblong-lanceolate, acuminate, oblique at base with one side ± rounded to subcordate, the other obtuse, 3–14 cm long, 7–25 mm wide, usually pubescent especially below (on BCI; sometimes glabrous elsewhere), the margins scabrid. Flowers in pedunculate, terminal or subterminal, umbelliform clusters, few to numerous in axils; peduncles 7–30(50) mm long (mostly 10–15 mm long), glabrous to hispidulous; pedicels very short or to 6 mm long, often glandular; sepals 3, ± glabrous, often glandular, broadly oblong, boat-shaped, 3.5–4.5 mm long; petals 3, white or pale lavender, usually equaling sepals; stamens 6, 3 long and sterile with anthers yellow, 3 short and fertile with anthers white; filaments of the sterile stamens with long, jointed, gland-tipped trichomes especially near apex; pistil glabrous; style short; stigma simple, brush-like, ± equaling the short functional anthers in height. Capsules subglobose, ca 2 mm long, 3-carpellate; seeds 2 per carpel, irregularly trigonous, ca 1 mm long, gray, foveolate with a depression on the side opposite the point of attachment. *Croat 9186.*

Common in the Laboratory Clearing. Flowers and fruits throughout the year, especially in the rainy season. The flowers open in midmorning and close in midafternoon, apparently regardless of weather conditions.

Central Mexico to Peru, Venezuela, and the Guianas; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Panamá, and Darién, from premontane wet forest in Chiriquí (Boquete) and Coclé (El Valle), and from tropical wet forest in Colón (Miguel de la Borda).

24. PONTEDERIACEAE

Aquatic, succulent herbs. Leaves opposite or whorled; petioles sheathing, sometimes inflated; blades simple, entire; venation parallel. Flowers bisexual, somewhat zygomorphic, in axillary spikes subtended by spathaceous leaf sheaths; perianth 6-parted, obscurely 2-seriate, bilabiate, the lobes basally connate, bluish, hyaline; stamens 6, obscurely 2-seriate; anthers 2-celled, introrse, dehiscing by vertical slits; ovary superior, 1- or 3-locular; 3-carpellate; placentation axile when 3-locular, parietal when 1-locular; ovules many, anatropous; style 1; stigma 3-lobed, 6-lobed, or moplike and capitate. Fruits achenes, utricles, or many-seeded, 3-celled capsules; seeds with copious mealy endosperm.

Pontederiaceae are distinguished by aquatic habitat and clusters of large, pale blue, somewhat zygomorphic flowers.

The type of heterostyly varies from place to place in *Eichhornia crassipes* (Schulthorpe, 1967) and *Pontederia rotundifolia.* Lowden (1973) found that populations of *P. rotundifolia* often had only one of the three style forms and suspected that many such populations are the result of a single introduction of seed followed by clonal establishment and a certain amount of self-pollination. H. Baker (pers. comm.) reports that such populations usually have flowers with medium-length styles or sometimes long styles, but never short styles. Absence or paucity of one of the style types in different areas suggests that cross-pollination is only rarely achieved (Schulthorpe, 1967).

The utricles are buoyant, and dispersal is believed to be by water currents (Schultz, 1942; Lowden, 1973). Vegetative reproduction is important to population establishment in *Eichhornia,* which produces new stems from the rhizome, and in *Pontederia* (Lowden, 1973). Van der Pijl (1968) reported that in other areas ducks may be active in the dispersal of *Pontederia.* The spinulose peri-

KEY TO THE SPECIES OF PONTEDERIACEAE

Leaves deeply sagittate-cordate; perianth usually less than 2.5 cm long .... *Pontederia rotundifolia* L.f.
Leaves not cordate at base; perianth usually more than 3.5 cm long:
  Petioles inflated (especially shorter ones); stems short, condensed, with long roots from base; perianth lobes entire ..... *Eichhornia crassipes* (Mart.) Solms
  Petioles not inflated; stems elongate, rooting from nodes; perianth lobes erose .....
  ..... *Eichhornia azurea* (Sw.) Kunth

gone bases are ideally suited for epizoochorous dispersal, as suggested by Lowden (1973).

Flowers are probably bee pollinated. Lovell (1920) reported that *Halictoides novae-angeliae* feeds on and pollinates only *Pontederia cordata* L. Flowers usually open soon after sunrise, but on cloudy days opening may be delayed (Agharkar & Benerji, 1930).

Seven genera and about 30 species; mostly in the tropics and subtropics but extending into temperate America.

EICHHORNIA Kunth

Eichhornia azurea (Sw.) Kunth, Enum. Pl. 4:129. 1843
Water hyacinth

Aquatic, usually rooted in soil, sometimes free-floating; stems elongate, with long, pendent roots at lower nodes. Petioles to 30 cm long, not markedly inflated; blades round to obovate, rounded or mucronate at apex, truncate to obtuse at base, to 15 cm long, lacking midvein. Spikes many-flowered, axillary, with a subensheathing spathe at base; flowers 6-parted; perianth ± funnelform, 3.5–5.5 cm long, purplish-blue with a yellow spot on the upper, expanded perianth lobe, the tube 2–3 cm long, glandular-pubescent, the lobes erose-margined, decurrent; stamens 6, unequal, the 3 shorter ones included; filaments adnate to tube, glandular-pubescent; style ca 2 cm long, glabrous; stigma red, capitate. Capsules with seeds 1–1.6 mm long, less than 1 mm wide. *Shattuck 409.*

Rare, along the shore. Flowers and fruits throughout the rainy season.

Mexico to Argentina; the Antilles. In Panama, known from tropical moist forest in the Canal Zone and its vicinity and in Bocas del Toro.

Eichhornia crassipes (Mart.) Solms in DC., Monogr. Phan. 4:527. 1883
Water hyacinth, Lechuga de agua

Aquatic, free-floating; stems short and condensed with many long roots at the base. Petioles 2–30 cm long, very inflated in short-petiolate leaves; blades ± round, short-acuminate to rounded at apex, obtuse to truncate at base, 1–6(8) cm long, lacking midvein. Spikes many-flowered, axillary, with a subensheathing spathe at base; perianth 6-parted, ± funnelform, 4–6 cm long, lavender, the upper lobe darker at base and with a yellow spot at center, the tube 1–1.5 cm long, the lobes not erose; stamens 6, unequal, the shorter 3 slightly exserted, the longer 3 well exserted; filaments adnate to tube, glandular-pubescent; ovary ca 8 mm long, 3 mm wide, gradually tapered to apex; ovules minute; style elongate; stigma capitate, mop-like. Capsules with seeds ca 1 mm long, ca 0.5 mm wide. *Croat 7905.*

Rare, around the edge of the island. Flowers from August to March, mostly in the late rainy season and especially in the early dry season.

The species is heterostylous, though a single population may have only one type of style. Too few observations have been made of the *Eichhornia* around the lakeshore of BCI to ascertain if more than a single style type exists there.

After the fruits have been floating for a day or so, water absorption causes them to split longitudinally from the pressure of the swelling mucilage (Parija, 1934).

United States to Paraguay; the Antilles. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Chiriquí.

PONTEDERIA L.

Pontederia rotundifolia L.f., Suppl. Pl. Syst. Veg. 192. 1781
Pickerelweed

Succulent aquatic; stems to 3 m long, prostrate or floating, finally ascending, rooting at lower nodes. Leaves emergent; petioles 17–54 cm long (those of the floral leaf shoot as short as 5 cm long); petiole sheaths with ligule to 7.5 cm long (those in axil of floral shoot to 24 cm long); blades ovate-cordate, reniform or sagittate, 15–34 cm long, about as wide as long, the sinus open or narrow, the veins closely spaced, radiating from apex of sinus but arcuate-ascending near margin. Spikes axillary, many-flowered; peduncles 6–25 cm long, spathate beneath flowers; flowers bilabiate, tristylous, congested at apex of the pilose rachis; perianth blue, 1.5–2.2 cm long, 6-lobed to near base, sparsely pubescent, the hardened bases spinulose-ridged, the largest lobe grooved with a bilobed yellow spot; stamens 6, unequal, in 2 groups of 3 each; anthers introrse, blue; filaments adnate to tube basally, glandular-pubescent near apex; style 1, of 3 possible lengths: (1) short with medium and long stamens; (2) medium with short and long stamens; or (3) long with short and medium stamens; stigma trilobate, each lobe bifid. Fruits ovoid, indehiscent utricles; seed 1, ovoid, 6–7 mm long. *Croat 7065.*

Locally abundant near the dock and rare elsewhere, in marshy areas especially on the south side of the island. Flowers and fruits throughout the year.

Small black bees have been seen visiting the flowers.

Guatemala to Paraguay. In Panama, known only from tropical moist forest in the Canal Zone (especially the Atlantic slope) and in Darién.

25. LILIACEAE

Shrubs. Leaves alternate, spiraled, petiolate; petioles sheathing; blades simple, entire; venation parallel-pinnate. Flowers bisexual, actinomorphic, in terminal, bracteate panicles or racemes; tepals 6, subequal, basally connate; stamens 6, epitepalous, opposite tepals; anthers 2-celled; ovary superior, 3-locular, 3-carpellate; placentation axile; ovules many, anatropous; style 1, simple; stigma small, capitate. Fruits many-seeded berries; seeds with copious endosperm.

Approximately 240–250 genera and 3,500–3,700 species; worldwide but less commonly tropical. The Smilacaceae (26), which are sometimes considered to be

in this family, are not included here. Liliaceae are well represented in Panama (for a tropical area), but only one cultivated species occurs on BCI.

CORDYLINE Commers. ex Adr. Juss.

Cordyline fruticosa (L.) A. Chev. ex Goepp., Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 25:53. 1855
Taetsia fruticosa (L.) Merr.

Shrub, to 2.5 m tall; stems sparingly branched. Leaves clustered at ends of stems, narrowly elliptic to linear, acuminate, tapered to base and decurrent on petiole, 15–35 cm long, 5–9 cm wide, glabrous, often reddish along margins and midrib. Flowers white, sessile, alternate on branches of open panicles to 30 cm long, each flower subtended by 3 small bracts; perianth tubular, 6-lobed about halfway to base, perpendicular to rachis; stamens 6, included; style slender, included. Berries ± globose, 3–5 mm diam, red at maturity. *Croat 6149.*

Cultivated in the Laboratory Clearing. Probably flowers chiefly in the rainy season (particularly May, July, and September). The fruits mature mostly in the dry season and the early rainy season.

Pollination system unknown. Fruits are well suited for bird dispersal.

Cultivated in tropical America. In Panama, known from tropical moist forest on BCI and in Colón; no doubt cultivated elsewhere also.

26. SMILACACEAE

Rhizomatous, tendriled vines; stems often prickly, woody at the base. Leaves alternate; petioles sheathing; blades simple, palmately veined or pliveined; stipules lacking. Flowers unisexual (dioecious), actinomorphic, in axillary umbels, solitary or in a short-branched series of umbels; tepals 6, free; stamens 6, free; anthers incompletely 2-celled, introrse; ovary superior, 3-locular, 3-carpellate; placentation axile; ovules 1 or 2 per locule, pendulous; styles 3. Fruits 1–3-seeded berries; seeds with hard endosperm.

Closely allied to the Liliaceae (25). These dioecious, mostly herbaceous vines generally have pliveined leaves and umbels of six-parted flowers.

The flowers have the bowl-shaped blossom typical of insect pollination.

Fruits are endozoochorous, dispersed probably by birds (Ridley, 1930) and, since the vines offer little support, by skillful climbers such as monkeys.

Four genera (only 1 in the New World) and about 300 species; widely distributed in tropical and temperate regions.

SMILAX L.

Smilax lanceolata L., Sp. Pl. pl. 1031. 1753
S. domingensis Willd.

Essentially similar to *S. spinosa* except the plant never armed except on older stems; the flowers larger, the tepals more than 4 mm long. *Croat 14955.*

Rare, in the forest.

Croat 14955 may be *S. spinosa* with an unusually large flower. *Shattuck 150* is a sterile plant—probably *S. spinosa,* since it has spines on the young stem. No other collections from BCI can be assigned to this species with certainty. Since fruiting specimens of *S. lanceolata* and *S. spinosa* are not distinguishable, the validity of this species seems in doubt.

Mexico to Panama; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Veraguas, Herrera, Panamá, and Darién; known also from premontane wet forest in Bocas del Toro and Panamá and from tropical wet forest in Bocas del Toro, Coclé, and Panamá.

Smilax mollis H. & B. ex Willd., Sp. Pl. 4:785. 1806

Vine, somewhat woody at base; stems terete, unarmed, persistently short-pilose or subtomentose. Petioles 1–3 cm long, densely pubescent; blades ovate to ovate-oblong, acute or apiculate at apex, cordate at base, 8–18 cm long, 3–9 cm wide, 7-veined at base, densely pubescent when young, persistently pubescent on underside of veins. Flowers greenish-white, in solitary axillary umbels (rarely in a short, branched series of umbels); peduncles, pedicels, and receptacles densely pubescent, the tepals glabrous except for tuft at apex; staminate umbels with peduncles 1–4 cm long; pedicels 3–4 mm long, inserted on a globose receptacle; tepals 6, narrowly oblong, ca 4 mm long, ca 1 mm wide; filaments 6, 2–3.5 mm long;

KEY TO THE SPECIES OF SMILAX

Plants pubescent, conspicuously so at least on stems, petioles and receptacles ..... *S. mollis* Willd.
Plants glabrous:
  Peduncles shorter than subtending petioles:
    Tepals less than 2.8 mm long; often spiny on younger stems ..... *S. spinosa* P. Mill.
    Tepals more than 4 mm long; never spiny except on oldest stems ..... *S. lanceolata* L.
  Peduncles longer than subtending petioles:
    Staminate flowers sessile, staminate umbels always solitary; pistillate flowers with 3 staminodia; secondary veins subparallel ..... *S. spissa* Killip & Mort.
    Staminate flowers pedicellate, staminate umbels often in branched series; pistillate flowers with 6 staminodia; secondary veins reticulate ..... *S. panamensis* Morong

Fig. 138. *Smilax mollis*

Fig. 139. *Smilax spissa,* staminate flowers

anthers ca 1 mm long. Pistillate umbels with peduncles 1–3 cm long, usually longer than the subtending petiole; pedicels 3–5 mm long; perianth segments 6, lanceolate-oblong, ca 3 mm long and 1 mm wide; staminodia 3; styles 3. Fruit clusters ca 5 cm diam; berries globose, 5–10 mm diam, green to red and finally purplish-black at maturity; seeds 1–3, embedded in a fleshy matrix. *Croat 6462.*

Occasional, in the forest. Flowers and fruits throughout the year.

Southern Mexico to Panama. In Panama, known from tropical moist forest in the Canal Zone, Colón, San Blas, Panamá, and Darién, from premontane wet forest in Chiriquí (Boquete), and from premontane rain forest in Darién (Cerro Pirre).

See Fig. 138.

Smilax panamensis Morong, Bull. Torrey Bot. Club 21:441. 1894
Zarza

Vine, climbing into the canopy, somewhat woody at base, glabrous; stems terete, armed when juvenile with broad-based spines to 2 cm long. Petioles 1–3 cm long; blades lanceolate or lanceolate-oblong to ovate or ovate-oblong, short-acuminate, obtuse to truncate or rounded at base, 10–23 cm long, 3–12 cm wide, 5–7-veined at base, all other veins reticulate. Flowers 6-parted, greenish-yellow or greenish-white, the umbels solitary and axillary or sometimes in a short, branched series; peduncles flattened, longer than subtending petioles; staminate umbels with peduncles 6–20 mm long; pedicels 4–8 mm long; tepals lanceolate, 4–6 mm long, ca 1.5 mm wide; filaments 6, 1–2 mm long; anthers linear, 2–2.5 mm long. Pistillate umbels with peduncles 1–2.5 cm long; pedicels 5–15 mm long; staminodia 6; styles 3. Berries globose, 7–12 mm diam, green to red and finally black, 1–3 seeded. *Croat 6475.*

Rare, in the forest. Flowers and fruits throughout the year.

Guatemala to Panama. In Panama, known from tropical moist forest in the Canal Zone and Darién and from premontane wet and lower montane rain forests in Chiriquí.

Smilax spinosa P. Mill., Gard. Dict. ed. 8, no. 8. 1768
Zarza

Somewhat woody vine, glabrous, usually armed with sparse, stout, recurved prickles 5–6 mm long, especially on older stems; young stems ± angulate. Petioles 5–20 mm long; blades ovate-oblong or ovate to lanceolate, acute or abruptly acuminate and apiculate at apex, acute to obtuse or cordate at base, 6.5–14 cm long, 2.5–9 cm wide, palmately 5–7-veined at base, occasionally aculeate on petioles and underside of major veins. Flowers 6-parted, cream-colored or greenish, in axillary umbels; peduncles 1–9 mm long, much shorter than subtending petioles; pedicels 4–13 mm long, interspersed with minute bracteoles on the globose receptacle; staminate umbels solitary or in a branched series of 3–5 umbels; tepals ovate-oblong, 2–2.8 mm long, 1–1.4 mm wide; stamens ca 1.5 mm long; filaments longer or shorter than anthers. Pistillate umbels solitary; tepals oblong-lanceolate, 1.5–2.8 mm long; staminodia 3 or 6, ca 1 mm long; styles 3. Berries subglobose, green to dull red or black at maturity, 5–10 mm long; seeds 1–3, embedded in a fleshy matrix. *Croat 4305, 14955.*

Rare, in the forest. Apparently flowers and fruits throughout the year.

Mexico to Panama; West Indies. Range within Panama uncertain due to confusion with *S. lanceolata;* known from tropical moist forest in the Canal Zone, Bocas del Toro, Veraguas, Los Santos, and Panamá and from premontane moist forest in the Canal Zone. Specimens that are probably this species are seen also from tropical moist forest in Darién and from premontane moist, tropical dry, and premontane rain (Cerro Jefe) forests in Panamá.

Smilax spissa Killip & Mort., Publ. Carnegie Inst. Wash. 461:273. 1936

Vine, ± glabrous overall, the older stems somewhat woody; stems terete, unarmed. Petioles 5–10(20) mm long, sheathed at base, with a pair of tendrils at apex of sheath; blades oblong or ovate-oblong, acuminate, rounded to obtuse at base, 6–18 cm long, 7–8 cm wide, 3-veined at base with an additional inconspicuous pair of submarginal veins, the secondary veins subparallel, connecting the primary veins. Flowers 6-parted, greenish-white, sessile, congested on globose, bracteate receptacle, in solitary, axillary umbels; peduncles longer than subtending petioles, the fruiting peduncles 1.5–2.5 cm long; staminate umbels on peduncles 2–4 cm long, always solitary; tepals unequal, the outer ovate-oblong, 3–4 mm long, ca 1.5 mm wide, the inner narrowly oval, 2–3 mm long, ca 1 mm wide; filaments 1–1.5 mm long; anthers linear, 1.5–2 mm long. Pistillate flowers with pedicels 1–2 mm long (ca 5 mm long in fruit); tepals 6, unequal, the outer narrowly ovate, 3–3.5 mm long, ca 1.8 mm wide, the inner slightly shorter, ca 1 mm wide; ovary ca 2 mm long, subglobose; staminodia 3, minute, oblong, ca 0.5 mm long and ca 0.2 mm wide; styles 3, ca 0.5 mm long, flattened, nearly as broad as long. Berries ± globose, ca 1.5 cm diam, green turning red and finally black, 1–3-seeded. *Croat 8772, 15260, Zetek 5587.*

Rare, in the forest. Flowers and fruits throughout the year.

Costa Rica and Panama. In Panama, known only from tropical moist forest in the Canal Zone.

See Fig. 139.

27. HAEMODORACEAE

Perennial herbs; rhizomes ± elongate, horizontal. Leaves alternate, sheathing the stem at the base; blades simple; venation parallel. Flowers bisexual, actinomorphic, in terminal panicles or scorpioid cymes; tepals 6, free, showy; stamens 3, free, opposite the inner tepals; anthers 2-celled, longitudinally dehiscent; ovary subinferior, 3-locular, 3-carpellate; placentation axile; ovules many;

style simple. Fruits many-seeded berries; seeds with copious endosperm.

Easily confused with the Liliaceae (25).

Some 22 genera with about 120 species; Southern Hemisphere and tropical and North America.

XIPHIDIUM Aubl.

Xiphidium caeruleum Aubl., Hist. Pl. Guiane Fr. 1:33, t. 11. 1775

Palma, Palma del norte, Palmita

Perennial herb, 30–80 cm tall; rhizome creeping then erect, weakly rooted. Leaves linear, equitant, 20–50 cm long, overlapping in two ranks, the lateral margins free only near base, fused toward apex, minutely serrulate near apex. Panicles 7–35 cm long, 3–16 cm wide, the branches few to many, circinately coiled in bud, held ± horizontal at maturity, the flowers on upper side; flowers white, distinctly pedicellate; tepals 6, narrowly ovate, 4–9 mm long, spreading at anthesis, long-persistent; stamens 3, ± erect; filaments flattened, ca 2 mm long; ovary globose; style simple, ca 4 mm long, slightly longer than ovary, becoming ± curved to one side. Berries dull red at maturity, ca 5 mm long; seeds numerous, red, ± rounded, irregularly dented, densely papillate, less than 1 mm diam. *Croat 11785.*

Common along trails in the forest, along the lake margin, and in clearings, often locally abundant. Flowers throughout the rainy season, especially in July and August. The fruits mature in the late rainy and early dry seasons.

This conspicuous plant appears flattened, with equitant, irislike leaves.

Flowers are open (dish-shaped) and seem well suited for pollination by small, unspecialized insects. The fruit, though appearing to be a capsule with three distinct fleshy valves, is apparently never dehiscent, even though the fruit easily separates into three parts. The whole top of the fruit is removed, generally, and at least part of the seeds are removed, apparently by some animal.

Mexico to Bolivia and Brazil; introduced into the West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién, from premontane moist forest in the Canal Zone and Panamá, and from premontane wet forest in Chiriquí.

28. AMARYLLIDACEAE

Erect or aquatic, glabrous herbs arising from bulbs. Leaves basal, simple; blades linear, succulent; venation parallel; stipules lacking. Flowers 1 to many, bisexual, actinomorphic, in umbels on leafless stalks; perianth tubular, 6-lobed, showy; stamens 6, attached to the perianth, united at base of filaments, 2-celled, versatile, dehiscing longitudinally; ovary inferior, 3-locular; placentation axile; ovules several, anatropous; style 1, slender; stigmas 3, or 1 and trifid. Fruits loculicidal, tardily dehiscent capsules; seeds with fleshy endosperm.

Recognized by their showy, lilylike flowers; often confused with both the Liliaceae (25) and the Iridaceae (30) in other areas, but this should cause no problem on BCI.

Flowers on *Crinum* and *Hymenocallis* are white with very long, slender, tubular corollas and are probably pollinated by hawk moths, though the flowers are open during the day and are no doubt visited by a variety of pollen feeders. Most smaller insects could not effect pollination, however, since the stamens and style are widely separated.

Fruits are probably water dispersed. Van der Pijl (1968) reported that some species of *Hymenocallis* have viviparous seeds that burst through the pericarp and may be deposited on the ground by the reclining shaft of the inflorescence. Seeds of *Crinum* are buoyant because of the lightness of the albumen (Ridley, 1930).

About 90 genera and more than 1,000 species; widespread in warm temperate regions, less numerous in the tropics.

AMARYLLIS L.

Amaryllis belladonna L., Sp. Pl. 293. 1753

Hippeastrum puniceum Urban

Bulbous perennial; bulb globose, producing runners or stolons. Leaves few, basal, strap-shaped, not developing

KEY TO THE TAXA OF AMARYLLIDACEAE

Leaves ca 1 cm wide or less; flowers solitary; perianth lobes 3–4.5 cm long, white; capsule 3-valved, ca 0.7 cm long and 1 cm wide; seeds 2 per carpel, flattened, shiny, black ..... *Zephyranthes tubispatha* Herb.

Leaves more than 2.5 cm wide; flowers 2–15; perianth lobes more than 7 cm long, orange-red or white; fruits not as above:

Flowers orange-red, 2–4 per inflorescence; cultivated in the Laboratory Clearing ..... *Amaryllis belladonna* L.

Flowers white, usually 4–12 or more per inflorescence; plants cultivated or aquatic along lake margin or in wet areas in forest:

Leaves less than 50 cm long; filaments united into a prominent, exserted, white, staminal tube, green toward apex; usually in wet areas in forest ..... *Hymenocallis pedalis* Herb.

Leaves usually 1–2 m long; stamens distinct, not connected by a membrane into an exserted tube, usually purple toward apex ..... *Crinum erubescens* Ait.

fully until after flowering, bluntly acute at apex, gradually tapered to sheathing base, 30–70 cm long, 1–5 cm wide. Scapes hollow, as long as or longer than leaves, with a pair of lanceolate bracts to 6 cm long at apex; flowers 2–4; pedicels to 7 cm long; perianth funnelform, showy, red-orange, greenish within near base, to 11 cm long and wide, the tube 2–3 cm long, the lobes 6–8 cm long, to 3.5 cm wide, the inner ones narrower; stamens 6, to 10 cm long, shorter than tepals, prominently arched toward center of perianth; filaments orange above middle; anthers ca 7 mm long; style ca 10 cm long; stigma exceeding stamens, capitate but obscurely 3-lobed. Fruits not seen. *Croat 14052.*

Cultivated at the Laboratory Clearing.

Mexico to South America; West Indies; Old World tropics. In Panama, cultivated at various places.

CRINUM L.

Crinum erubescens Ait., Hort. Kew 1:413. 1789
Lirio

Large aquatic herb; bulb ovoid, 7–10 cm diam. Leaves basal, strap-shaped, mostly acute at apex, 1–2 m long and to 8.5 cm wide, thick and succulent, broadly channeled. Flowering scapes stout, usually somewhat shorter than leaves; involucral bracts 7–11 cm long, pointed; flowers 4–12 per inflorescence, sessile; perianth salverform, 15–25 cm long, white, usually tinged with maroon, often persisting in fruit, the tube slender, green, the lobes 6, lanceolate, 7–11 cm long; stamens 6, long-exserted, to 7 cm long or more, white at base, maroon above; anthers versatile, more than 1 cm long; style maroon, exceeding stamens; stigma weakly trilobate. Capsules fleshy, irregularly rounded, to 7 cm long; seeds 2–4, naked, of very irregular size and shape, mostly ca 5 cm long. *Croat 11803.*

Locally abundant, usually in protected areas. Flowering plants are apparently restricted to the shoreline. The species may be found in flower and fruit during any part of the year and shows no marked seasonality, though perhaps the greatest flowering activity occurs during the dry season and the early rainy season. The same population may have both flowering and fruiting inflorescences simultaneously.

The buoyant seeds are usually washed ashore, where they germinate, but they have been reported to germinate while still afloat.

Widespread, often cultivated, in tropical America. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro and Darién and from tropical wet forest in Bocas del Toro.

See Fig. 140.

HYMENOCALLIS Salisb.

Hymenocallis pedalis Herb., App. 44. 1821

Glabrous herb; bulb subcylindrical, to 6 cm diam including leaf bases. Leaves basal, numerous, ascending-spreading, tightly ensheathing one another at base, ± succulent, deciduous, the basal part persisting; blades oblong-oblanceolate, acuminate and ± flat near apex, gradually tapered toward the canaliculate, subpetiolar base, 20–45 cm long, 3–7 cm wide. Inflorescences to 15-flowered, usually held well above leaves; scapes to 45 cm long, compressed, glaucous, arising from middle of rosette of leaves, 2.5–3 cm by 1–1.5 cm in cross section; involucral bracts narrowly triangular, 4–10 cm long; flowers several, salverform, white, to 31 cm long, sweetly aromatic at anthesis, the tube to 18 cm long and 5 mm wide, green and glaucous except near apex beneath lobes; perianth lobes 6, lance-linear, to 12 cm long and 7 mm wide, spreading, gradually tapered to apex; stamens 6, widely exserted; filaments 6–7 cm long (free portion), green near apex, white below middle and fused into an exserted funnelform tube; anthers ca 1.5 cm long; pollen orange, tacky; style simple, green, slightly longer than stamens, at first erect, finally deflected to one side; stigma weakly 3-lobed. Fruits ovoid with the corolla persistent, the carpel wall thin; ovules 2, ovoid or almond-shaped, enlarging to ca 3 cm long; seeds buoyant, the seed coat soft, green, leathery. *Croat 17085.*

Rare, in the forest, possibly persisting from previous cultivation, usually in moist places but not in standing water. Though the plants have been seen elsewhere in flower during most of the year, they flower principally during the rainy season. An individual plant transferred to the greenhouses at the Missouri Botanical Garden flowered for about 2 weeks during late October and early November. Although no pollination took place, ovaries developed somewhat for 2–3 weeks and then shriveled. One year later the same plant flowered during the second and third weeks of October. A total of seven flowers were produced, one or two per day; flowers opened in the evening and lasted most of the following day before withering. At anthesis flowers are sweetly aromatic. Artificial pollination between sexual parts of the same flower and between other simultaneously opened flowers resulted in good fruit set. Within 2 weeks of pollination ovules had burst through the wall of the thin carpel. The fruits enlarged until they reached ca 3 cm in length, in about 1 month. The seeds then became loosened. The first fruits fell by the second week of November, the last by the end of November. By this time the inflorescence had drooped until it was lying on the ground.

Crinum erubescens is similar, but its leaves are much larger and ensiform, the colored part of its filaments and the style are maroon rather than green, and the prominent staminal tube of *Hymenocallis* is lacking. The species is confused with *H. littoralis* Salisb., which was reported by Traub (1962) from Mexico, Colombia, and the Guianas. *H. pedalis* is distinguished from *H. littoralis* by having the perianth lobes free from the staminal tube, whereas in *H. littoralis* the perianth lobes are adnate to the base of the staminal tube.

Mature fruits remain green but are very buoyant, suggesting that they probably are loosened by stream currents and carried away for dispersal.

Belize (*fide Yuncker et al. 8843*), Panama to Brazil.

Fig. 140. *Crinum erubescens*

Fig. 142. *Hymenocallis pedalis,* naked ovules bursting from ovary wall—those at right appearing like fruits

Fig. 141. *Hymenocallis pedalis*

In Panama, known principally from tropical moist forest on the Atlantic slope, but also from tropical moist forest in the Perlas Islands (Panamá).

See Figs. 141 and 142.

ZEPHYRANTHES Herb.

Zephyranthes tubispatha Herb., App. 7:96. 1821

Glabrous, acaulescent herb, 10–50 cm tall. Leaves arising from an underground bulb, this globose, to ca 3 cm diam; blades linear, narrowly acute at apex, to 50 cm long and 3–9 mm wide, moderately thick, canaliculate and often purplish near ground level. Scapes terete, hollow, ± equaling leaves, bearing 1 flower, the single cylindric spathe with a tube to 2 cm long, narrowly attenuate on one side to a deeply cleft tip; pedicel slender, to 5 cm long; flower white; perianth tube less than 5 mm long, the lobes obovate or oblanceolate, acute to bluntly acuminate at apex, 3–4.5 cm long, 6–16 mm wide; filaments 1.5–2.5 cm long, inserted at base of tube; anthers yellow, linear, attached below middle; style slender, 2.5–3.7 cm long, trifid; stigma lobes linear, to 2.5 mm long, narrowly tapered and weakly recurved at apex, the stigmatic surface on upper edge, chiefly in outer two-thirds of lobes. Capsules 3-valved, ca 8 mm long and 10 mm wide, yellowish or brown; seeds 6, 2 per carpel, ± ovoid, ca 6–7 mm long, somewhat flattened, shiny, black. *Croat 14889, 17365.*

Growing in the Laboratory Clearing, apparently not the result of cultivation. Flowers in the early rainy season (May to August). The fruits develop quickly, probably within one month of flowering.

Nothing is known of the dispersal of the seeds. Since they are shiny and black, they might be picked by birds, or, just as likely, they may merely spill out of the capsule.

Southern United States, Guatemala, Panama, Peru, and Argentina; Jamaica; no doubt more widespread. In Panama, known only from tropical moist forest on the Atlantic slope in Bocas del Toro, the Canal Zone, and San Blas (Puerto Obaldía).

29. DIOSCOREACEAE

Twining herbaceous vines arising from tubers. Leaves alternate or partly opposite, petiolate; blades mostly simple, sometimes 3–5-lobed, the margins entire; venation palmate; stipules lacking. Flowers unisexual (dioecious), actinomorphic, in axillary, bracteate fascicles, panicles, or spikes, the inflorescences often several per node; perianth 6-lobed, greenish, persistent; stamens 6, epipetalous, in 2 series, the outer fertile, the inner sometimes reduced to staminodia; anthers 2-celled, introrse or extrorse, basifixed, dehiscing longitudinally; ovary inferior, 3-locular, 3-carpellate; placentation axile; ovules 2 per cell, anatropous; styles 3. Fruits winged or angled, 3-valved, loculicidal capsules; seeds winged, disk-shaped or samaroid, with endosperm.

In Panama the family consists only of *Dioscorea.* The leaves lack parallel veins and thus are not typically monocotyledonous.

Flowers of *Dioscorea* are usually inconspicuous and often poorly known. They are open, with easy access to the nectaries.

The usually winged fruits are much more conspicuous than the flowers. The wing flutters when the wind is blowing, dislodging and dispersing the seeds. Most *Dioscorea* vines flower in the late rainy and early dry seasons, with the fruits maturing in the dry season. Though *D. urophylla* flowers in the rainy season, its seeds are also dispersed in the dry season.

Five, six, or more genera and 600–750 species; widely distributed.

DIOSCOREA L.

Dioscorea is recognized by its scandent habit, by its tiny, dioecious, six-parted, greenish flowers arranged in spikes or racemes, and by its three-winged or three-angled capsules with winged seeds. Among the diagnostic characters of many species is the presence or absence of plate-shaped glands and pellucid lineations. The Smilacaceae (26) are also twining with small green, dioecious flowers, but differ in having the flowers arranged in umbels and the fruits fleshy.

Dioscorea alata L., Sp. Pl. 2:1033. 1753

Ñame de agua, Ñame, Yam, Winged yam

Dioecious, twining vine; stems stout, 4-winged, twining to the right, the wing extending onto petiole. Leaves opposite; petioles 5–14 cm long; blades ovate-cordate, acuminate, with a broad to narrow basal sinus, 10–21 cm long, 6–14 cm wide; glands small, dark, scattered; veins (7)9–11(13), palmate. Staminate inflorescences in narrow axillary panicles 20–30 cm long; pistillate inflorescences stout simple spikes, solitary in axils, to 25 cm long; rachis glabrous; flowers yellow; tepals 6, very thick-

KEY TO THE SPECIES OF DIOSCOREA

Stems and petioles winged:
- Leaf blades with apical lobe deeply 3–5-lobed; rachis pubescent ..... *D. trifida* L.f.
- Leaf blades with apical lobe not lobed; rachis glabrous ..... *D. alata* L.

Stems and petioles not winged:
- Leaves more than 20 cm long and 12 cm wide, sparsely pubescent only on secondary and tertiary veins of lower surface; inflorescence paniculate; staminate flowers solitary; fruits more than 5 cm wide ..... *D. haenkeana* Presl

Leaves less than 20 cm long, less than 12 cm wide, glabrous or with pubescence not restricted to secondary and tertiary veins; fruits less than 3 cm wide:
- Blades not pellucid-lineolate; rachis pubescent or with minutely scabrid ribs:
  - Rachis and flowers densely pubescent; fertile stamens 6; lower side of blade with veins smooth, bearing dark plate-shaped glands near base ..... *D. sapindoides* Presl
  - Rachis merely minutely scabrid on ribs; flowers glabrous; fertile stamens 3; lower side of blade with veins minutely scabridulous (with magnification), eglandular ..... *D. polygonoides* Willd.
- Blades pellucid-lineolate; rachis glabrous and smooth:
  - Lower surface of blade eglandular; rachis minutely scabridulous; flowers with 3 stamens and 3 bifid staminodia ..... *D. polygonoides* Willd.
  - Lower surface of blade with glands either numerous and all over (best seen under 10× magnification) or large, whitish, and crateriform near axils of lateral veins below; stamens 6:
    - Glands of lower surface minute, all over; staminate flowers solitary, sessile; pistillate flowers with 6 minute staminodia; fruits oblong, usually tuberculate, acute to obtuse at apex, rounded to subcordate at base ..... *D. urophylla* Hemsl.
    - Glands of lower surface crateriform, whitish, restricted to area along veins especially near base; staminate flowers on short, stalked fascicles (sometimes appearing solitary as only one flower opens at a time); pistillate flowers lacking staminodia; fruits usually obovate, smooth, truncate to emarginate at apex, abruptly tapered at base ..... *D. macrostachya* Benth.

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ened, ca 3 mm long; style 3, the branches bifid. Capsules 3-winged, suborbicular or broader than long, smooth; seeds winged. *Croat 11616.*

Occasional in the Laboratory and Lighthouse Clearings, apparently persisting from cultivation.

Stems and tubers contain the alkaloid dioscorine, which may paralyze the central nervous system (Blohm, 1962).

Native to southern Asia; introduced generally throughout the tropics.

Dioscorea haenkeana Presl, Rel. Haenk. 1:135. 1827

Dioecious twining vine, climbing into canopy; stems terete, smooth except for some very fine longitudinal ribs (at least when dried). Leaves alternate; petioles 8–12 cm long, ± terete; blades ovate, acuminate, cordate at base (sinus ca 4–6 cm deep), 16–30 cm long, 11–20 cm wide, upper surface glabrous, rugose in age, the lower surface with sparse, inconspicuous, dark, plate-shaped glands; veins 9–11, conspicuous, palmate, the major veins arcuate-ascending, impressed above on older leaves, the secondary veins nearly perpendicular to primary ones, the tertiary reticulations less conspicuous, all veins minutely papillate, the secondary and tertiary veins sparsely pilose. Panicles axillary, about as long as leaves; staminate flowers solitary at nodes, sessile or with a pedicel 1–2 mm long; perianth ca 1.5–2 mm long; bracts sharply acuminate, ca 1.5 mm long; pistillate flowers not seen. Capsules ca 3.5 cm long and 6 cm wide, the inner surface of the valves brown, shiny; seeds disk-shaped, ca 2 cm or more in diam, the seminiferous areas at the center. *Croat 11880a, Montgomery 15.*

Collected on Drayton and Wheeler Trails and near the Laboratory Clearing from the top of the canopy. Flowers have been seen in August and September. Old fruits have been found on the ground in late August, however, which indicates that plants may flower as early as July.

Panama and Peru; this is the first report from Central America.

Dioscorea macrostachya Benth., Pl. Hartweg. 73. 1839

Dioecious twining vine, glabrous; stems twisting to the right. Leaves alternate; petioles slender, 2–7 cm long; blades ovate-cordate, narrowly acuminate, with a broad or narrow sinus at base, 4–12 cm long, 2–9.5 cm wide, usually obscurely pellucid-lineate, with a few, scattered, rounded, crateriform, whitish glands on lower surface especially in axils of veins; veins usually 9, palmate. Flowers unisexual; staminate inflorescences usually solitary in leaf axils, 4–12(30) cm long, simple or branched; flowers solitary, borne on short-stalked fascicles, usually with a single open flower and 1 or more buds; peduncles 0.5–3 mm long, usually with a slender bract about midway; perianth segments violet-purple except sometimes greenish on margins, broadly ovate, to 1 mm long, spreading at anthesis; stamens 6, all fertile, borne on the hypanthium at the center of the flower; anthers about as broad as long, dehiscing extrorsely or upward; filaments stout, shorter than the width of the anther; pistillode stout, slightly exceeding stamens. Pistillate inflorescences usually solitary and unbranched, commonly somewhat longer than staminate ones, usually to 20 cm long; pistillate flowers solitary, ± sessile, to 5 mm long at anthesis, bearing 1 or 2 lanceolate bracts at base; perianth lobes as in staminate flowers; staminodia lacking; styles 3, short and stout, each with a pair of short, divergent branches; ovary sharply 3-angled, soon curved upward along the pendent rachis. Capsules 3-winged, 2–3 cm long, tan, smooth, the valves obovate to broadly oblong, truncate to emarginate at apex, abruptly tapered and short-stipitate at base; seeds flat, ± oblong, 8–12 mm long, 5–8 mm wide, winged all around, brown, one side usually straight, the seminiferous area to 5 mm long and 3.5 mm wide. *Shattuck 680.*

Apparently rare on the island, though moderately common in surrounding areas of the Canal Zone. Flowers throughout most of the year, especially in the very late rainy season and in the dry season (November to March). The species may flower twice per year, since there seems to be a second burst of flowering in the early rainy season. Most fruits probably mature during the late dry and early rainy seasons.

Although Standley reported *D. macrostachya,* the specimen he cited (*Shattuck 582*) was *D. polygonoides.*

Mexico to Panama. In Panama, known principally from tropical moist, premontane wet, and tropical wet forests on the Atlantic slope, but also from premontane wet forest at higher elevations on the Pacific slope in Panamá and from tropical moist forest in Veraguas and Darién; apparently rare in premontane moist forest in the Canal Zone on the Pacific slope.

Dioscorea polygonoides H. & B. ex Willd., Sp. Pl. 4:795. 1806

Dioecious twining vine; stems, petioles, and inflorescences weakly ribbed, the ribs minutely scabrid; stems twisting to the left. Leaves alternate; petioles 1.5–6 cm long; blades ovate-orbicular to ovate, narrowly acuminate, sometimes falcate, deeply to broadly cordate at base, mostly 4–11 cm long, 2.5–8.5 cm broad, obscurely pellucid-lineolate, eglandular; veins (9)11, palmate, the cauline veins 3, the veins of lower surface often minutely scabrid (especially after drying); juvenile plants often with a single ovate-cordate leaf arising from an underground stem, the petiole to 1.3 cm long, the blade often mottled with gray; leaves of the juvenile climbing stems larger than on adults, to 22 cm long and 13.5 cm wide, the petiole to 8 cm long. Inflorescences axillary; rachises minutely scabrid; flowers to 2 mm broad; staminate spikes 2–4 in leaf axils, 10–30 cm long, usually unbranched, sparsley flowered; flowers greenish, sessile, in few-flowered fascicles, the perianth segments ovate, 1–1.3 mm long, united in lower half, each with a ± prominent medial vein; stamens 3, inserted on perianth; anthers extrorse, separated by a broad connective; staminodia 3, bifid at apex, about as long as stamens; ovary rudiment conspicuous. Pistillate spikes solitary or paired, unbranched, less than 15 cm long, the flowers sessile; stamens lacking; ovary ca 3 mm long; styles 3, minute, conical; stigmas bifid. Capsules 3-winged, obovate to oval, 2.5–3 cm long, to ca 2 cm wide, glabrous; seeds winged all around. *Croat 12877, Shattuck 582.*

Occasional, in the forest and at the margins of clearings; probably about as abundant as *D. urophylla* with which it is confused. Seasonal behavior uncertain. Apparently flowers in the early dry season (December to February); the fruiting season is not known.

Standley cited *Shattuck 582,* which is this species, as *D. macrostachya.* Morton in the *Flora of Panama* (1945) reported that the species lacks pellucid lineations. Though they are not as prominent as in *D. urophylla,* pellucid lineations are usually present, at least after the specimens are dried.

Mexico to Peru and Brazil; West Indies. In Panama, known only from tropical moist forest in the Canal Zone and in adjacent Panamá.

Dioscorea sapindoides Presl, Rel. Haenk. 1:33. 1830

Dioecious twining vine, extending into trees in the forest; stems slender, terete, usually sparsely and inconspicuously pubescent, twisting to the right. Leaves alternate, thin; petioles 3–5(8) cm long, pubescent, flattened above, minutely ribbed marginally, somewhat angulate on lower side, both ends thickened; blades ovate-oblong, abruptly acuminate, cordate at base, (4)9–15(19) cm long, 5.5–11 cm wide, glabrous, not pellucid-lineate, bearing dark, scattered, platelike glands on lower surface especially at base in vein axils; veins 9(11) (cauline veins 3), palmate, impressed above, raised below (intervenous areas sometimes becoming achlorophyllous in age); juvenile plants with leaves mottled green above, violet-purple below, the basal lobes sometimes ± truncate. Inflorescences axillary; rachises, pedicels, perianth segments, and ovaries short-pilose; staminate inflorescences 1–3 per axil, the rachis angulate, 5–25(30) cm long, usually simple; flowers in numerous, short, several-flowered racemes, the pedicels short, each subtended by a narrowly triangulate bract; perianth to 2 mm long, 6-lobed ca two-thirds of the way to base, glabrous within; stamens 6, less than 1 mm long, included; filaments connate into a tube. Pistillate inflorescences unbranched, solitary or paired, 6–30 cm long, the flowers 5–6 mm long, the perianth to 2 mm long, lobed to about middle, glabrous within; staminodia 6, minute; styles 3, ca 0.7 mm long, stout; stigmas bifid. Capsules 3-winged, oblong, obtuse to rounded at apex, rounded to subcordate at base, to 2 cm long and 1.1 cm wide, glabrous or sparsely short-pilose along median at maturity; seeds oblong, samaroid, 10–13 mm long, 4–5 mm wide. *Croat 12804, 12837.*

Rare; known only from the vicinity of Fairchild Point and the Lighthouse Clearing. Flowers in the late rainy and early dry seasons (October to December). The fruits probably mature in the dry season.

Mexico, Costa Rica, and Panama; no doubt in other parts of Central America as well. In Panama, ecologically variable; known chiefly from premontane moist forest in the Canal Zone and Panamá, but also from tropical moist forest in the Canal Zone and Panamá and from premontane wet forest in Panamá (on the summit of Cerro Campana).

Dioscorea trifida L.f., Suppl. Pl. Syst. Veg. 427. 1781
Ñame, Yampi, Yam

Dioecious twining vine, nearly glabrous; stems conspicuously 4-winged on the angles. Leaves alternate; petioles to 15 cm long; blades cordate, 3–5-lobed, 6–23 cm long, as broad as long, glabrous to minutely puberulous on upper surface and on the veins below, pellucid-lineolate, not obviously glandular, the lobes acute to acuminate, the terminal lobe with 3 veins; veins 9–13, palmate. Staminate spikes axillary, 2–5 per axil, their flowers greenish,

solitary, short-pedicellate, the ovary pubescent; tepals 6, oblong-lanceolate, to 2.7 mm long; stamens 6, all fertile, ca 1.3 mm long, attached to tepals; anthers introrse; pistillate flowers not seen. Capsules 3-winged, ca 2.7 cm long and 1.7 cm wide (*fide* Morton (1945) in *Flora of Panama*), puberulent. *Croat 7242.*

Cultivated at the Laboratory Clearing. Seasonal behavior uncertain. Probably flowering and fruiting in the dry season.

Native to South America; cultivated widely, at least from Guatemala to Peru and Brazil, and also in the West Indies. In Panama, known from tropical moist forest in the Canal Zone and Panamá and from premontane moist forest in Panamá.

Dioscorea urophylla Hemsl., Biol. Centr.-Amer. Bot. 3:361. 1884

Bejuco de saina

Dioecious twining vine, glabrous; stems usually twisting to the left, with short broad-based spines at the base of larger leaves. Leaves alternate to opposite; petioles 3.5–9.5 cm long (to 14 cm long on juvenile plants); blades ovate, narrowly long-acuminate, truncate to weakly cordate at base, 5–14 cm long, 3–8.5(14) cm wide, thin, conspicuously pellucid-lineolate and glandular-dotted on lower surface (glands sparse to lacking on upper surface); veins 7–9, palmate. Staminate spikes 1–3 per axil, to ca 50 cm long (usually less than 10 cm), unbranched or branched (especially when long); flowers greenish-yellow, solitary, sessile; tepals oblong, 2–3 mm long, acute at apex, connate at base, spreading at anthesis; stamens 6 (in 2 whorls of 3 each), ca 1.3 mm long, inserted on and held at about same level as tepals; anthers introrse; pollen golden, tacky; pistillode much shorter than filaments, trilobate. Pistillate spikes 1 per axil, 10–20 cm long; flowers sessile; tepals 6, 2–3 mm long; stamens 6 (probably nonfunctional but with some pollen), adnate to lower part of tepal, ca 0.7 mm long; ovary glabrous, ca 3.5 mm long; style single, 1.3–2 mm long, conical; stigmas bilobed, flattened. Capsules 3-winged, oblong-elliptic, acute or apiculate at apex, ± rounded below, 2.3–3 cm long, 1.3–1.6 cm wide, 3-valved, the valves coriaceous, tuberculate (especially medially); seeds samaroid, 2–2.5 cm long (including wing), 6–8 mm wide, brown. *Croat 6704, Foster 1177.*

Occasional, in the forest. Flowers principally in the rainy season (June to September, occasionally as early as April). The fruits mature during the following dry season (December to April).

Capsules of this species are almost identical to those of *D. cymosula* Hemsl., which can be distinguished by having the persisting flower and pedicel densely pilose, whereas *D. urophylla* is wholly glabrous. The species is most easily confused with *D. polygonoides* and *D. macrostachya.*

Panama and Peru; probably in intervening regions as well. In Panama, known from drier regions of tropical moist forest in the Canal Zone (both slopes) and Herrera, Panamá, and Darién; known also from premontane moist forest in the Canal Zone and Panamá and from premontane wet forest in Colón (Santa Rita Ridge).

See Fig. 143.

30. IRIDACEAE

Perennial, rhizomatous herbs. Leaves alternate, basal, sessile; blades simple, entire; venation parallel; stipules lacking. Flowers soon withering, bisexual, actinomorphic, borne in a few-flowered, bracteate cluster arising from below apex of leaflike peduncle; sepals 3, free, showy; petals 3, free, showy; stamens 3; filaments free; anthers 2-celled, extrorse, basifixed, dehiscing by longitudinal slits, coherent to the style; ovary inferior, 3-locular, 3-carpellate; placentation axile; ovules numerous, anatropous; style 1, 3-branched; stigmas transverse, basal. Fruits 3-valved, loculicidal capsules; seeds many, arillate, with copious endosperm.

About 60–70 genera and 800–1,500 species; widely distributed. (Adams (1972) reported the higher number and Willis (1966) the lower number.)

NEOMARICA Sprague

Neomarica gracilis (Herb.) Sprague, Bull. Misc. Inform. 1928:280. 1928

Marica gracilis Herb.

Rhizomatous herb, 50–100 cm tall, glabrous. Leaves basal in a 2-ranked, fan-shaped cluster; blades ensiform, long-acuminate, tapered to base, 30–70 cm long, 1–2 cm wide, the midrib conspicuously raised. Flowering scapes leaflike, the peduncle appearing lateral and overtopped by the terminal leaflike spathe 30–40 cm long; peduncles 1–3 cm long, ensheathed at base with spathes 1–3 cm long; flowers 2–5, 3–5 cm long, soon withering, the tube obsolete; sepals 3, obovate, spreading, white with yellow and brown to purple markings at base; petals 3, much smaller, oblanceolate, spreading to about the middle, then prominently arched upward and inward toward center of flower, prominently reflexed at apex, yellowish with prominent purple transverse markings, especially toward apex; sexual parts not available for study. Capsules oblong, 2–3 cm long, green; seeds many, red, irregular, ca 5 mm long. *Croat 4130.*

Rare, in the forest. Flowers from January to June, principally in March and April. The fruits mature from June to January, principally from August to December.

Flowers are rather specialized and are open for only one day (Bailey, 1949). They seem suited to bee pollination. Flowering stems fall over and root at the tips (*fide* collection label of *Standley 31341*). The fruits have arillate seeds.

Mexico to Brazil. In Panama, known from tropical moist forest in the Canal Zone and Colón and from premontane wet forest in Coclé (El Valle).

31. MUSACEAE

Stout, unbranched, rhizomatous herbs; stems very short or formed by closely imbricated, sheathing petioles. Leaves alternate, distichous (*Heliconia*) or spiral (*Musa*); blades simple, entire; venation pinnate and at about a 90° angle to midrib. Flowers bisexual (*Heliconia*) or unisexual (monoecious in *Musa*), weakly zygomorphic, closely congested and arranged colaterally in racemes

KEY TO THE TAXA OF MUSACEAE

Leaves and flowers spirally arranged; flowers unisexual by abortion, the staminate flowers at the apex of the inflorescence soon falling; calyx tubular; fruit an elongate, indehiscent berry (the banana); plants cultivated at the Laboratory Clearing ..... *Musa sapientum* L.
Leaves and flowers distichously arranged (i.e., in 2 ranks); flowers bisexual; calyx not tubular (of 3 sepals, free or partially united to corolla); fruits tardily dehiscent capsules, rounded to oblong, less than 2 cm long ..... *Heliconia*

(*Musa*) or of many-flowered cincinni subtended or enveloped by conspicuous, colorful, distichous bracts (*Heliconia*); perianth of 6, ± united segments in 2 series, the inner showy; stamens 6, including 1 sterile staminodium, often petaloid; anthers 2-celled, dehiscing longitudinally; ovary inferior, 3-locular, 3-carpellate; placentation axile; ovules many and anatropous (*Musa*) or solitary and basal (*Heliconia*); style 1; stigma lobed or 3. Fruits fleshy, usually blue capsules dehiscing into 3 cocci (*Heliconia*) or a long berry (*Musa*); seeds with endosperm.

Members of the family are easily confused with the Marantaceae (33) in juvenile or sterile stages, since that family may also have similar, broad, banana-like leaves. The Musaceae have a canaliculate petiole, however, whereas in the Marantaceae the petioles have a hardened callus (round in cross section) on the upper part and are occasionally geniculate.

Flowers are narrowly tubular and produce abundant nectar. Those of *Heliconia* are generally white, green, or yellow, but attract hummingbirds because of their colorful red bracts (Chapman, 1931; Stiles, 1975).

The often blue, fleshy capsules of *Heliconia* are frequently exserted from the bracts by an elongating, often white pedicel. Despite the fact that fruits appear to be capsular, they are taken before dehiscing. The fruits are dispersed by birds. Stiles (1975) recorded 27 birds (chiefly manakins) that disperse these fruits in Costa Rica; the most important were *Manacus candei, Pipra mentalis,* and *Pipro morpha oleagina* (pers. comm.). Aggregated species such as *H. latispatha* are pollinated by territorial hummingbirds (usually not hermits), whereas isolated forest species are pollinated by wandering, nonterritorial hummingbirds (usually hermits) (Linhart, 1973; Stiles, 1975). Nectar production for *Heliconia* increases during the morning and usually levels off by midday, whereas visits by hummingbirds decrease rapidly as the morning progresses (Stiles, 1975).

Five genera and 150 species; widespread in the tropics.

HELICONIA L. (Platanillo)

Heliconia catheta R. R. Smith, Phytologia 30:65–66. 1975

Caulescent rhizomatous herb, 3–5 m tall, of musaceous habit; stem flattened, ca 5 cm diam by 3 cm or less; stem, petiole, and midrib pruinose. Petioles 50–100 cm long, stout; blades oblong, abruptly acuminate at apex, obtuse-truncate to cordate at base with one lobe longer than the other, 50–135 (175) cm long, (15) 20–36 cm wide, glabrous; veins 4–6 mm apart. Inflorescence pendent from uppermost leaves, hanging 70–100 cm long from stout

KEY TO THE SPECIES OF HELICONIA

All bracts of the inflorescence, except perhaps the lowermost, overlapping to some extent (on fully opened inflorescences):
  Bracts overlapping for most of their length, entirely red, mostly blunt or short-acuminate at apex ..... *H. mariae* Hook.f.
  Bracts overlapping only at their base, usually red but with greenish or yellowish margins, long-acuminate at apex ..... *H. wagneriana* O. G. Petersen
Bracts of the inflorescence relatively distant, not overlapping except before fully opened:
  Inflorescences pendent:
    Bracts with free margins and apex both yellow or yellow-green, the length of the upper bract margins broadly concave; middle bracts more than 10 cm long ..... *H. catheta* R. R. Smith
    Bracts red throughout, the length of the upper margins ± straight to convex; middle bracts less than 10 cm long ..... *H. pogonantha* Cuf.
  Inflorescences erect:
    Bracts densely villous ..... *H. irrasa* R. R. Smith
    Bracts essentially glabrous:
      Bracts spirally arranged, broadened at base, concealing flower pedicels ... *H. latispatha* Benth.
      Bracts not spirally arranged, narrow at base, exposing flower pedicels:
        Bracts red, the lower ones often leafy; flowers yellow; lower portion of ovary and fruit yellow; leaf blades green on underside; plants usually of shoreline and clearings ... . *H. vaginalis* Benth.
        Bracts green, the lower ones usually not leafy; flowers pink or red; lower portion of ovary and fruit white; leaf blades maroon on underside; plants cultivated .... *H. metallica* Hook.

Fig. 143. *Dioscorea urophylla*

Fig. 144. *Heliconia irrasa*

Fig. 145. *Heliconia latispatha*

erect peduncle more than 30 cm long and to 1.5 cm diam; most parts minutely pubescent; peduncle and rachis bright red, the rachis strongly flexuous; bracts (10)12–20, spirally arranged, red except for broad yellow band on distal and free margins, usually pubescent only near base, 2–5.5 cm high at their base, tapered to a point, the free margin broadly concave along its length; basal bracts (those nearest peduncle) to 30 cm long (often green), the remaining bracts decreasing in length, 8–10 cm long at apex of inflorescences, sometimes deciduous, the lowermost internodes 5–6 cm long; pedicels ca 1 cm long (to 2.5 cm in fruit); flowers yellow, 6–10 per bract; perianth 4–6 cm long with tips protruding from the bract. Fruits at first yellow, turning blue, ca 2 cm long and less than 1.5 cm wide, puberulent, protruding through bracts at maturity; seeds 3, oblong, black, warty. *Croat 6387.*

Occasional, in clearings, in open areas along trails, and especially along the shore. Flowers from June to September. The fruits mature from July to October. Both flowers and fruits may be present on the same inflorescence.

Distinguished by the pruinose stems and petioles and by the pendent inflorescences with widely spaced, red and yellow bracts. Standley (1933) and Woodson and Schery (1945a) confused this species with *H. platystachya* Baker, a South American species, which has fewer and shorter branch bracts with smaller flowers and occurs at higher elevations.

Known only from Panama in tropical moist forest in the Canal Zone, Colón, Chiriquí, Panamá, and Darién.

Heliconia irrasa Lane ex R. R. Smith, Phytologia 30:68–70. 1975

Caulescent, rhizomatous herb, 1.5–2(3) m tall, of musaceous habit; stem slender, to ca 5 cm diam. Petioles to ca 50 cm long, woolly-pubescent around sheath; blades oblong to oblong-ovate, acuminate, obtuse to rounded at base, 30–100 cm long, 7–30 cm wide; major veins 3–7 mm apart. Inflorescence erect, or nodding in fruit, densely villous-woolly throughout; peduncle 15–30 cm long; rachis moderately flexuous; bracts usually 6–8, the lowermost often leafy, the others spirally arranged, 6–17 cm long, long-acuminate, usually curling on ends, broadest near base, densely villous, 2–6 cm high, orange to yellowish-brown, the free margin red and undulate; internodes of lower bracts 2–3 cm long; flowers 5–6 cm long; perianth yellow, 4–5.2 cm long. Fruits broadly triangular, ca 1 cm long, ca 6 per bract, greenish to yellow, becoming purple. *Croat 12194.*

Occasional, in moist shady areas of the older forest. Flowers primarily from June to September, sometimes as early as April. The fruits mature mostly from September to December.

Distinguished by the erect inflorescence with yellowish, densely pubescent bracts that are often curled on the ends.

Known only from Panama from tropical moist forest in the Canal Zone, Colón, Panamá, and Darién, from premontane moist forest in Coclé and Panamá, and from tropical wet forest in Colón and Coclé (La Mesa).

See Fig. 144.

Heliconia latispatha Benth., Bot. Voy. Sulphur 170. 1846

Platanillo, Guacamaya

Caulescent, rhizomatous herb, 1.5–3 m tall; stem flattened, 4–5 cm wide by 2–2.5 cm thick. Petioles often somewhat pruinose, 30–40 cm long; blades broadly oblong, rounded and cuspidate at apex, rounded to truncate at base, 50–100 cm long, 15–30 cm wide; veins 4–10 cm apart, branching from midrib at ca 90° angle. Inflorescence glabrous, erect; peduncle 15–30 cm long; rachis strongly flexuous, usually greenish; bracts broad at base, long-acuminate, spirally arranged, the lower 1–3 bearing leaves (occasionally with blades to 1 m long), the leafless ones 4–25 cm long, 2–3.5 cm high at base, red or orange except the lower proximal margin yellowish-green; flowers 4–5 cm long, orange to yellow with green margins, lying ± flat in bract and mostly concealed by it. Fruits purple at maturity, broadly oblong, weakly trigonous, 8–10 mm long, emerging from bracts, the pedicels remaining concealed; seeds 3, ca 7 mm long. *Croat 6368.*

Very common in the Lighthouse and Laboratory Clearings and occasional on the shore; a ubiquitous species along roadsides and the railroad right-of-way in the Canal Zone. Flowers throughout the rainy season, rarely during the dry season. Stiles (1975) reported that the species flowers mostly from May to August in Costa Rica. The fruits develop within about 1 month and are abundant on some plants during the middle to late rainy season.

Recognized by its erect, glabrous inflorescence with much-spiraled, broad, red bracts often leafy at the base.

Mexico to Colombia, Venezuela, and Ecuador; possibly elsewhere in South America. In Panama, known from tropical moist forest on both slopes in the Canal Zone and in probably all provinces.

See Fig. 145.

Heliconia mariae Hook.f., J. Proc. Linn. Soc., Bot. 7:69. 1864

Beef-steak heliconia

Caulescent, rhizomatous herb, 3–6 m tall; stem flattened, to 12 cm broad and 4–6 cm thick. Petioles 50–100 cm long above the sheath; blades elliptic, blunt and cuspidate at apex, slightly lobed to rounded at base, to 2 m or more long and 60 cm wide (sometimes smaller on lower part of plant); veins 8–20 cm apart. Inflorescence glabrous or minutely pubescent, pendent on stout peduncle 50 cm or more long, with about 40 cm of peduncle exposed, the fertile part 20–80 cm long, 10–13 cm wide, tapering only slightly to apex; bracts 20–70, red, distichous, all but the lowermost closely imbricated and 3.5–8 cm long, broadest in the middle, acute to acuminate at apex; flowers only slightly protruding from bracts, white at base, reddish at apex, 2.5–4 cm long; ovary white, becoming lavender to blue. Fruits oblong, ca 1.5 cm wide and 9 mm wide, 3-angled, bright blue, exserted on a fleshy white peduncle, 3-seeded; seeds oblong, 8–10 cm long, 3–4 mm wide, covered with a fleshy white matrix. *Croat 8689.*

Known only from the vicinity of the Laboratory Clearing, usually at the edge of the forest and along Creek #8.

Fig. 146. *Heliconia mariae*

Fig. 147. *Heliconia pogonantha*

Probably flowering and fruiting throughout the year, but new inflorescences begin to open in the middle to late rainy season. Some flowers and mature fruits are generally present on the same inflorescence.

The only species of *Heliconia* on the island with a pendent inflorescence and imbricated bracts.

Belize to Panama and northern South America. In Panama, known from tropical moist forest in the Canal Zone (Atlantic slope), Bocas del Toro, Colón, and Darién.

See Fig. 146.

Heliconia metallica Planch. & Lind. ex Hook., Bot. Mag. 88, t. 5315. 1862

Caulescent, rhizomatous herb, 1–3 m tall; stem to ca 5 cm diam. Leaves much like *H. vaginalis* but very dark green above, maroon below, 20–120 cm long and 9–25 cm wide. Inflorescence glabrous, erect; peduncle to 50 cm long; bracts 5–7, green, glabrous or long-tomentose, 2.5–8 cm long, 1.5 cm or less deep; rachis ± straight; flowers reddish-pink, 4–5 cm long; all flowers parts extending above bracts; pedicel and lower half of ovary white, the upper rim becoming green in fruit. Fruits truncate, ca 1 cm long, green at apex, white at base, becoming blue at maturity; seeds ± pyramidal, ca 6 mm long and wide, gray-brown, rough. *Croat 16562.*

Cultivated in the Laboratory Clearing south of the Animal House near the edge of the forest. Introduced to the island from El Valle. Probably flowering all year, but especially in the dry and early rainy seasons.

Distinguished by the greenish bracts, reddish-pink flowers, and purplish lower blade surfaces.

Panama and Colombia, possibly elsewhere in South America. In Panama, known from tropical moist forest in the Canal Zone and Darién, from premontane wet forest in Coclé (El Valle) and Panamá (Cerro Campana), and from tropical wet forest in Coclé (La Mesa) and Darién.

Heliconia pogonantha Cuf., Arch. Bot. Sist. 9:191. 1933
H. pendula Wawra

Caulescent, rhizomatous herb, 3–5(6) m tall. Petioles ca 1 m long; blades broadly oblong, acute to acuminate, rounded at base and sometimes inequilateral, 1.5–2 m long and ca 50 cm wide, sometimes glaucous on underside. Inflorescence pendulous, red, 0.5–1(2) m long, inconspicuously puberulent; rachis flexuous; bracts broadly ovate, 6–18 cm long, red, strongly reflexed at anthesis; flowers 8–30, yellow, ca 4.5 cm long. Fruits pedicellate, ca 1 cm long, bluish. *Croat 12422.*

Cultivated at the Laboratory Clearing; introduced to the island by Dressler from the Caribbean slope. The inflorescence begins to emerge at the beginning of the rainy season, requiring nearly 1 month to become fully extended. The flowers emerge from the bracts before the inflorescence is fully extended and may still be present into the dry season of the following year. Stiles (1975) reported the species to flower all year in Costa Rica. The fruits develop within about a month.

Although possibly confused with *H. longa* (Griggs) Winkl., this species has branch bracts that are fleshy, not coriaceous, and only slightly longer than high. *H. longa* has coriaceous branch bracts that are long and slender (the longer ones four or more times longer than broad).

Costa Rica and Panama. In Panama, known from tropical wet forest along the Caribbean slope and in the Canal Zone.

See Fig. 147.

Heliconia vaginalis Benth., Bot. Voy. Sulphur 171. 1846

Caulescent, rhizomatous herb, 1–3 m tall, glabrous except the midrib of younger leaves minutely furfuraceous. Petioles often marked with maroon and sheathing stem to base of leaves; blades elliptic-oblong, long-acuminate at apex, obtuse to rounded below, mostly 30–100 cm long, 12–20 cm broad (the lowermost often tiny), dark green above, lighter below, the minute cross-veins visible. Inflorescence glabrous, erect; peduncle at least 3 cm long; bracts distichous, 6–9, red, 12–18 mm high at base, the lower ones often leafy and to 40 cm long, the uppermost 3–4 cm long; rachis somewhat flexuous; flowers 4–5.5 cm long, yellow except the tip green; pedicels and lower part of ovary yellow, the upper edge of ovary dark green, protruding above bract, prominently so in fruit. Fruits conspicuously truncate, ca 1 cm high, about as broad as long; immature fruit yellow with apex and peduncle green, mature fruits bluish-purple; seeds minute, brown. *Croat 11137.*

Occasional; particularly common on the shoreline, also common in clearings, rare in the forest. Perhaps the most common *Heliconia* on the island. Flowering and fruiting to some extent throughout the year, especially in the rainy season. Most plants have many fruits in various stages of development between the late rainy and early dry seasons.

Distinguished by the narrow, solid red, leafy bracts and yellow flowers.

Mexico to Ecuador. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, San Blas, Panamá, and Darién, from premontane wet forest in Colón (Río Providencia) and Panamá (Cerro Campana), and from tropical wet forest in Coclé (La Mesa).

Heliconia wagneriana O. G. Petersen in Mart., Fl. Brasil. 3(3):12. 1890

Caulescent, rhizomatous herb, to 6 m tall; stem flattened. Petioles mostly 40–60 cm long above vagination, the younger ones often with white waxy covering; blades oblong, short-acuminate at apex, broadly rounded to obtuse at base, 90–140 cm long, 20–30 cm broad. Inflorescence erect; peduncle stout, 15–50 cm long; bracts 6–12, usually pale red with greenish or yellowish margins, to 5 cm high at base, mostly 7–21 cm long, gradually long-acuminate, uniformly ascending, the lowermost often leafy; flowers 4–6 cm long, the tube white basally, greenish apically, curved toward apex; fertile stamens 5, exserted, equaling style. Fruits oblong, ca 1.5 cm long, blue, protruding on elongating, tubular, white pedicel at maturity. *Croat 6970.*

Known only from the vicinity of the Laboratory Clear-

ing. Flowers and fruits throughout the year, especially in the dry season. Stiles (1975) reported the species to flower only during the dry season in Costa Rica.

Distinguished by the moderately short, erect, stout inflorescence with closely imbricating bracts. Although described in *Flora Brasiliensis* by Petersen, it is listed there as only from Panama.

Probably pollinated by hummingbirds.

Honduras to Panama; Trinidad. In Panama, known from tropical moist forest in the Canal Zone, Colón, San Blas, Chiriquí and Darién, from premontane wet forest in Coclé, and from tropical wet forest in Bocas del Toro (Río Guarumo).

MUSA L.

Musa sapientum L., Syst. Nat. ed. 10, 1303. 1759
Banana

Caulescent, rhizomatous herb, to 6 m tall; stem round, to 15 cm thick, tapering upward. Leaves spiraled, the stout successive sheaths forming the trunk; blades broadly elliptic, to more than 2 m long, both the petiole and the lower surface of blade white-waxy. Inflorescence a terminal spike, emerging from leaf sheaths, drooping to pendent; flowers unisexual, in flat clusters beneath broad, spirally arranged, purplish bracts, the distal clusters on the rachis functionally staminate, the proximal clusters functionally pistillate; flowers of both sexes with the calyx tubular, the corolla of 1 petal; staminate flowers and bracts deciduous; stamens usually 6, 1 a staminodium. Fruit a fleshy elongate berry.

Cultivated in the Laboratory Clearing.

Juvenile plants are similar to *Heliconia,* but the species may be distinguished by its round stem and petioles, which are continuous with the margin of the blade.

Native to India, but now widely cultivated in the tropics.

32. ZINGIBERACEAE

Perennial rhizomatous or tuberous herbs, usually aromatic. Leaves alternate, spiraled, or distichous (*Renealmia*), sessile to petiolate; petioles sheathed, ligulate; venation closely spaced, parallel-pinnate. Flowers bisexual, zygomorphic, in terminal or scapose, bracteate, spiciform inflorescences; calyx trilobate; petals 3, unequal, showy, the posterior lobe largest, or corolla trilobate; fertile stamen 1; sterile stamens 2, united (opposite the fertile anther) into a petaloid labellum (the labellum small in *Renealmia*); anther 2-celled, dehiscing longitudinally; ovary inferior, 3-locular, 3-carpellate (2-locular and 2-carpellate in *Dimerocostus*); placentation axile; ovules many, anatropous; style 1; stigma capitate or bilamellate. Fruits usually 3-valved, loculicidal capsules (irregularly dehiscent in *Zingiber;* 2-valved and tardily dehiscent in *Dimerocostus*); seeds many, arillate, with copious hard endosperm.

Zingiberaceae are distinguished by their spirally or distichously arranged leaves with nearly parallel veins and by their closely bracteate terminal inflorescences with usually showy flowers bearing a single petaloid stamen. They may also be distinguished by their usually capsular fruits with many small arillate seeds.

Hummingbirds pollinate the small red or red-orange tubular flowers of *Costus pulverulentus* and *C. scaber.* They possibly pollinate *Renealmia cernua* and *R. alpinia,* which have short, tubular, reddish-orange flowers. Other species of *Costus,* including *C. allenii, C. guanaiensis,* and *C. laevis,* are pollinated by both male and female bees of the genera *Euglossa, Eulaema,* and *Euplusia* (Maas, 1972; Dodson, 1966). Both male and female bees of *Euglossa ignita, Eulaema meriana, E. speciosa, E. polychroma,* and *Euplusia surinamensis* visit flowers of *Costus villosissimus* (Dodson, 1966).

The fruits are eaten by animals. The soft, white, generally indehiscent capsules of *Costus* are exposed against the generally red inner bract surface as the bracts reflex at maturity. The seeds are shiny, black, and bear a lacy, sticky aril ideally suited to sticking to the beaks of birds. The fruits are eaten by other animals as well. Monkeys have been observed eating fruits of *Renealmia cernua* (Oppenheimer, 1968). Inflorescences of *Renealmia* are produced near the ground, perhaps more because of the pollination system than because of the dispersal strategy (van der Pijl, 1968).

About 50 genera with 1,500 species; tropics and subtropics.

KEY TO THE TAXA OF ZINGIBERACEAE

Leaves distichous (2-ranked); flowers less than 3 cm long;
  Corolla yellow-green, the lip trilobate; leaves less than 2.5 cm wide; inflorescences spikes bearing closely spaced, green bracts ..... *Zingiber officinale* Rosc.
  Corolla yellow or red, the lip not trilobate; leaves mostly more than 2.5 cm wide; inflorescences not as above ..... *Renealmia*
Leaves spirally arranged; flowers more than 3 cm long:
  Flowers white, very large; calyx 3–3.5 cm long, becoming brown and extending well above the bracts (at least in fruit); ovary bilocular ..... *Dimerocostus strobilaceus* O. Kuntze subsp. *strobilaceus*
  Flowers variously colored but never entirely white; calyx less than 2 cm long, never exserted, even in fruit; ovary trilocular ..... *Costus*

KEY TO THE SPECIES OF COSTUS

All bracts with foliaceous appendages; plants growing in clearings or open areas:
- Flowers yellow; plants densely ferruginous-villous-hirsute, the trichomes on the bracts to 2 mm long ..... *C. villosissimus* Jacq.
- Flowers white, often striped with red in the labellum; plants puberulus, the trichomes to 1 mm long ..... *C. guanaiensis* Rusby var. *macrostrobilus* (K. Schum.) Maas

Bracts lacking appendages or only the lower ones appendaged; plants usually growing in the forest:
- Plants rarely more than 1 m tall; inflorescences fusiform (sharp-pointed at apex); margins of bracts dilacerating into fibers; plants common; flowers red, tubular, 50–70 mm long ..... *C. pulverulentus* Presl
- Plants usually 1.5–3.5 m tall; inflorescences ± cylindrical; margins of bracts usually not dilacerating into fibers; plants infrequent:
  - Plants densely brownish-pilose; labellum yellowish striped with red or reddish striped with yellow; bracts green ..... *C. allenii* Maas
  - Plants glabrous or nearly so:
    - Inflorescences 1–3.5(4.5) cm wide; flowers tubular, 3–4 cm long; labellum inconspicuous, exceeding corolla at most a few mm, less than 20 mm wide; midrib on upper side of leaves densely strigillose; bracts red to orange-red ..... *C. scaber* R. & P.
    - Inflorescences 3–7(9) cm wide; flowers 5–9 cm long; labellum conspicuous, greatly exceeding corolla, more than 50 mm wide; midrib on upper side of leaves glabrous; bracts green to yellowish-green in the exposed part ..... *C. laevis* R. & P.

COSTUS L.

The genus is distinguished by the unbranched stems and the spirally arranged leaves bearing a prominent sheath, which encircles the stem. In some species the stem itself may be spiraled. Flowers are compacted into a conelike terminal spike (in ours) and appear singly or few at a time over a long period. The fleshy capsules are usually white and contrast sharply with the usually red interior surface of the bracts as the bracts fold out in age to expose the fruits.

Costus allenii Maas, Fl. Neotr. Monogr. no. 8, Zingiberaceae, Costoideae 61. 1972

Plants to 2(3.5) m tall, often in moderately large populations, brownish-pilose on most parts, especially on sheaths, petioles, and lower midrib of leaves; stem ca 1.5 cm diam. Leaves nearly sessile, oblanceolate-elliptic, caudate-acuminate, tapered to obtuse base, mostly 25–40 cm long, 9–16 cm wide. Inflorescences ± ovoid, 4.5–6.5(11) cm long, 3.5–4.5(7) cm wide; bracts rounded, 3–4 cm long and wide, green, the covered portion red, the upper ones inconspicuously pubescent, the lowermost conspicuously villous and with reduced leaves, the upper margin thin, glabrous, and reddish, the callus green; bracteole 2–2.5 mm long; calyx 8–10 mm long, the lobes 2–4 mm long; corolla white, ca 5 cm long, the lobes obovate, ca 3.5 cm long, 1.5–2.0 cm wide; labellum 5.5–7 cm long, pale red striped with yellowish-white or pale yellow striped with red at apex, yellowish-white at base, unequally trilobate, the central lobe heavily tinged with yellow at base; petals 3, lanceolate-elliptic, obtuse to apiculate, yellowish-white, ± transparent, 1.5–5 cm long; stamen 3–4.5 cm long, reddish and reflexed at apex; style borne between the 2 thecae, its broad stigma held just above the thecae. Fruiting inflorescence and fruits similar to *C. laevis;* capsules ellipsoid, 8–20 mm long, glabrous or puberulous at apex; seeds black. *Croat 16198.*

Infrequent, but sometimes locally abundant along streams or in marshy areas. Apparently flowering and fruiting during the rainy season.

Most easily confused with *C. laevis* because of the similar color of the labellum. It is distinguished, however, by being densely and softly pubescent, while *C. laevis* is nearly glabrous; *C. laevis* is also a much larger, stouter plant. Maas (1972) suggested this may be a hybrid of *C. villosissimus* and *C. laevis.*

Pollinated by large bees, as are *C. laevis* and *C. guanaiensis.*

Panama, Venezuela, Colombia, and Ecuador. In Panama, known from tropical moist forest in the Canal Zone and from premontane wet forest in Colón, Coclé (El Valle), and Panamá (Cerro Jefe).

Costus guanaiensis Rusby var. **macrostrobilus** (K. Schum.) Maas, Fl. Neotr. Monogr. no. 8, Zingiberaceae, Costoideae 52. 1972

C. friedrichsenii sensu Woods. non O. G. Petersen

Plants moderately stout, usually densely puberulent, 2–4(6) m tall; stem straight, usually 2–5 cm diam, the lower 1.5–2 m leafless. Leaves narrowly ovate to narrowly obovate, gradually acuminate, narrow and cuneate to rounded at base, all but the uppermost 30–65 cm long, 7–17 cm wide, shortening at apex and merging inconspicuously with leaflike bracts, puberulent on both surfaces, the trichomes soft, to 1 mm long. Inflorescence broadly ovoid; bracts green (red at base within), all with foliaceous tips, 1.5–6 cm long or more, the outermost pubescent like the leaves, those on inner whorls glabrous; bracteole 2.5–4 cm long, red; calyx to 16(22) mm long,

Fig. 148. *Costus guanaiensis* var. *macrostrobilus*

Fig. 149. *Costus laevis*

Fig. 150. *Costus pulverulentus*

Fig. 151. *Costus pulverulentus,* fruiting inflorescence

red, with 3 acute lobes; corolla white, 7–8.5(10) cm long, 3–3.5 cm wide, the lobes 3, almost free; stamen 5–8 cm long; labellum 7.5–11 cm long, white with red to pink lines, sometimes white-pubescent within on either side of stamen, its central lobe fimbriate, usually marked with yellow. Capsules 1–3.5 cm long; seeds irregularly 3-sided to round, 2–3 mm long, black, enveloped in a white lacerate aril. *Croat 6388.*

Apparently uncommon; collected at Rear #8 Lighthouse Clearing. Flowers in the rainy season, chiefly from June to September. The fruits are shed usually by the end of the rainy season.

Distinguished by having foliaceous tips on all bracts.

Guatemala and Belize to Guyana, Brazil, and Peru. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién, from premontane moist forest in the Canal Zone and Panamá, from premontane wet forest in Chiriquí, and from tropical wet forest in Panamá.

See Fig. 148.

Costus laevis R. & P., Syst. Veg. 3. 1798

Stout, essentially glabrous plant, 1–3.5(6) m tall; stem 1.5–3 cm diam, the lower part leafless. Petioles lacking or to 3 cm long; blades oblanceolate, gradually long-acuminate, cuneate at base, mostly 44–53 cm long, 10–16 cm wide; basal and apical leaves much smaller, the lowermost reduced to bulbous projections. Inflorescence ovoid to oblong, somewhat narrowed at both ends, 5–10 cm long (to 25 cm long in fruit), 3–7(9) cm wide; bracts glabrate to appressed-pubescent, red, lacking leaflike appendages or with only the lowermost bearing leaflike appendages, the others rounded to broadly oblong and green at apex; bracteole 2–3 cm long; calyx 8–13(20) mm long, red or white, trilobate; corolla 5–9 cm long, white or faintly red and yellowish at base; labellum 6–9.5 cm long, 4–5.5 cm wide at apex, unequally trilobate, the middle lobe curved forward and lacerate, its color variable, usually red to maroon with white lines or white to yellowish with red markings, the center yellowish within; stamen red and recurved at apex, 3.5–5 cm long, the margin minutely toothed. Capsules white, ellipsoid, 1–2.5 cm long, sharply contrasting with inner surface of opened bracts at maturity; seeds subglobose to irregularly 3-sided, 2–3 mm long, black, enveloped in a fleshy lacerate aril. *Croat 15586.*

Occasional, in the forest, especially in open areas of tree falls and along streams. Flowers in the rainy season, chiefly from June to September. The fruits are usually shed by late in the rainy season or in the earliest part of the dry season (December).

Probably pollinated by euglossine bees. At maturity the fruiting inflorescence may be as much as 15 cm broad when the bracts are spread open. This species is the tallest *Costus* on the island. It is often nearly leafless for the first 2 m.

Guatemala south to western South America as far as Bolivia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Panamá, and Darién, from premontane wet forest in Bocas del Toro, Coclé, and Panamá, and from tropical wet forest in Colón.

See Fig. 149.

Costus pulverulentus Presl, Rel. Haenk. 1:41. 1830

C. sanguineus Donn. Sm.

Plant usually about 1 m or less tall; stem commonly spiraled, less than 1 cm diam, often reddish at least near base. Leaves moderately few and well spaced (except the uppermost), narrowly obovate, abruptly acuminate at apex, narrowed to broadly-cuneate at base, 12–26(30) cm long, 4–9.5(12) cm wide, essentially glabrous or puberulent on underside, the sheath-ligule extended above the leaf base, its upper side fringed with dilacerating fibers. Inflorescence usually 3–7 cm long, ellipsoid to sharply pointed; bracts 2.5–4.5 cm long, red to orange-red (rarely greenish), the margins dilacerating into fibers, the innermost usually glabrous on outer surface except at margin; bracteole ca 2 cm long, red; flowers tubular, red, 5–7 cm long, ca 1 cm wide; calyx red, shallowly trilobate, 7–10 mm long, persistent in fruit; corolla lobes ± oblong, 1–1.5 cm wide, flared to 4 cm wide above, the center lobe barely exceeding stamen; labellum shorter than stamen, 5-lobed, the 3 central lobes narrow and toothlike. Capsules ellipsoid, 1–2.5 cm long; seeds many, black, 2–3 mm long, irregularly rounded to irregularly 3-angled, covered with a shredded white aril. *Croat 9222.*

Abundant in the forest, particularly along trails, but also in old tree-fall areas. Flowering mostly in the middle to late rainy season, especially from July to October. The fruits are shed by the late rainy season or early dry season. A second but distinctly smaller flush of flowering occurs in the dry season (March and April), with the fruits being shed at the beginning of the rainy season.

Maas (1972) indicated considerable variability in the height of this species, 0.5 to 2.5 m and rarely to 3.5 m tall. On BCI it is rarely more than 1 m tall. The species may be confused only with *C. scaber.*

Pollinated by hummingbirds.

Mexico to Colombia, Venezuela, and Ecuador. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí (Burica Peninsula), Los Santos, Panamá, and Darién and from premontane wet forest in Coclé (El Valle).

See Figs. 150 and 151.

Costus scaber R. & P., Syst. Veg. 2, pl. 3. 1798

Slender herb, mostly 1.5–2(3) m tall, usually in clusters of 3–8 plants; stem usually less than 1 cm thick, sometimes spiraled at apex; stems, lower leaf surfaces, and inflorescence bracts usually inconspicuously puberulent. Leaves ± sessile, mostly narrowly elliptic-obovate, acuminate at apex, narrowed to rounded or subcordate at base, all but the uppermost 10–25(30) cm long and 3–6(11) cm wide; midrib on upperside densely strigillose. Inflorescence 5–12 cm long, 2.5–4.5 cm wide, oblong, bluntly rounded at apex; bracts red to red-orange, obtuse

at apex, 2–3.5 cm long and wide, usually puberulent, the margin thin, glabrous but opaque, only the covered part dilacerating into fibers, the callus prominent, green or yellowish; bracteole 1–1.5 cm long, reddish; flowers orange-red, 3–4 cm long, ca 1 cm wide; calyx reddish, 3–7 mm long, shallowly trilobate, the lobes obtuse; corolla lobes oblong-obovate, thin, ca 1 cm wide, red; labellum red or red-orange, oblong-obovate (when spread out), thick, slightly exceeding corolla lobes, the margins curved upward, partially enclosing stamen; stamen about as long as labellum, usually yellow at apex; style fit in slot between the 2 thecae of anther, obcordate and thickened apically; stigma rounded at apex, consisting of 2 flaps, the margins ciliate. Capsules ellipsoid to subglobose, 7–12 mm long, glabrous to densely puberulous at apex; seeds black. *Croat 14868.*

Occasional, in the old forest, usually in old tree-fall areas or along trails; often in large local stands. Flowers in the rainy season, chiefly in June and July, but some flowering continues throughout the rainy season. The fruits are shed mostly in the late rainy and early dry seasons.

Pollinated by hummingbirds.

Mexico to the Guianas, Brazil and Bolivia; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro (Isla Colón), Colón (Isla Grande), Panamá, and Darién and from premontane wet forest in Chiriquí, Coclé, and Panamá.

Costus villosissimus Jacq., Fragm. Bot. 55, pl. 80. 1809

C. hirsutus Presl

Cañagria, Caña de mico

Plant 2–3(6) m tall, conspicuously ferruginous villous-hirsute especially on blades, upper part of sheaths, and tips of inflorescence bracts. Petioles very short; blades oblong-elliptic, acuminate, cuneate to inconspicuously subcordate at base, 15–30(62) cm long, 5–13(14) cm wide. Inflorescence 5–10 cm long (to 20 cm in fruit); bracts green, 5–8 cm long, the lowermost longer, leaflike, the tips spreading or recurved, acute, foliaceous, unexposed parts of bracts red on both surfaces at least in fruit; bracteole 1.5–3 cm long; flowers with all parts yellow (rarely with white corolla); corolla lobes narrow, 6–7.5 cm long, to 3.7 cm wide; labellum 8–10 cm long; anther to 8 cm long, the thecae well below apex. Capsules white, ellipsoid, 15–25 mm long, minutely puberulous at apex; seeds black. *Croat 11722.*

Very common along roadsides in parts of the Canal Zone adjacent to BCI and probably abundant on the island at one time; seen recently only a few times along the shore and in sign clearings, but to be expected sporadically in larger clearings. Beginning to flower in late March or April, reaching a peak of flowering in June or July, and continuing until October. The fruits mature mostly in the middle to late rainy season.

Pollinated by large bees.

Costa Rica to Colombia, Venezuela, the Guianas, Ecuador, and Peru; West Indies (Jamaica and Lesser Antilles). In Panama, known from tropical moist forest in the Canal Zone, Colón, San Blas, Herrera, Panamá, and Darién, from tropical dry forest in Panamá (Taboga Island), from premontane moist forest in the Canal Zone (Ancón Hill), and from premontane wet forest in Chiriquí, Coclé, and Panamá.

DIMEROCOSTUS O. Kuntze

Dimerocostus strobilaceus O. Kuntze subsp. **strobilaceus,** Rev. Gen. 2:687. 1891

D. uniflorus (Poepp. ex O. G. Petersen) K. Schum.

Cañagria

Stout herb, 3–4(6) m tall; stem 1–4 cm diam, often leaning and somewhat spiraled, bearing leaves only near apex. Leaves sessile or on obscure petiole, closely spiraled, oblong-oblanceolate, narrowly acuminate, gradually narrowed to base, 20–50 cm long, 6–10 cm wide, glabrous above, minutely sericeous or glabrous below, the midrib prominently impressed above, raised below; leaf sheaths densely pubescent, ciliate on upper edge. Inflorescence spiciform, ± spirally contorted, 15–30 cm long, 5–9 cm broad; bracts numerous, closely sheathing, 2–3 cm long, usually with a linear callus near apex; bracteole surrounding each flower, bilobed, winged laterally, exceeding bracts; calyx green becoming brown in fruit, coriaceous, sericeous, 3–3.5 cm long at anthesis, 2 of 3 lobes with linear callus; flowers white, usually only 1 open at a time; corolla lobes 3, narrowly oblong, 5.5–7(8) cm long; labellum 8–11 cm long and broad, the center of the tube opposite the stamen yellow; stamen solitary, 3–4 cm long; ovary sericeous, ca 1 cm long at anthesis, to 4 cm in fruit. Fruits tardily dehiscent, 2-celled capsules, green above, whitish below; seeds numerous, closely packed in irregular rows, shiny and black, ca 4 mm long, oblong, angulate, flat above, with a rounded apical depression. *Croat 5100.*

Occasional, in the forest, usually in open places along trails; locally common along the shore. The flowers and fruits are seen all year, though perhaps with heaviest flowering late in the dry season and during the rainy season. Individual plants often have both flowers and fruits in various stages, but occasionally plants are seen with fruits and without flowers or buds.

A conspicuous species, distinguished from *Costus* by its stiff calyces, which turn brown and persist in fruit. The fruits eventually weather and dehisce.

Honduras to Ecuador and Peru. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién and from tropical wet forest in Colón.

RENEALMIA L.f.

Renealmia alpinia (Rottb.) Maas, Acta Bot. Neerl. 24:474. 1975

R. exaltata L.f.

Large herb, 2.5–4 m tall. Leaves distichous, oblong-elliptic, acute or weakly acuminate at apex, decurrent at

KEY TO THE SPECIES OF RENEALMIA

Inflorescences arising directly from the rhizome (scapose), paniculate (at least not conelike), red; leaves often more than 10 cm wide ..... *R. alpinia* (Rottb.) Maas

Inflorescences terminal at apex of stem, conelike, orange; leaves usually less than 10 cm wide ..... *R. cernua* (Sw.) Macbr.

Two other species of *Renealmia* that could be expected on BCI are *R. occidentalis* (Sw.) Sweet and *R. mexicana* Ulotr. ex O. G. Petersen.

base onto obscure petiole, to 84 cm long and 19 cm wide (mostly less), the sheath and ligule slightly longer than base of petiole. Inflorescence scapose, arising from rhizome near base of stems, 2–45 cm tall, the base enveloped with imbricate bracts, these 1–10 cm long and deciduous; flowers red, to 2.7 cm long, weakly pubescent, arranged in short panicles to ca 5 cm long; calyx thin, trilobate in upper third, the lobes narrowly acute; corolla trilobate, the lobes rounded, ± cucullate; labellum scarcely exceeding corolla, pale yellow, with 4 short lobes at apex, the inner pair of lobes often acute, the outer pair round; stamen solitary, thick, shorter than corolla; apex of style much thickened. Capsules 3-locular, ± ellipsoid, to 3.5 cm long and 2 cm wide, red, drying with many closely spaced, prominent, longitudinal striations; valves fleshy, 3 mm thick; seeds many, white, 3–4 mm long, bearing a long, sticky, arillate appendage at base. *Croat 6483.*

Infrequent, in the forest, usually occurring in tree-fall areas, not persisting long after being completely shaded. Seedlings of the species are more abundant. Flowers and fruits within the rainy season. The flowers bloom over a long period, chiefly from July to September. Mature fruits may be present on an inflorescence that is still producing flowers.

Belize to Brazil; the Antilles. In Panama, known from tropical moist forest in the Canal Zone and Darién, from premontane wet forest in Chiriquí and Coclé, and from tropical wet forest in Colón.

See Fig. 152.

Renealmia cernua (Sw.) Macbr., Field Mus. Nat. Hist., Bot. Ser. 11:14. 1931

Aromatic herb, 1.5–2.5(3) m tall. Leaves distichous; petioles sheathed, the sheath patterned with small rectangular areas, often extending beyond base of blade; blades oblong to oblong-elliptic, gradually to abruptly acuminate, 4–40 cm long, 2–12 cm wide; veins closely spaced and prominent on underside. Inflorescence sessile or short-pedunculate at apex of stem, 4–15 cm long, conelike, ovoid to oblong; bracts usually orange, persistent, boat-shaped, 2–3 cm long; calyx acutely trilobate, to 1.5 cm long; corolla tubular, trilobate, orange to yellow, to ca 2.5 cm long when mature, slightly exceeding bracts; labellum orange, trilobate, only slightly longer than corolla; style thick at apex. Capsules ovoid to ellipsoid, ± equaling length of fruiting calyx, prominently striate with whitish lines, topped by the persistent green calyx exserted well above the bracts. *Croat 11882.*

Common in all parts of the forest. Flowers from the late dry season through the rainy season, chiefly from June to September. The fruits mature mostly in the middle to late rainy season, from August to December. Juvenile inflorescences are common by the beginning of the dry season in December.

The fruits are reported as fleshy, irregularly dehiscent capsules, but I have never seen them dehisce. They are probably dispersed by birds.

Guatemala to Peru. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, San Blas, Chiriquí, Panamá, and Darién, from premontane wet forest in Colón, Chiriquí, Coclé, Panamá, and Darién, from tropical wet forest in Colón and Darién, from premontane rain forest in Coclé, and from lower montane rain forest in Chiriquí.

See Fig. 153.

ZINGIBER Boehm.

Zingiber officinale Rosc., Trans. Linn. Soc. London 8:348. 1807

Common ginger

Herb, ca 1 m tall; rhizome tuberous, aromatic. Leaves distichous, sessile, lanceolate to linear-lanceolate, gradually narrowed to both ends, sheathing at base, 15–30 cm long, 1.5–2.5 cm wide, thin. Inflorescences spicate, usually arising from the root (sometimes from stems), shorter than the stems; peduncles bracteate, their bracts merging with the bracts of the spike; spikes 4.5–7 cm long, 1.5–2.5 cm broad; floral bracts ovate, ca 2.5 cm long, green, the margin scarious; corolla yellow-green, cylindrical, the tube enlarged at apex, the lobes lanceolate, ca 2 cm long, longer than lips; lip deflexed, purple with yellow spots; fertile stamen solitary, the filament short, the connective usually produced into a long spur exceeding the lip. Capsules 3-valved, rupturing irregularly. *Croat 6349.*

Cultivated at Rear #8 Lighthouse Clearing. Flowers apparently in the rainy season.

Probably native to the Pacific islands, but cultivated throughout tropical regions of the world. In Panama, collections have been made only from BCI.

33. MARANTACEAE

Perennial, caulescent or acaulescent herbs, rarely aquatic; roots often tuberous. Leaves alternate, distichous or basal; petioles pulvinate at apex, sheathing the stem at base; blades simple, entire; venation pinnate. Inflorescences

Fig. 152. *Renealmia alpinia*

Fig. 153. *Renealmia cernua*

KEY TO THE TAXA OF MARANTACEAE

Plants stemless, the leaves arising from the ground ..... *Calathea* (in part)
Plants with a stem, at least part of the leaves arising from the stem:
Apex of blade oblique, the tip markedly offset from center; pulvinus with annular ring at base ..
..... *Ischnosiphon pruinosus* (Reg.) O. G. Petersen
Apex of blade not markedly oblique, the tip not offset from center; pulvinus without annular ring at base:
Blades pruinose beneath (covered with white waxy layer; on older specimens, the waxy layer is no longer visible):
Leaves often more than 50 cm long and 25 cm wide, obtuse or rounded at apex; spikes 3–5 cm broad, the bracts nearly as broad as high ..... *Calathea lutea* (Aubl.) Schult.
Leaves seldom more than 35 cm long and 20 cm broad, acuminate to caudate at apex; spikes less than 1 cm broad, the bracts much higher than broad .....
..... *Ischnosiphon leucophaeus* (Poepp. & Endl.) Koern.
Blades not pruinose beneath (sometimes weakly pruinose in *Thalia geniculata*):
Spikes markedly flattened and more than 4.5 cm broad ..... *Calathea insignis* O. G. Petersen
Spikes ± cylindrical or somewhat flattened and less than 1 cm wide:
Plants aquatic or at least occurring at edge of shoreline marshes; flowers purple, in open paniculate inflorescences; uncommon ..... *Thalia geniculata* L.
Plants never aquatic, generally within forest or in clearings:
Plants with numerous leaves forming a close spiral at the apex of a stout, canelike stem; most blades less than 12 cm broad; bracts orange, in open paniculate inflorescences, deciduous ..... *Stromanthe jacquinii* (R. & S.) Kenn. & Nic.
Plants never with leaves forming a close spiral at the apex of a stout stem; blades usually more than 12 cm broad; bracts persistent in capitate inflorescences:
Flowers cream-colored; lower surface of blade softly pilose; major veins scarcely raised (not pleated), midrib pubescent in furrow above; sheath glabrate .....
..... *Calathea marantifolia* Standl.
Flowers purple; lower leaf surface glabrous; major lateral veins raised, leaf pleated; midrib glabrous above; sheath densely pilose ... *Calathea latifolia* (Link) Klotzsch

bracteate panicles or racemes, often capitate, usually terminal, sometimes arising directly from the rhizome; bracts usually congested, spirally arranged; spikes more or less terete; flowers bisexual, zygomorphic; sepals 3, free; corolla deeply 3-lobed; stamens petaloid, the androecium basically of 2 whorls, the outer whorl usually with 1–3 staminodia, the inner whorl with 1 fertile stamen and 1 or 2 staminodia; anther 1-celled, lateral, dehiscing by a vertical slit; ovary inferior, 3-locular (usually only 1 locule fertile), 3-carpellate; placentation axile; ovules 1 per locule, seemingly basal; style 1, simple, (may be twisted, lobed, etc.); stigma terminal. Fruits loculicidal capsules; seeds 1–3, often arillate, with copious endosperm.

Members of the family share with the Cannaceae and Musaceae (31) usually broad leaves, with the closely parallel, fine lateral veins much less prominent than the midrib. They may be distinguished by the pulvinate, terete petiole, the very asymmetrical flowers with much modified, often petaloid staminodia, and the short, spirally arranged bracts (or, if distichously arranged, the compound inflorescence).

The flowers of most Marantaceae are bee pollinated (Kennedy, 1973). After alighting on the flower, the bee commences to feed, thus triggering a small flap on the cucullatum that acts as a release for the springlike style, which bears a loose mass of pollen just below the stigma. The pollen is deposited into a depression in the style before anthesis. The style springs forward, striking the bee on the "chin," first with the stigma (picking up pollen deposited there during a previous visit) and then with the pollen load. In some species, such as *Calathea marantifolia* and *C. latifolia,* the flower buds do not open until forced open by a bee. *Calathea insignis* is visited by both sexes of *Euglossa ignita, E. dodsoni, E. gorgonensis,* and *E. hansoni,* as well as by *Eulaema cingulata* and *E. polychroma.* All visits are to collect pollen (Dodson, 1966). On BCI most species of Marantaceae are pollinated by *Euglossa imperialis,* but sometimes also by *Eulaema cingulata* (H. Kennedy, pers. comm.). I have seen large tabinid flies visiting *Calathea inocephala. Calathea panamensis* has flowers that are cleistogamous (H. Kennedy, pers. comm.). *Stromanthe jacquinii* is visited by hummingbirds (H. Kennedy, pers. comm.).

The fruits are capsular, and some usually develop to maturity while the plant is still flowering. Seeds usually emerge from the capsule by swelling of the pedicel and become exposed as the bracts are reflexed or weather away; they are probably bird dispersed.

About 30 genera with 350–400 species; mostly in damp, shady, tropical or subtropical habitats.

CALATHEA G. Meyer

Calathea inocephala (O. Kuntze) Kenn. & Nic., Ann. Missouri Bot. Gard. 62:501. 1975

C. barbillana Cuf.; *Phyllodes inocephalum* O. Kuntze

Acaulescent herb, to more than 2 m tall. Petioles ca 1.5 m long, round, vaginate on lower part, the pulvinus 10–16

KEY TO THE SPECIES OF CALATHEA

Plants stemless, the leaves arising from the ground:
- Plants more than 1 m tall; leaf blades glabrous beneath, the midrib above glabrous, often with lighter green band running the length of the blade between midrib and margin when still juvenile; adult blades 25–45 cm broad; inflorescences globose, ca 6 cm wide ..... *C. inocephala* (O. Kuntze) Kenn. & Nic.
- Plants less than 1 m tall; leaf blades minutely to conspicuously pubescent beneath; midrib above pubescent; blades mostly less than 15 cm broad; inflorescences usually not globose, usually less than 4 cm wide:
  - Blades pubescent above, marked with several brown or dark green spots along the blade between the midrib and the margins; bracts of inflorescence 2-ranked; plants cultivated in the Laboratory Clearing ..... *C. villosa* (Lodd.) Lindl.
  - Blades glabrous above except midrib; leaf uniformly green above; bracts of inflorescence spirally arranged:
    - Blades green beneath; leaf sheaths wide, spreading, subglabrous, extending to base of pulvinus; inflorescence sessile, more than 4 cm long; flowers yellow ... *C. panamensis* Standl.
    - Blades often maroon beneath; leaf sheaths puberulent, narrow, ending well below the pulvinus; inflorescence long-pedunculate (7 cm or more), held as high as or higher than leaves; flowers white ..... *C. micans* (Math.) Koern.

Plants with a stem, at least part of the leaves arising from the stem:
- Blades pruinose beneath ..... *C. lutea* (Aubl.) Schult.
- Blades not pruinose beneath:
  - Spikes markedly flattened and more than 4.5 cm broad ..... *C. insignis* O. G. Petersen
  - Spikes ± cylindrical or somewhat flattened and less than 1 cm wide:
    - Flowers cream-colored; lower blade surface softly pilose; major veins scarcely raised (not pleated), midrib pubescent in furrow above; sheath glabrate ..... *C. marantifolia* Standl.
    - Flowers purple; lower leaf surface glabrous; major lateral veins raised, leaf pleated; midrib glabrous above; sheath densely pilose ..... *C. latifolia* (Link) Klotzsch

cm long, darker green in color; blades very broadly elliptic, blunt at apex, truncate to rounded at base, 45–100 cm long, 25–45 cm wide, ± concolorous, the very margin often reddish; veins about 10–15 mm apart, branching from midrib at 45° angle; blades of juvenile plants occasionally with streaked, light green bands midway between midrib and margin. Inflorescences ± globose, 6–12 cm long, ca 6 cm wide; peduncles 50–80 (150) cm long; bracts many, ca 5 cm long, becoming very weathered; flowers densely aggregated, pale orangish-yellow or cream-colored, 5 cm long, soon perishing. Capsules orange, pedicellate, strongly 3-sided, less than 2 cm long and about as broad; seeds 1–3, irregularly oblong-ovoid, ca 1 cm long, 7–8 mm wide, violet-blue, with an irregular white aril at base. *Croat 16576.*

Common in the forest, at least as a juvenile plant. Flowers from mid-April to September, mostly in June after the rainy season has begun. The fruits develop to maturity by August and may constitute most of the head by late in the flowering season; the last fruits persist until about mid-January.

Easily recognized by its short broad leaves and globular inflorescences, which often age and weather while the plant is still flowering. Sterile plants may be confused with *C. lutea,* but the blades are never pruinose on the underside as in that species. Unlike most species of *Calathea,* the fruits are a conspicuous feature of the plant.

Mexico to Peru. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, Coclé, Panamá, and Darién and from premontane wet forest in Chiriquí.

Calathea insignis O. G. Petersen in Mart., Fl. Brasil. 3(3):124. 1890

Caulescent, moderately stout herb, 2–3 m tall; stems ± swollen at base of petiole. Petioles long, often scabrid and brown near base; blades ovate to ovate-elliptic, short-acuminate, rounded or obtuse at base, usually more than 1.5 times longer than broad, 35–70 cm broad, dark green on upper surface with pale green midrib, glabrous except the midrib appressed-pubescent on upper surface. Inflorescences terminal on stem; spikes 1–3, laterally flattened, broadly oblong, 15–40 cm long; peduncles to 25 cm long, 4.5–6 cm broad; bracts greenish-yellow, 2-ranked, perpendicular to the rachis, broadly reniform, glabrate, the upper edge rounded; flowers pale yellow, 2.5–3.5 cm long. Fruits similar to those of *C. latifolia. Aviles 85b.*

Though long known to be present on Orchid Island, a population of the species was discovered by Foster near Barbour Trail 1500 only recently. Flowers principally in the rainy season (June to November), but also in March and April at higher elevations in Panama. The fruits develop soon and are usually already of mature size while the plant is still in flower.

The species prefers a moist habitat, often occurring in coastal and estuarine flood plains elsewhere in Panama; it does not grow well in deep forest. It is an invading species.

Coastal areas from Mexico to Colombia and Peru. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Panamá, and Darién, from premontane wet forest in Bocas del Toro, Colón,

and Coclé, and from tropical wet forest in Bocas del Toro and Colón.

Calathea latifolia (Willd. ex Link) Klotzsch in R. Schomb., Reisen Brit.-Guiana 3:918. 1848

C. allouia var. *violacea* sensu Woods. non Lindl.

Bijao, Faldita morada, Sal, Sweet corn root

Caulescent, 1–2 m tall; roots bearing large, edible tuber-like storage organs. Petioles with short-pilose sheath, the pulvinus to 7.5 cm long, somewhat brownish; blades ovate to oblong-ovate, obtuse to short-acuminate, rounded to subtruncate at base, ca 70 cm long and 30 cm wide, bicolorous, frequently with light purple bands between midrib and margin, the surface glabrous, pleated; midrib glabrous to minutely puberulent, the lateral veins sparsely puberulent, raised. Spikes solitary, ovoid to cylindrical, 6–14 cm long, 3–5.5 cm wide; peduncle 7–30 cm long; bracts reniform, spiral, closely imbricated, to 2.5 cm high and 4 cm broad, green and maroon, the apex ± rounded; flowers not opening spontaneously, borne in pairs with as many as 13 pairs subtended by a single bract; petals unequal, obovate-elliptic, purple, ca 2 cm long; calyx to 3.5 cm high, whitish at base, purple above or with tips tinged with pale violet, persistent in fruit, turning darker purple, the lobes unequal, free; staminodia white to cream-colored, shorter than corolla, sometimes tinged with purple at apex. Capsules obovoid, ca 1 cm long; seeds usually 3, trigonous, rugose, ca 5 mm long, bearing a basal aril ca half as long as seed. *Croat 4271, 11989.*

Adult plants uncommon in the forest, more common in clearings; juvenile plants sometimes common. Flowers throughout the rainy season (July to December). The fruits develop to mature size in about 2 months and are usually present in the same inflorescence throughout much of the flowering season.

Plants of this species may be distinguished by the light purple bands that extend over much of the blade midway between the margin and the midrib, chiefly on the lower surface. The other distinguishing feature is the short-pilose pubescence on the sheaths, which is usually visible to the naked eye. In contrast, the sheaths of *C. marantifolia* vary from glabrous to rather densely pubescent; the trichomes are generally appressed, and always very inconspicuous, scarcely or not at all visible to the naked eye. Juvenile plants can be distinguished from other species by having the sheath villous at least at its apex. The cream-colored flower form of *C. latifolia*, which occurs elsewhere in the Canal Zone, lacks the purple bands on the leaf. Woodson and Schery in the *Flora of Panama* (1945b) mistakenly reported this species as a variety of *C. allouia* (Aubl.) Lindl. (*C. allouia* var. *violacea*). This name is based on a misinterpretation of *Calathea violacea* Lindl., which is restricted to Brazil. The plant is fairly shade tolerant.

On BCI *C. latifolia* is pollinated by the bee *Euglossa imperialis* (elsewhere by *Eulaema cingulata* and *Eulaema nigrita*) (H. Kennedy, pers. comm.).

Panama, Colombia (Meta Valley near the Macarena), and Venezuela (drier costal areas); Trinidad. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién, from premontane moist forest in the Canal Zone and Panamá, from premontane wet forest in Colón, Chiriquí, Coclé, and Panamá, and from tropical wet forest in Colón.

See Fig. 154.

Calathea lutea (Aubl.) Schult., Mant. 1:8. 1822

Hoja blanca

Caulescent herb, 2–3 m tall, mostly glabrous. Petioles 1.2–2 m long, the sheath less than 2 m long, geniculate at petiole, the pulvinus to 17 cm long, brownish; blades broadly elliptic to almost rounded, obtuse or abruptly acuminate at apex, obtuse to truncate and abruptly decurrent at base, mostly 50–100 cm long (to 150 cm) and 25–60 cm wide, prominently whitish-pruinose on lower surface, the margins held ± erect. Inflorescences emerging from sheath of subtending leaf; peduncles 6–17 cm long, unbranched; spikes oblong, ± flattened, 10–30 cm long, 3–5 cm broad; bracts yellowish when young, reddish or bronze in age, 2-ranked, imbricate, nearly orbicular, 3.5–5 cm long, often lobed at apex with mucronate point; staminodia usually pale yellow, occasionally whitish; petals 4–4.5 cm long. Fruits capsules; seeds orange, with a brilliant orange aril. *Croat 6992.*

Almost never in the forest except in tree-fall areas; occasional on creek beds and shoreline soil deposits. Flowers and fruits throughout the year, but activity is greatest during the early rainy season. The fruits develop quickly.

Distinguished by its leaves, which are white beneath, and by its oblong, somewhat rounded spikes. This is the most aggressive species of the genus, according to H. Kennedy (pers. comm.).

The species has been seen pollinated by euglossine bees and is robbed of nectar by hummingbirds.

Coastal areas from Mexico to Peru and Brazil; principally in coastal marshes and disturbed areas along both coasts. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Chiriquí, Los Santos, and Darién, from tropical dry forest in Coclé, from premontane wet forest in Chiriquí and Panamá (Cerro Campana), and from tropical wet forest in Colón (near Portobelo).

See Fig. 155.

Calathea marantifolia Standl., J. Wash. Acad. Sci. 17:250. 1927

C. allouia (Aubl.) Lindl. sensu Woods. (1942) non Aubl.; *C. lagunae* Woods.

Caulescent herb, 1–2 m tall. Blades oblong to oblong-elliptic, abruptly short-acuminate, obtuse to rounded at base, to 45 cm long and 25 cm wide, the edges turned upward, the upper surface glabrous, the midrib with a line of hirsute pubescence, the lower surface dull, short-pilose, the pubescence diminishing but extending onto petiole and sheath, the sheath almost glabrate. Spikes broadly oblong, at apex of leafy stem, solitary; peduncles to 21 cm long; bracts minutely pubescent, very broad, scarcely 1 cm high, persistent; flowers cream, 4–5 cm long, not opening spontaneously; sepals ca 2.5 cm long,

Fig. 154. *Calathea latifolia*

Fig. 155. *Calathea lutea*

Fig. 156.
Calathea panamensis

white to yellowish, persisting in fruit. Fruits obovate; seeds 3, slate-gray with white aril. *Croat 12222.*

Occasional in the forest and rare in clearings. Flowers mostly from June to October; may flower much later in tropical wet forests. The fruits soon mature to adult size and, according to H. Kennedy (pers. comm.), are dispersed in about 2 months.

Juvenile plants may be recognized by the soft short-pilose pubescence on the leaf surfaces. This species has been confused with *C. macrosepala* K. Schum., which occurs in Veraguas and Los Santos Provinces.

Guatemala to Ecuador. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, Coclé, Panamá, and Darién and from tropical wet forest in Colón (Río Guanche).

Calathea micans (Math.) Koern., Cat. 126. 1862
C. microcephala (Poepp. & Endl.) Koern.

Acaulescent, to 30 cm tall. Petioles often equaling blades, short-pilose; leaf sheaths puberulent, narrow, ending well below pulvinus; blades ovate to oblong-elliptic, acute to short-acuminate, acute to rounded at base, 6–15 cm long, 2.5–8 cm wide, glabrous above except the midrib, short-pilose and usually purple below. Spikes small, long-pedunculate, equal to or longer than leaves, 1.5–2.5 cm long; bracts few, lanceolate or ovate-lanceolate, spirally arranged; flowers white or the labellum tinged purple. Fruits not studied. *Croat 6638.*

Common locally, but apparently restricted to certain areas of the older forest. Flowers throughout the year in Panama, but in regions such as BCI with a prominent dry season plants die back altogether during the dry season and reappear shortly after the rainy season begins.

Guatemala to Peru and Brazil. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Darién, from premontane wet forest in Colón and Coclé, and from tropical wet forest in Veraguas (Atlantic slope) and Coclé.

Calathea panamensis Rowl. ex Standl., J. Wash. Acad. Sci. 15:4. 1925

Acaulescent, to 65 cm tall; roots bearing edible tubers. Petioles broadly winged to base of pulvinus, somewhat shorter than blade; blades oblong or obovate-elliptic, shortly and abruptly acuminate to blunt at apex, obtuse or rounded at base, 25–38 cm long, 6–15 cm wide, often ± asymmetrical, dark green and glabrous above except the midrib, paler and moderately pubescent with soft trichomes below. Inflorescences terminal, arising among leaf sheaths, sessile or very short-pedunculate; bracts mostly 3–7 cm long, lanceolate, spirally arranged; flowers yellow, cleistogamous, ca 5 cm long, exserted ca 1.5 cm, the tube very slender, ca 3.5 cm long; corolla lobes ± unequal, to 17 mm long, 5–9 mm wide, elliptic and boat-shaped; staminodia petaloid, irregular, shorter than petals, united with filament; anther ca 3.2 mm long; style stiff, curved. Capsules ca 1 cm long; seeds 3, brown, ca 5 mm long, the aril with 2 lateral, pointed appendages. *Croat 11786.*

Uncommon in the forest, but locally abundant in a few places along trails, notably on Hood, Van Tyne, and Wheeler trails. The plant dies back during the middle of the dry season and reappears the following rainy season, about May. Flowers mostly from June to October. The fruits apparently develop quickly, but their time of dispersal is unknown.

Recognized by its small size and its yellow flowers inconspicuously situated below the leaves. The flowers are cleistogamous, and reproduction is by means of autogamy.

Costa Rica (Guanacaste) and Panama. In Panama, known from seasonally dry parts of tropical moist forest in the Canal Zone, Panamá and Darién and from premontane moist forest in Panamá. BCI has about the upper limit of rainfall for the species.

See Fig. 156.

Calathea villosa (Lodd.) Lindl., Edward's Bot. Reg. 31, pl. 14. 1845

Moderately pubescent, acaulescent herb, to 80 cm tall; roots with tubers. Petioles 1.5–6 cm long; blades oblong-elliptic to obovate, short-acuminate, obtuse at base, 15–60 cm long, 8–15 cm wide, pubescent on upper surface, with 5–7 dark-green markings equally spaced on blade between margin and midrib. Inflorescences on leafless scape usually overtopping leaves; bracts 4–7, 2-ranked, not imbricate, 2–3 cm long; flowers yellow, autogamous, 3.5–4 cm long. Fruits not studied. *Croat 10913.*

Cultivated at the Laboratory Clearing. Flowers during the rainy season, beginning about July.

Costa Rica to Brazil. In Panama, known from seasonally dry parts of tropical moist forest and from premontane moist forest in the Canal Zone and Panama; known also from premontane wet forest in Panamá (Cerro Campana).

ISCHNOSIPHON Koern.

Ischnosiphon leucophaeus (Poepp. & Endl.) Koern., Bull. Soc. Imp. Naturalistes Moscou 35(1):91. 1862

Caulescent herb, 1–2 m tall. Leaves chiefly basal; petioles to 65 cm long; blades broadly oval, gradually to abruptly acuminate, 15–33 cm long, 12–20 cm wide, glabrous, pruinose on underside. Spikes usually in clusters of 2–6, sessile, narrowly cylindrical, 10–15 cm long, to 1 cm broad; bracts oblong, narrow and 2.5–3 cm high, somewhat pruinose; flowers white, 3–4 cm long. Fruits not studied. *Croat 4360.*

Uncommon, in the forest. Flowering and fruiting throughout the rainy season (May to December).

Recognized by its very narrow, cylindrical spikes.

Panama to Brazil. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Panamá, and Darién and from tropical dry forest in Panamá (Taboga Island).

Ischnosiphon pruinosus (Reg.) O. G. Petersen, Bot. Tidsskr. 18:264, pl. 18. 1892
Pleiostachya pruinosa (Reg.) K. Schum.

Caulescent herb, 2–3 m tall. Petioles 39–84 cm long, at least those bearing inflorescences in their axils vaginate

Fig. 157. *Ischnosiphon pruinosus*

Fig. 158. *Thalia geniculata*

Fig. 159. *Thismia panamensis*

more than three-fourths their length, ± pubescent up to the callus, glabrous above, the pulvinus with a raised annular ring 5–7 cm below the blade; blades elliptic-oblong, 25–85 cm long, 12–28 cm wide, with one side 4–8 cm narrower, very oblique and falcate-cuspidate at apex, obtuse at base, the lower edges often held erect, the midrib and the underside of blade maroon (sometimes green or with only a maroon band along one margin). Inflorescences 2 or 3 pedunculate clusters per leaf axil; peduncles 14–43 cm long, the branches flattened, each subtended by a bract 5–14 cm long; spikes flattened, green, 9–19 cm long, to 2 cm broad, at first pruinose; flowers exserted from tightly appressed bracts, 4–5 cm long, white, the outer staminodium to ca 1 cm wide, violet-purple, the cucullatum pale yellow, the staminodium callosum tinged with violet-purple at apex. Fruits 1-seeded capsules ca 13 mm long, apparently falling out of the weathered and drooping inflorescence; seeds 3-sided, 7–8 mm long. *Croat 4116.*

Frequent in the forest, often in open places such as tree-fall areas. Flowers principally from July to October; fruiting inflorescences persist into the early dry season before weathering away.

Pollinated by the bee *Euglossa imperialis.*

Belize to Panama. In Panama, known from tropical moist forest on both slopes of the Canal Zone and in Bocas del Toro, Chiriquí (Burica Peninsula), Panamá, and Darién; known also from premontane moist forest in Veraguas and Panamá and from premontane wet forest in Chiriquí.

See Fig. 157.

STROMANTHE Sond.

Stromanthe jacquinii (R. & S.) Kenn. & Nic., Ann. Missouri Bot. Gard. 62:501–2. 1975

S. lutea (Jacq.) Eichl. non Aubl.

Platanillo de montana

Caulescent rhizomatous herb, 1–2 m tall. Leaves 2-ranked, atop a leafless stem 30–185 cm tall; petioles mostly 19–37 cm long, the sheath narrow, extending more than halfway to blade, often to base of pulvinus, the pulvinus 15–25 mm long; blades oblong-elliptic, abruptly short-acuminate, broadly obtuse to rounded at base, mostly 26–46 cm long, 9–18 cm wide (smaller on juveniles), faintly pleated, all veins ± equal. Inflorescence usually solitary, arising from a leaf sheath, held above the leaves; peduncle 50–75 cm long; spikes diffusely and paniculately compound, the rachis closely flexuous; bracts orange, mostly broadly ovate, 1–2.5 cm long, soon deciduous; flowers ca 1 cm long, pedicellate, in pairs on a common stalk, subtended by a bracteole; sepals 3, free, ca 7 mm long, slightly shorter than petals; petals united at base, white with red markings; staminodia petaloid, slightly shorter than petals. Fruits ca 1 cm long; seed 1, black, on a short white aril. *Croat 11815.*

Uncommon in the forest and at the edge of the forest along the lake. Flowers mostly throughout the rainy season (June to December), principally in September; rarely flowering earlier (in the dry season) elsewhere in Panama at higher elevations. The fruits develop rapidly and are present on the same inflorescence with the flowers, soon shedding to expose the rachis.

Costa Rica to Venezuela. In Panama, known principally from tropical moist forest in the Canal Zone, Colón, San Blas, Panamá, and Darién; known also from premontane wet forest in the Canal Zone, Colón, and Panamá, from tropical wet forest in Colón, Panamá, and Darién, and from premontane rain forest in Darién (Cerro Pirre).

THALIA L.

Thalia geniculata L., Sp. Pl. 1193. 1753

Swamp lily, Platanillo

Caulescent, perennial herb, usually 2–3 m tall. Leaves both basal and cauline; petioles usually much longer than blade; blades broadest at base, gradually tapering, ovate to ovate-lanceolate, gradually or abruptly short-acuminate at apex, obtuse or rounded at base, 20–75 cm long, 5–30 cm wide, glabrous, sometimes ± pruinose on underside. Inflorescences widely branched, very diffuse panicles, many-flowered; peduncles often very long, exceeding leaves; rachis of spikes sharply flexuous, the internodes 5–10 mm long; bracts 1–2.5 cm long, usually bluish, caducous; flowers in pairs subtended by a pair of unequal bracts, green or bluish, caducous, the longest 1.5–2.5 cm long, sessile; sepals 3, oblong to obovate, violet at least medially, rounded at apex; labellum obovate, clawed, ca 2 cm long, the blade lavender, to 1.2 cm wide; petals very irregular, violet; ovary obovate, ca 2.5 mm long; style spirally twisted, spring-loaded, bearing two slender appendages. Fruits nutlike, indehiscent, 1-seeded. *Croat 5455, Shattuck 971.*

Rare; restricted to undisturbed marshy areas along the shore. Flowers throughout the year, but especially in the dry season. The fruits develop quickly and often share the same inflorescence, as in *Stromanthe jacquinii.*

Florida and Mexico to Argentina; Greater Antilles. In Panama, known principally from tropical moist forest on the Pacific slope in the Canal Zone, Chiriquí, Panamá, and Darién; known also from tropical dry forest in Herrera and Panamá, from premontane moist forest in Panamá, and from premontane wet forest in Chiriquí.

See Fig. 158.

34. BURMANNIACEAE

Saprophytic, colorless herbs arising from a tuberous underground part. Leaves lacking. Flowers bisexual, zygomorphic, solitary, terminal, bracteate; perianth urceolate-campanulate, 6-lobed; stamens 6, attached to the perianth tube, alternating with small, triangular appendages; filaments attached to the appendages; anthers sessile, 2-celled, dehiscing transversely; ovary inferior, 1-locular, 3-carpellate; placentas 3, parietal, stalked;

ovules many; style 1, thick-filiform, trifid, bearing terminal stigmas. Fruit a fleshy capsule; seeds very numerous, with little endosperm.

The single tiny saprophyte on BCI is not confused with any other species.

Eleven genera with about 100 species; tropics and subtropics.

THISMIA Griff.

Thismia panamensis (Standl.) Jonk., Monogr. Burm. 234. 1938

Ophiomeris panamensis Standl.

Small, white to flesh-colored, saprophytic herb, 4–12 cm tall, arising from a tuberous root, leafless; stem slender, 1-flowered. Flower urceolate-campanulate, subtended by 4 bracts ca 4 mm long; perianth 6-lobed, to 12 mm long, zygomorphic, persisting in fruit, the bulged part with 3 slits, the outer lobes short and reflexed, the inner lobes spreading, tapered to filiform purplish appendages 3–4 cm long, the throat 3–4 mm diam, surrounded by a 6-lobed rim; stamens 6, to 5.5 mm long, pendent below throat, emarginate at apex, each bearing a pair of small lateral appendages, the thecae borne on their outer surface (against inner wall of perianth); ovary inferior; style to 3.5 mm long, 3-branched, the branches densely pubescent and longer than the unbranched part, the stigmatic part terminal. Capsule fleshy, to ca 3 mm long; seeds very numerous, minute. *Croat 10848.*

Frequent in the forest. Flowering and fruiting from June to September; not obvious at other times of the year.

The flower is specialized and probably pollinated by small insects. The small fleshy fruit may be dispersed by small birds, or perhaps the minute seeds are carried by insects. Van der Pijl (1968) suggested earthworms as possible dispersers of seeds in the family.

Known only from Panama, from tropical moist forest on BCI and from tropical wet forest in Colón (near Portobelo).

See Fig. 159.

35. ORCHIDACEAE

Terrestrial or epiphytic, perennial herbs (*Vanilla* scandent), very rarely saprophytic, usually with pseudobulbs. Leaves alternate, distichous or spiraled; blades simple, entire, fleshy, obscurely veined, rarely the leaves lacking and the roots photosynthetic. Flowers bisexual (rarely unisexual and monoecious (*Catasetum*) or dioecious (*Mormodes, Catasetum*), zygomorphic, in bracteate, generally simple racemes (panicles in *Oncidium*); sepals 3, free, somtimes showy; petals 3, the central petal (the lip)

KEY TO THE TAXA OF ORCHIDACEAE

- Plants terrestrial:
  - Leaf blades more than 30 cm long; sepals more than 6 mm wide:
    - Flowers white, ± globose, very fleshy; sepals often about as wide as long; fruits more than 1.5 cm wide; leaves mostly more than 6 cm wide ..... *Peristeria elata* Hook.
    - Flowers greenish, not globose, not very fleshy; sepals much longer than wide; fruits less than 1.5 cm diam; leaves mostly less than 6 cm wide ..... *Eulophia alta* (L.) Fawc. & Rendle
  - Leaf blades less than 30 cm long; sepals usually less than 6 mm wide:
    - Leaves very reduced on stem *or* leaves in a basal rosette, often not present at time of flowering:
      - Flowers more than 1.5 cm long; scape bracts 2–2.5 cm long; both stem and scape bracts pubescent ..... *Spiranthes lanceolata* (Aubl.) León
      - Flowers less than 1 cm long; scape bracts and stem not as above; both stem and scape bracts usually glabrous:
        - Plants to 15 cm tall, usually leafless at time of flowering, ± saprophytic; lip 7–8 mm long ..... *Triphora gentianoides* (Sw.) Ames & Schlechter
        - Plants 15–40 cm tall, usually bearing leaves at time of flowering, not saprophytic; lip 4–5.5 mm long ..... *Liparis elata* Lindl.
    - Leaves borne along stem, always present at time of flowering (not to be confused with scape bracts), either usually more than 5 cm long or, if less, ± ovate:
      - Plants usually less than 15 cm tall; leaves narrowly to broadly ovate, less than 2.5 cm long; flowers 1–3, terminal ..... *Triphora mexicana* (S. Wats.) Schlechter
      - Plants 20–100 cm or more tall; leaves narrowly elliptic to almost linear, usually more than 4 cm long; flowers usually much more numerous or not terminal:
        - Inflorescence of axillary racemes or panicles at usually leafless nodes, much shorter than leaves; flowers lacking a spur; leaves conspicuously petiolate ..... *Palmorchis powellii* (Ames) Schweinf. & Corr.
        - Inflorescence of terminal racemes held above leaves; leaves not conspicuously petiolate:
          - Flowers green or green and white; lip less than 12 mm long, bearing a conspicuous spur ..... *Habenaria*
          - Flowers brick-red or orange; lip more than 12 mm long, lacking a spur ..... *Epidendrum radicans* Lindl.

- Plants epiphytic, normally growing in trees or on rocks (fallen epiphytes may thrive in exposed positions, but this will cause little confusion on BCI):
  - Plants fleshy-leaved vines ..... *Vanilla*
  - Plants not vines:
    - Plants lacking both pseudobulbs and leaves, the gray-green roots functioning as photosynthetic organs ..... *Campylocentrum pachyrrhizum* (Reichb.f.) Rolfe
    - Plants with pseudobulbs and/or normal leaves:
      - Inflorescence terminal on stem or pseudobulb or restricted to upper leaf axils (may appear upper-axillary in *Maxillaria* but then inflorescence arising from base of pseudobulb):
        - Leaves plicate (with several folds longitudinally):
          - Inflorescence normally with only 1 or 2 flowers open at a time; flowers more than 2 cm long ..... *Sobralia*
          - Inflorescence many-flowered; flowers less than 1 cm long:
            - Leaf blades ± elliptic, thin, rosulate at apex of short pseudobulb; pseudobulbs inconspicuous, usually enveloped by leaves ..... *Liparis elata* Lindl.
            - Leaf blades lanceolate, not thin, scattered along stem, the lower deciduous; pseudobulb lacking ..... *Elleanthus longibracteatus* (Griseb.) Fawc.
        - Leaves conduplicate (folded once along midrib):
          - Leaves solitary on each stem, the stems not thickened:
            - Flowers less than 3 mm long; leaves prominently striate longitudinally when dry ..... *Stelis crescentiicola* Schlechter
            - Flowers more than 4 mm long; leaves not prominently striate when dry ... *Pleurothallis*
          - Leaves 2 to several on each stem, *or* the stems definitely thickened:
            - Lip adnate to the column for the length of the column; stems usually slender with several or many leaves ..... *Epidendrum* (except *E. rousseauae* Schlechter)
            - Lip at least partly free from the column:
              - Pseudobulbs cigar-shaped, hollow; flowers white or pink, cleistogamous ..... *Caularthron bilamellatum* (Reichb.f.) Schult.
              - Pseudobulbs various and solid *or* pseudobulbs lacking:
                - Leaves or leaf scars usually numerous, scattered on stem:
                  - Leaves equitant (laterally flattened, V-shaped); flowers white or yellow; column wings lateral, not surpassing anther; stem not thickened ... *Lockhartia*
                  - Leaves normal; flowers rose-colored, serial on a condensed raceme; column wings surpassing anther; stem thickened ..... *Dimerandra emarginata* (G. Meyer) Hoehne
                - Leaves few (usually 1–3), terminal on stem or pseudobulb (*Scaphyglottis* forms a series of superimposed pseudobulbs, but each bears terminal leaves):
                  - Pseudobulbs club-shaped, stalked; leaves 2 or 3, about 3 times longer than broad; flowers orchid-lavender ..... *Cattleya patinii* Cogn.
                  - Pseudobulbs ovoid or ellipsoid; leaves more than 3 times longer than broad; flower color various:
                    - Flowers usually more than 1 cm long (to 8 mm in *E. triptera*); lip entire, cordate, concave; flowers white with purplish lines or spots on lip ..... *Encyclia*
                    - Flowers less than 7 mm long; lip not as above:
                      - Stems with a single ovoid pseudobulb; flowers in a raceme or panicle, yellow or greenish-yellow; lip with mealy powder ..... *Polystachya*
                      - Stems with several swollen, superimposed segments (slender pseudobulbs); flowers clustered at tips of segments; lip not with mealy powder ..... *Scaphyglottis*
      - Inflorescence lateral on stem, usually from base of stem or pseudobulb:
        - ◆ Leaves plicate (*Xylobium foveatum* sometimes appearing conduplicate):
          - ■ Leaves several, scattered along pseudobulb:
            - Pseudobulbs cigar-shaped, pendent, stalked; flowers fleshy, with a trilobate lip and 8 pollinia ..... *Chysis aurea* Lindl.
            - Pseudobulbs oblong or cigar-shaped, erect, not stalked; flowers usually unisexual, the staminate flowers with "sensitive" columns, ejecting the 2 pollinia violently when triggered:
              - Lip ± saccate in both staminate and pistillate flowers; staminate column pointed, usually with 2 slender "antennae" beneath; inflorescence from base of pseudobulb; old pseudobulbs spiny above after leaves have fallen ..... *Catasetum*
              - Lip not saccate; column lacking antennae, pointed, with a slender apical bristle, connivent with lip in staminate flowers; inflorescence usually from middle of pseudobulb, the flowers asymmetrical, both column and lip twisted, the staminate and pistillate flowers usually similar; old pseudobulbs not spiny ..... *Mormodes powellii* Schlechter

■ Leaves few, terminal on pseudobulb:
Peduncles each with a single flower (but several peduncles produced at once) . . . . . *Lycaste powellii* Schlechter
Peduncles with several or many flowers:
Each pseudobulb with a single leaf; flowers small (12–20 mm diam), the lip concave . . . . . *Sievekingia suavis* Reichb.f.
Each pseudobulb with 2 or 3 leaves:
Inflorescence erect; lip trilobate, fleshy, simple; flowers cream-colored . . . . . *Xylobium foveatum* (Lindl.) Nich.
Inflorescence pendent; lip complex; flowers yellow to brown with red or purple markings:
Flowers large (ca 10 cm diam), 2–4; lip forming a cup containing a clear liquid produced by glands at base of lip . . . . . *Coryanthes maculata* Hook.
Flowers small (3–4 cm diam), numerous; lip not cuplike . . . . . *Gongora*

◆ Leaves conduplicate:
Plants lacking pseudobulbs (often present in *Ionopsis,* but minute and ensheathed by leaves), the leaves thin or laterally flattened:
Stems longer than leaves:
Leaves laterally flattened; flowers yellow or white . . . . . *Lockhartia*
Leaves normal:
Inflorescence of many white, spurred flowers (one-sided and toothbrushlike) . . . . . *Campylocentrum micranthum* (Lindl.) Maury
Inflorescence of single flowers . . . . . *Dichaea*
Stems much shorter than leaves:
Leaves normal (± linear in *Ionopsis satyrioides*):
Inflorescence of several to many flowers . . . . . *Ionopsis*
Inflorescence of 1 flower:
Leaves less than 12 cm long; flowers less than 12 mm long . . . . . *Masdevallia livingstoneana* Reichb.f.
Leaves more than 12 cm long; flowers more than 30 mm long . . . . . *Cochleanthes lipscombiae* (Rolfe) Garay
Leaves laterally flattened; plants fanlike:
Inflorescence of few to many white or green flowers . . . . . *Ornithocephalus*
Inflorescence with proportionately large yellow flowers produced serially . . . . . *Psygmorchis pusilla* (L.) Dods. & Dressl.
Plants with pseudobulbs *or* the leaves very thick and fleshy:
Flowers always 1 per inflorescence (though many 1-flowered peduncles may be produced at one time):
Sepals much larger than petals or lip, connivent to about middle, abruptly reflexed; peduncle erect, much taller than pseudobulbs; flowers brownish-purple . . . . . *Trigonidium egertonianum* Lindl.
Sepals and petals subequal, the sepals not abruptly reflexed at middle; inflorescence usually shorter than pseudobulbs or subequal:
Column with a fringed hood at apex; lip trumpet-shaped; pseudobulbs 1-leaved, with spotted sheaths . . . . . *Trichopilia maculata* Reichb.f.
Column lacking apical hood (or if hooded the margin entire); lip never trumpet-shaped; pseudobulbs with sheaths not spotted . . . . . *Maxillaria*
Flowers usually few, several, or many, produced serially on the same peduncle:
Lip united with column for length of column; flowers green . . . . . *Epidendrum rousseauae* Schlechter
Lip at least partly free from column:
Pseudobulbs more or less 4-angled, usually widely separated on a creeping rhizome; rachis of inflorescence thick, fleshy; small flowers sessile on the rachis, the flower diam less than that of the rachis . . . . . *Bulbophyllum pachyrrhachis* (Reichb.f.) Griseb.
Plants not with this combination of features; rachis never thick and fleshy:
Flowers very flat, yellow and brown; lip with a fleshy, lumpy callus; column with lateral, fanlike wings; inflorescence a many-flowered panicle, much surpassing leaves (inflorescence equal to or shorter than leaves in *Oncidium stipitatum* with long, terete leaves) . . . . . *Oncidium*
Plants not with this combination of features:
▲ Pseudobulbs with 2 or 3 terminal leaves, the leaves markedly flattened:
Lip adnate to basal half of column and then abruptly diverging; pseudobulbs stalked; sepals and petals acute, but not long-acuminate; plants common on tree trunks . . . . . *Aspasia principissa* Reichb.f.
Lip free from column; pseudobulbs not stalked; sepals and petals long-acuminate, spidery; plants rare . . . . . *Brassia caudata* (L.) Lindl.

▲ Pseudobulbs with only 1 terminal leaf *or* the terminal leaf aborted:
Anther parallel with axis of column; inflorescence many-flowered, often pendent; lip clawed; column without a fringed hood over anther; flowers white or green ..... *Notylia*
Anther terminal and caplike on column:
Base of lip saccate, retrorse; pseudobulbs very reduced ..... *Trichocentrum capistratum* Linden & Reichb.f.
Base of lip not saccate and retrorse; pseudobulbs usually conspicuous (scarcely wider than leaf in *Trichopilia subulata*):
Pseudobulbs narrowly cylindric; apex of column with a fringed hood; flowers white; lip more or less enclosing column or fringed ..... *Trichopilia subulata* (Sw.) Reichb.f.
Pseudobulbs compressed, ellipsoid; apex of column lacking fringed hood; lip neither enclosing column nor fringed ..... *Leochilus scriptus* (Scheidw.) Reichb.f.

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usually larger; 1 or more sepals sometimes forming a nectariferous spur; stamens forming a column with the stigma either 1 and terminal or 2 and lateral; anthers 2-celled, introrse; ovary inferior, 1-locular, 3-carpellate; placentation parietal; ovules numerous, anatropous; stylar portion of the column stout, with 3 sessile stigmas or stigmatic lobes. Fruits 3-valved, longitudinally dehiscent capsules; seeds many, lacking endosperm.

Orchidaceae are characterized by the unusual, zygomorphic flowers of three sepals and three petals, one of which is very different from the rest, and by the stamen(s) united to the style. Other distinguishing features include the usually epiphytic habit, the swollen, pseudobulbous stems, and the usually ribbed, capsular fruits with many tiny seeds.

Orchids are more highly modified and specialized for insect pollination than any other family (Baker, 1963). Species-specific attraction of pollinators is characteristic of the more highly evolved species of orchids (Dodson et al., 1969; Dressler, 1968a). There are often no other barriers to cross-pollination of many genera of orchids, and artificial hybrids are common (Proctor & Yeo, 1973). Most orchids are adapted to bee pollination. Genera of BCI orchids with known bee pollinators include *Aspasia, Bulbophyllum, Catasetum, Cochleanthes, Coryanthes, Dichaea, Encyclia, Epidendrum, Eulophia, Gongora, Lockhartia, Lycaste, Maxillaria, Mormodes, Notylia, Oncidium, Ornithocephalus, Peristeria, Sievekingia, Sobralia, Spiranthes, Trichocentrum, Trigonidium, Vanilla,* and *Xylobium.* Because so many of the species on BCI have known pollinators, a record of these specific pollinators will be found with the respective species. All reports of pollination are taken from Dodson (1965b) or Dressler (1968a) or are known through personal communication from R. Dressler. Probably the most important pollinators of orchids on BCI are bees of the genera *Euglossa, Eulaema,* and *Euplusia* (tribe Euglossinae). Bees visit flowers to collect pollen and/or nectar, but in general pollen is collected by the female bees. Male euglossine bees often collect floral fragrances from flowers and may as a result be important in pollination; moreover, they may be particularly important in long-range dispersal of pollinia, since they do not remain affiliated with the brood and are wide-ranging (Williams & Dodson, 1972). Many of the floral fragrances have been isolated as pure chemicals and are found to attract certain bees even when dissociated from the flowers that produce them (Hills, Williams & Dodson, 1968).

Birds are probably responsible for pollination of orange-flowered species of *Elleanthus.* Elsewhere birds have been reported visiting *Masdevallia,* but not the BCI species. Flies are also reported as pollinators of *Bulbophyllum, Masdevallia, Pleurothallis,* and *Liparis.*

The genus *Habenaria* is pollinated by moths, though at least one species elsewhere is visited by butterflies. *Epidendrum difforme* is pollinated by the moth *Amastus acona.*

Wasps, which pollinate *Leochilus, Brassia,* and *Encyclia,* are in general much less effective pollinators than bees. The lip of the orchid forms a landing platform for bees and wasps. The basal part of the lip leads the pollinator down the front of the column. Upon backing out of this "tunnel," the pollinator usually gets some stigmatic liquid on its back. A little farther on it contacts the pollinia, which sticks to its back. In more advanced orchids other mechanisms, including springlike traps, are employed in depositing the pollinia on the insect (Dodson et al., 1969).

Ants associated with some orchid species probably do not pollinate, but may be useful to the plant in preventing predation by phytophagous insects.

Most species have seeds that are wind dispersed, but *Vanilla* has fleshy fruits dispersed by animals (Ridley, 1930; van der Pijl, 1968). In most species the capsule splits by three or six lateral slits, but remains attached at the apex. Wind passing through the fruits carries the seeds away.

At least 600 genera and 20,000 species; worldwide but with the greatest diversity in the tropics.

ASPASIA Lindl.

Aspasia principissa Reichb.f., Bot. Zeitung (Berlin) 10:367. 1852

A. epidendroides var. *principissa* (Reichb.f.) P. H. Allen

Epiphyte; pseudobulbs oblong-elliptic, flattened, to 16 cm long and 4.5 cm wide, 2-leaved, stipitate, with leaflike imbricating bracts at base. Petioles conduplicate; blades lanceolate to ligular, 10–41 cm long, 1.7–5.5 cm wide.

Fig. 160. *Aspasia principissa*

Fig. 162. *Brassia caudata*

Fig. 161. *Brassia caudata*

Racemes 1 or 2, erect, few-flowered, from base of pseudobulb; sepals and lateral petals lanceolate to oblong, acute at apex, pale green striped with brown or purple, to 4 cm long, the petals slightly broader than sepals; lip ± fiddle-shaped, to 2.5 cm wide, white to pale yellow with pink or lavender streaks, wavy on margin, clawed at base, the claw fused to column at base then diverging abruptly; column to 2.5 cm long. Fruits narrowly fusiform, ribbed, to 8 cm long, usually bearing the persistent sepals. *Croat 8496.*

Common in the forest, sometimes occurring on tree trunks near the ground. Flowers principally in the dry season (late December to mid-May), mostly from mid-January to mid-February.

Pollinated by the bees *Eulaema* and *Exaerte* (*fide* Dressler, pers. comm.).

Guatemala to Panama. Widespread in tropical moist forests throughout Panama.

See Fig. 160.

BRASSIA R. Br.

Brassia caudata (L.) Lindl., Edward's Bot. Reg. 10, t. 832. 1824

Epiphyte; pseudobulbs linear to oblong-elliptic, ca 14 cm long and 3.5 cm wide, flattened with sharp edges, 2(3)-leaved, with 4–6 usually papery bracts at base. Petioles conduplicate; leaves ligular to elliptic-oblong, 16–27 cm long, 2.5–8 cm wide, symmetrical to strongly asymmetrical at apex. Inflorescences 1 or 2, unbranched, arching, 6–12-flowered, to 35 cm long, from lateral base of pseudobulb; sepals caudate-acuminate and spreading, light yellow-green, the longer lateral ones 12–30 cm long; petals similar to sepals but much shorter; lip oblong-lanceolate, acuminate at apex, free from column; sepals, petals, and lip similarly mottled with violet-purple near base, the basal part of lip with 2 short, erect teeth in front of 2 erect orange-tipped lamina. Fruits oblong-elliptic, to 7 cm long and 1.3 cm wide, ± acuminate on both ends, 5-ribbed. *Croat 11780, 14628.*

Apparently rare. Most plants in Panama were seen in flower in the early rainy season (May to August). The fruits may develop to mature size by August, but the time of dehiscence is unknown.

Widespread; Florida and Mexico to Venezuela, Brazil, and Bolivia; Greater Antilles. In Panama, known from tropical moist forest in the Canal Zone, Chiriquí, Los Santos, Panamá, and Darién.

See Figs. 161 and 162.

BULBOPHYLLUM Thouars

Bulbophyllum pachyrrhachis (Reichb.f.) Griseb., Fl. Brit. W. Ind. 613. 1864

Epiphyte, 10–45 cm tall; pseudobulbs short, subconical, strongly 4-angulate, well spaced along creeping rhizome. Leaves 2, linear-lanceolate, conduplicate, 7–20 cm long, to 2.4 cm wide. Inflorescences from base of pseudobulb, erect or arching, 10–45 cm long; rachis thick and fleshy; flowers many, small and inconspicuous, green-yellow spotted with purple, sessile in pits of rachis, subtended by ovate bracts; sepals ovate, 4–5 mm long, the dorsal sepal free, arching over the column, the lateral ones connate at base and adnate to base of column; petals ca one-third as long as sepals, oblong-elliptic; lip entire, fleshy. Fruits ovoid, ca 1 cm long and 6 mm wide, bearing many closely-spaced ribs. *Shattuck 777.*

Not seen in recent years on BCI. Elsewhere flowers and fruits principally in the dry season (December to May). Populations of plants have been seen in March with individuals bearing either flowers or full-sized fruits, indicating that the species may flower more than once a year.

Mexico to Panama; Greater Antilles, Trinidad. In Panama, known from tropical moist forest in the Canal Zone, Veraguas, and Panamá.

CAMPYLOCENTRUM Benth.

Campylocentrum micranthum (Lindl.) Maury, J. Bot. (Morot) 3:273. 1889

C. panamense Ames

Epiphyte; pseudobulbs lacking; stems unbranched, to 35 cm long. Leaves alternate, conduplicate, distichous, 4–9 cm long, 1.2–2 cm wide, articulate at base, ultimately deciduous below, alternating along stem with long, thickened, whitish roots. Inflorescences short, recurved, densely flowered racemes from base of roots; flowers small, secund and distichously arranged on scape, white or greenish; sepals to 4.5 mm long, ± linear; petals to 4 mm long; lip trilobate, to 4.5 mm long, produced at base into a spur ca 4 mm long. Fruits ± oblong, somewhat curved, longitudinally grooved, 6–9 mm long. *Croat 4623.*

Fairly common in the forest and around clearings, preferring sunlight. Plants flower for a moderately long period of time and may bear fruits on lower inflorescence branches while still in flower, in the late dry and early rainy seasons, mostly from April to June. Peak fruiting

KEY TO THE SPECIES OF CAMPYLOCENTRUM

Leaves regular, borne along slender stems ..... *C. micranthum* (Lindl.) Maury
Leaves lacking, the roots gray-green, chlorophyllous ..... *C. pachyrrhizum* (Reichb.f.) Rolfe

Other species of *Campylocentrum*, e.g., *C. poeppigii* Rolfe, may also appear on the island (R. Dressler, pers. comm.).

season is unknown, but plants with developed fruits appear to be most common during the rainy season and early dry season.

R. Dressler (pers. comm.) believes that *C. panamense* Ames, treated here as a synonym, may be a distinct species occurring in the forest, while *C. micranthum* is the plant found in clearings.

Mexico to Trinidad, Guyana, Brazil, and Peru; Greater Antilles. In Panama, reported from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Panamá, and Darién.

Campylocentrum pachyrrhizum (Reichb.f.) Rolfe, Orchid Rev. 11:246. 1903

Leafless epiphyte; roots chlorophyllous, flattened, thin, 20–30 cm long, ca 2 mm wide. Racemes short, usually 2–3 cm long, densely flowered; floral bracts prominent, dark brown, the margins erose, persisting on fruiting inflorescences; flowers to 1.5 mm long; sepals very pale cream, subequal, to 4.5 mm long and 1.5 mm wide, acute at apex, the ventral margin of lateral sepals strongly inrolled; petals to 4 mm long and 1 mm wide, white, the ventral margin inrolled in lower half; lip white, spurred, shorter than petals, narrowly acute, the lower edges inrolled, the spur nearly as long as the blade, extending well below the sepals. Fruits ovate-oblong, prominently ridged, ca 6 mm long. *Shattuck 844.*

Rare; collected once by Shattuck at Gross Point. His collection, made in late March, bears mature fruits.

Florida, West Indies, Trinidad, French Guiana, Venezuela, and Panama (no doubt in Colombia as well). In Panama, only from the Canal Zone (BCI and Summit Garden).

See Fig. 163.

CATASETUM L. C. Rich. ex Kunth

Catasetum bicolor Klotzsch, Allg. Gartenzeitung 22:337. 1854

Monoecious epiphyte; pseudobulbs subconic or cylindrical, 4–9.5 cm long, 2.5–4 cm wide, enveloped by the imbricating, persistent leaf bases. Leaves plicate, elliptic-lanceolate, acute or acuminate, deciduous at the end of the growing season. Flowers unisexual, dimorphic, the staminate and pistillate flowers on separate racemes from base of pseudobulb, greenish-brown with tinges of maroon, the petals darker than the sepals; staminate inflorescences arched or pendent, to 15 cm long, the sepals and petals subequal, ± lanceolate, to 3 cm long, the lip short, white to pale yellow with reddish-brown spots, prominently saccate, bearing 3 narrow lobes at apex and 2 additional slender lobes near base; pistillate racemes ± rare, few-flowered, 8–10 cm long, erect, the sepals coriaceous, elliptic-lanceolate, acute, the petals similar to sepals, the lip fleshy, yellowish-green, forming a deep pocket, the apex broadly triangular. Fruits not seen. *Zetek s.n.* (collected in 1942).

Collected only once on the island. Flowers throughout the rainy season and in the early dry season (June to January).

The species is vegetatively identical to *C. warczewitzii* Lindl. & Paxt., a species thus far unknown on BCI.

Pollinated by *Euglossa cordata* (Dodson, 1967a; Dressler, 1968a), by *E. cyanaspis* (Dressler, 1968a), and by *E. variabilis* (R. Dressler, pers. comm.).

Panama to Venezuela and Brazil. Apparently a wide-ranging species ecologically; on the basis of few collections, it appears that the species ranges from tropical moist forest at elevations of 24 m, such as around Gatun Lake, to tropical wet forest and premontane rain forest at elevations of more than 1,000 m. In Panama, known from Colón (Cerro Santa Rita) and Chiriquí (Volcan Chiriquí).

Catasetum viridiflavum Hook., Bot. Mag. 69, t. 4017. 1843

Monoecious or dioecious epiphyte; pseudobulbs large, fusiform, to 25 cm long, enveloped by leaf bases, the older leafless ones persisting. Leaves 6–12-plicate, elliptic-lanceolate, acuminate, 20–48 cm long, 3.5–12 cm wide. Flowers unisexual, dimorphic, on separate, stout racemes from base of pseudobulb; staminate inflorescences erect or arching, 25–70 cm long; staminate flowers 2–12, lacking aroma, to 5 cm long, pale green, aging yellow, the sepals oblong to oblanceolate, acuminate to cuspidate, to 5 cm long, the petals ovate, acuminate, to 4.5 cm long, the lip very firm, subglobose, to 3.5 cm long, green but inside of distal margin yellow (the color fading through to outer surface), the lateral margin ciliate, weakly spurred at base, the column beaked and exserted from lip, the lower edge with 2 antennae, one curved laterally, the other extending out into the spur depression, the anther beaked, ca 1.5 cm long, the pollinia ovoid, ca 6 mm long, ejected from column with considerable force; pistillate racemes infrequent, stouter than staminate racemes; pistillate flowers 2–4, similar to staminate flowers but the sepals and petals fleshy and smaller (to 2.5 cm long), the lip rounded at base, 3–4 cm long, persisting in fruit. Fruits fusiform, heavy and fleshy, to 9 cm long, bluish-green, with 5 broad ribs. *Croat 5515, 5546, 11298.*

Common on tree stumps in the lake; occasionally high in trees in the forest. Flowers from the late dry season

KEY TO THE SPECIES OF CATASETUM

Lip of staminate flowers 1 cm or less, with 5 elongate lobes (3 apical, 2 basal) . . . . . *C. bicolor* Klotzsch
Lip of staminate flowers 2 cm or more, lacking elongate lobes . . . . . *C. viridiflavum* Hook.

Fig. 163. *Campylocentrum pachyrrhizum*

Fig. 164. *Catasetum viridiflavum*

Fig. 165. *Cochleanthes lipscombiae*

(April) to the late rainy season (November), mostly from May to September. The fruits develop to full size by November, probably dehiscing chiefly during the dry season.

Recognized by the large pseudobulb and the plicate leaves, as well as by the thick waxy flowers and large fruits.

Pollinated by *Eulaema cingulata* (Dodson, 1965a) in the early morning hours (Dressler, 1968; Hills, Williams & Dodson, 1972).

Allen (1949) reported that the pollinia are ejected with any disturbance of the anther or antennae. My investigations of three different flowers show that only the applicator is released from its position in the column by forceful movement of the base of the antennae. The anther can easily be removed without releasing the translator arm from its position, and the distal parts of the antennae can be moved violently without reaction. However, any movement of the sticky white applicator after its release from the column causes the translator arm to release violently. These flowers were possibly immature.

Known only from Panama in tropical moist forest in the Canal Zone, Colón, Veraguas (Coiba Island), and Panamá and from premontane wet forest in Coclé (hills south of El Valle).

See Fig. 164.

CATTLEYA Lindl.

Cattleya patinii Cogn., Dict. Icon. des Orch. t. 25. 1900
C. skinneri Batem. var. *autumnalis* P. H. Allen

Epiphyte (or elsewhere semiterrestrial), to 40 cm tall; pseudobulbs fusiform to cylindrical, usually narrowed toward base, 15–30 cm long, usually 2-leaved from apex, enveloped by leafy bracts at base. Leaves conduplicate, elliptic to oblong-lanceolate, obtuse, coriaceous, 10–15 cm long, 3.5–5.5 cm wide. Inflorescences simple, terminal, few-flowered, erect racemes subtended by spathaceous bracts; flowers large and showy, both the sepals and petals 3–5 cm long, orchid-lavender, the petals broader; lip sessile, very deep orchid-lavender, folded along the edges forming a tube around the column 3–4.5 cm long. Fruits 5–7 cm long, narrowly tapered on both ends, not prominently ridged.

Rare; R. Dressler has seen the species on BCI, but no collections have been made. Flowers in the dry season, mostly from January to March. The fruits develop during the dry season and shed their seeds by early in the rainy season. Costa Rican and Guatemalan collections bearing the name *C. skinneri* Batem. show flowers from January to March.

Recognized by its large, terminal, showy, purplish flowers, the lip large, tube-shaped, and darker than the petals and sepals.

Costa Rica to Colombia and Venezuela; Trinidad. In Panama, range uncertain; known from tropical moist forest in the Canal Zone, Los Santos, and Darién and from premontane moist forest in Panamá (around Bejuco).

CAULARTHRON Raf.

Caularthron bilamellatum (Reichb.f.) Schult., Bot. Mus. Leafl. 18:42. 1958
Diacrium bilamellatum (Reichb.f.) Hemsl.

Epiphyte, 20–65 cm tall; stems pseudobulbous, fusiform to cylindrical, to 16 cm long, hollow and often inhabited by ants, enveloped by close, short bracts, bearing 1–4 strap-shaped leaves at apex. Leaves conduplicate, 6–20 cm long, to 2.5 cm wide. Inflorescences terminal, few-flowered, long-pedunculate racemes; peduncles 5–45 cm long, bearing numerous short sheaths; flowers white or pink, often cleistogamous, pedicellate, 1 or few open at a time; sepals 11–16 mm long, slightly longer and narrower than the petals, thickened toward apex, equaling lateral petals; lip free from the column, with 2 horns on upper side near base. Fruits elliptic, ribbed capsules, 2.5–3 cm long at maturity. *Croat 7762, 8709.*

Occasional over trees at the margin of the lake, and infrequent within the forest. Flowering chiefly in February and March (rarely into the early rainy season). The fruits develop to full size by March, and seeds are usually shed by late in the dry season.

Mexico to Panama and across northern South America to Trinidad. In Panama, a lowland, principally coastal species known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, and Chiriquí, Panamá, and Darién and from tropical wet forest in Colón.

CHYSIS Lindl.

Chysis aurea Lindl., Edward's Bot. Reg. 23, t. 1937. 1837

Epiphyte; stems pseudobulbous, cylindrical, fusiform or club-shaped, branched, often pendent, 5–50 cm long, 1–2 cm wide. Leaves plicate, lanceolate, acute or acuminate, 6–40 cm long, to 5 cm wide, moderately thin, ± undulate, the persistent imbricating bases enclosing stems. Racemes short, usually solitary from axils of new leaf growth; floral bracts pale green, the veins light violet-purple; flowers 3–7, 2.5–4 cm long; sepals fleshy, yellow at apex, yellow-cream at base, 2–3 cm long; petals less fleshy than sepals, about as long as lateral sepals, creamy white with red veins and spotting in apical half; lip yellow or white, trilobate, the middle lobe sometimes purple with paler markings; pollinia 8. Fruits narrowly ellipsoid, 5 cm long and 2.5 cm wide, ribs broad.

Apparently rare on BCI and throughout Panama. Reported by R. Dressler (pers. comm.) for the island, but no collections seen. Seasonal behavior uncertain. Probably flowers and fruits principally during the dry season.

Though still somewhat uncertain, Fowlie (1971) believed Panamanian material belongs to *C. aurea*, of Venezuela and Colombia, and that it is distinct, therefore, from *C. maculata* (Hook.) Fowlie, a species ranging from Costa Rica north to Nicaragua and perhaps Honduras.

Panama, Colombia, and Venezuela. In Panama, known

only from tropical moist forest in the Canal Zone (BCI and the Pipeline Road north of Gamboa).

COCHLEANTHES Raf.

Cochleanthes lipscombiae (Rolfe) Garay, Orquideologia 4:152. 1969

Caespitose epiphyte; pseudobulbs lacking. Petioles conduplicate, 6–7 cm long, occasionally persisting; leaves moderately thin, elliptic-oblanceolate, acuminate to acute, mostly 12–30 cm long, tapering to petiole, the lowermost bractlike. Inflorescences 1-flowered, arching or somewhat pendulous, bracteate scapes 6–15 cm long, from axils of lowermost bracts; flowers large, with clovelike aroma; sepals white, 3–3.5 cm long, the laterals directed downward, the dorsal erect and recurved; lateral petals similar to dorsal sepal, directed outward; lip to 4.5 cm long and 3.5 cm wide, white tinged with violet on margin and with violet lines on face within, the lateral margins incurved around column; column white, shorter than lateral lobe of lip, 12–18 mm high. Fruits not seen. *Croat 12711.*

Apparently rare, occurring in the forest. Seasonality uncertain. It has been reported to flower at the end of the dry season (*Powell 11*), but has been collected in flower on BCI in late November. An individual plant transplanted to Summit Garden flowered twice, a few weeks apart, early in the dry season (January and February).

Allen (1949) reported that the flowers are fragrant during the morning. They are pollinated by the bee *Eulaema meriana* (R. Dressler, pers. comm.).

Known only from Panama, principally from tropical moist forest in the Canal Zone, but also from premontane wet forest in Coclé (El Valle).

See Fig. 165.

CORYANTHES Hook.

Coryanthes maculata Hook., Bot. Mag. 58, t. 3102. 1831

Epiphyte; pseudobulbs subcylindrical, strongly ridged and tapering to apex, 6.5–15 cm long, 2-leaved at apex. Leaves lanceolate, 30–60 cm long, 4–10 cm wide, plicate, strongly veined. Racemes 30–60 cm long, pendent from base of pseudobulbs; flowers 2–4, ca 10 cm diam, showy, of variable color and complex shape; sepals and petals membranaceous, usually similarly colored, clear yellow to pale brown with a few purplish spots or pale purple or reddish-brown; lip very fleshy, complexly 4-parted, waxy, yellow, forming a cup containing a clear liquid produced by glands at the base of the lip. Fruits not seen.

Apparently rare; reported by R. Dressler (pers. comm.) for the island, but no specimens have been collected. Herbarium collections give evidence that the species flowers during spring (dry-season) months.

According to Allen (1949) the plants are usually found high in trees but often also on ant nests in association with *Epidendrum imatophyllum.* The unique pollination of this species was described by P. H. Allen in the *Flora of Panama* (Ann. Missouri Bot. Gard. 36:66–67. 1949). The bee *Euglossa cordata* was observed visiting this species in Trinidad (Dodson, 1965b) and in Panama (Dressler, 1968a).

Costa Rica to Venezuela, the Guianas, Brazil, and Peru; Trinidad. In Panama, known from tropical moist forest in the Canal Zone and adjacent Panamá.

DICHAEA Lindl.

Dichaea panamensis Lindl., Gen. & Sp. Orch. Pl. 209. 1833

Caespitose epiphyte; pseudobulbs lacking, stem unbranched, 4–18 cm long. Leaves conduplicate, 2-ranked, narrowly linear-lanceolate, acute or acuminate, sheathing at base, 1–2(4) cm long, to ca 5 mm wide. Flowers numerous, solitary from leaf axils, on slender pedicels to 1.5 cm long, white spotted with lavender (sometimes completely lavender elsewhere), to 1.5 cm long; sepals acute to acuminate, the lateral ones falcate; petals shorter and broader than sepals; lip sagittate, recurved, the lateral lobes folded over the column; column short; pollinia held beneath a purple, caplike flap. Fruits narrowly obovate, ca 1 cm long, weakly ribbed. *Croat 8099.*

Abundant in the forest, often growing in dense mat, occasionally in association with *Masdevallia livingstoneana* and species of *Pleurothallis.* Flowers throughout the dry season, especially in February and March, rarely during the dry season elswhere in Panama.

Easily recognized by its small size and distichous leaves, most of which subtend a small flower.

Probably pollinated by the bee *Euglossa cordata* (Dressler, 1968a).

Mexico to Venezuela and Peru, probably also in Ecuador; according to Ospina (1958) it ranges along the entire Pacific coast of Colombia. In Panama, ecologically wide-ranging; known from tropical moist forest in the Canal Zone, Bocas del Toro, and Panamá, from premontane wet forest in Coclé (El Valle), and from tropical wet forest along the Caribbean slope in Veraguas and Colón.

Dichaea trulla Reichb.f., Beitr. Orch. Central Amer. 104. 1866

D. powellii Schlechter

Erect or ± pendent, epiphytic herb; pseudobulbs lacking; stem unbranched, 15–45 cm long, enveloped by condup-

KEY TO THE SPECIES OF DICHAEA

Leaves 1–2(4) cm long ..... *D. panamensis* Lindl.
Leaves 6–13 cm long ..... *D. trulla* Reichb.f.

Fig. 166. *Dimerandra emarginata*

Fig. 167. *Encyclia chacaoensis*

licate leaf bases, the terminal portion bearing 6–12 leaves. Leaves distichously imbricating; blades spreading, linear-ligular, acute to acuminate, 6–13 cm long, to 6 mm wide, articulated at base, eventually deciduous. Flowers few, solitary from leaf axils; pedicel with a cucullate bract at apex; sepals and petals subequal, ± lance-elliptic, pale yellow-green, to 1.3 cm long and 4 mm wide, ± acute; lip purplish or green marked with purple, the claw at base broad and ligular, the blade somewhat expanded, trilobate, folded into an open-sided tube, the lateral lobes retrorse; column shorter than lip. Capsules glabrous, shiny, smooth, to 1.6 cm long. *Shattuck 1012.*

Apparently rare, in the forest. Known to flower in the early rainy season (May to August).

Easily distinguished from *D. panamensis* by having flowers many times shorter than the leaves.

Honduras to Venezuela, Guyana, and Brazil. In Panama, known from tropical moist forest in the Canal Zone and from premontane wet forest in Colón and Panamá; no doubt occurring in tropical moist forest in Darién since it has been collected in Colombia (Chocó, near the Panamanian border).

DIMERANDRA Schlechter

Dimerandra emarginata (G. Meyer) Hoehne, Bol. Agric. (São Paulo) 34:618. 1934

Epidendrum stenopetalum Hook.

Caespitose epiphyte, 15–40 cm long; pseudobulbs lacking; stems leafy, slender, with prominent longitudinal grooves, often somewhat flexuous; internodes usually prominently ribbed, often swollen. Leaves conduplicate, linear to oblong, 2.5–11(14) cm long, 0.4–1.5 cm wide, unequally, shallowly bilobed at apex. Flowers rose-colored, in 1 to few, short, few-flowered racemes; sepals and petals nearly alike, 10–13 mm long, acute or acuminate; lip ± obovate, 11–13 mm long. Capsules ellipsoid, ca 2.5 cm long, prominently ribbed. *Croat 4682, Shattuck 221.*

Common in the forest, usually rather high in trees. Flowers in the rainy season (August to December). The fruits reach full size by January and dehisce at least by April; some fruits persist without dehiscing well into the rainy season.

Mexico to Central America, Venezuela, Trinidad, the Guianas, Brazil, and Ecuador. In Panama, known from tropical moist forest along both slopes of the Canal Zone and in Bocas del Toro, Panamá, Herrera (Las Minas), and Darién.

See Fig. 166.

ELLEANTHUS Presl

Elleanthus longibracteatus (Lindl. ex Griseb.) Fawc., Fl. Pl. Jam. 38. 1893

E. trilobatus Ames & Schweinf.

Epiphytic (or elsewhere terrestrial); pseudobulbs lacking; stems slender and reedlike, to 120 cm tall. Leaves ± equidistant on stem, somewhat lanceolate, acuminate, to 18 cm long, plicate, becoming bractlike near apex; basal leaves deciduous. Inflorescences terminal, dense, many-flowered, bracteate, congested racemes to 9 cm long; lower bracts to 2.5 cm long, the upper ones reduced; flowers white or yellowish, ca 8 mm long; dorsal sepal apiculate, the lateral sepals somewhat oblique, acute; petals linear-oblong, obtuse, to 7 mm long; lip trilobulate, 6–7.5 mm broad, fimbriate-lacerate in outer half, the base with a pouchlike enlargement. Fruits elliptic-oblong, 1–2 cm long. *Shattuck 201.*

Apparently rare, collected once on Pearson Trail. Seasonal behavior not determined. The species has been collected in flower in the Canal Zone in May.

Costa Rica to Colombia. In Panama, known principally from tropical wet forest in Colón (Portobelo) and Panamá (Cerro Campana); known also from tropical moist forest in the Canal Zone and Panamá.

ENCYCLIA Hook.

Encyclia chacaoensis (Reichb.f.) Dressl., Phytologia 21:436. 1971

Epidendrum ionophlebium Reichb.f.

Repent or caespitose epiphyte, to 40 cm tall; pseudobulbs usually narrowly ovoid, 3–9 cm long. Leaves 2(3), borne at apex of pseudobulb, ligulate or elliptic, obtuse at apex, 10–35 cm long, 1.5–4 cm broad. Inflorescences terminal, to 15 cm long, bearing few to several flowers; flowers greenish to white; sepals 1.4–3.5 cm long; petals somewhat shorter, elliptic-oblanceolate to oblanceolate, acute or acuminate; lip to 2.2 cm long, ovate to orbicular, obtuse to apiculate at apex, clawed at base, colored as the petals but with purplish stripes. Fruits winged at maturity. *Shattuck 799.*

Not seen on the island in recent years. Flowering collections from Panama were all made between January and July.

Mexico to Venezuela. In Panama, known from tropical moist forest in the Canal Zone, Veraguas, and Los Santos and from premontane wet forest in Chiriquí.

See Fig. 167.

KEY TO THE SPECIES OF ENCYCLIA

Pseudobulbs bearing 1 leaf ..... *E. chimborazoensis* (Schlechter) Dressl.
Pseudobulbs bearing 2 or more leaves:
  Flowers less than 1 cm long, the lip ± trilobate; leaves less than 15 cm long and 2 cm wide .... *E. triptera* (Brongn.) Dressl. & Poll.
  Flowers more than 2 cm long, the lip not trilobate; leaves usually more than 15 cm long and 2 cm wide ..... *E. chacaoensis* (Reichb.f.) Dressl.

Encyclia chimborazoensis (Schlechter) Dressl., Phytologia 21:440. 1971

Repent or caespitose epiphyte, to ca 40 cm high; pseudobulbs narrowly oblong, somewhat flattened, stipitate at base, 5–9 cm long, to 1.3 cm wide and 8 mm thick, borne on a flexuous stem. Leaves solitary from apex of pseudobulb, conduplicate, ligulate, acute to obtuse, (10)14–20(30) cm long, (1.5)2–3(5) cm wide, coriaceous. Inflorescences terminal, few-flowered, to 15 cm long, ensheathed at base, the sheath to 2.5 cm long; flowers with sweet, intense aroma, subtended by a narrowly acute bract; sepals narrowly lanceolate, acuminate, to 3 cm long; petals oblanceolate, acuminate, to 1.7 cm long; both sepals and petals greenish-white to yellowish in age, dotted near base with violet-purple; lip broadly ovate, to 1.8 cm long and 1.1 cm wide, narrowly long-acuminate, striped throughout with violet-purple, the lateral margins upturned. Fruits not seen. *Croat 15573, Shattuck 551.*

Rare, in the forest. Flowering usually November to January (R. Dressler, pers. comm.).

Central Panama through western Colombia to Ecuador. In Panama, known from tropical moist forest on BCI and from premontane wet forest in Coclé (El Valle).

Encyclia triptera (Brongn.) Dressl. & Poll., Phytologia 21:438. 1971

E. pygmaea (Hook.) Dressl.; *Epidendrum pygmaeum* Hook.

Small, repent epiphyte, the rhizome creeping; pseudobulbs cylindrical to fusiform, 2–10 cm long, scattered along the rhizome, 2-leaved at apex. Leaves narrowly elliptic to oblong-oval, obtuse to acute, to 15 cm long and 2 cm broad. Inflorescences short, sessile in upper leaf axils; bearing few to several flowers; flowers inconspicuous; sepals and petals pale green; sepals to 12 mm long; petals linear, acute, to 8 mm long and 1 mm broad; lip ± trilobate, white with 1–3 purplish spots or streaks on the middle lobe, ± rounded and clawed, 3–8 mm long. Fruits not seen. *Dressler s.n. (STRI).*

Rare. The few Panamanian collections indicate that the species flowers in the rainy season.

Florida and Mexico to Brazil; Trinidad, Greater Antilles. In Panama, known from tropical moist forest in the Canal Zone and Darién and from premontane wet forest in Chiriquí and Coclé (El Valle).

EPIDENDRUM L.

Epidendrum anceps Jacq., Select. Stirp. Am. 224, t. 138. 1763

Epiphyte, 15–100 cm tall; pseudobulbs lacking; stem unbranched, usually somewhat 2-edged. Petioles articulate below blade; leaves conduplicate, ligulate to elliptic-lanceolate, acute or obtuse, 4–25 cm long, 1–5 cm wide, largest on the middle of the stem. Inflorescences simple or branched, terminal, racemose or subcapitate; peduncles very long, 10–45 cm long, longer than rachis, 2-edged, covered with scarious sheaths; flowers greenish- or brownish-yellow; sepals 5–10 mm long and 2–4 mm wide; petals slightly shorter and to 1.5 mm broad, sometimes reduced, threadlike, and nearly as long as sepals; lip somewhat cordate, the claw adnate to the column and somewhat enclosing it at apex. Fruits not seen. *Croat 9793.*

Uncommon, usually occurring rather high in trees; abundance is perhaps underestimated, since its flowers are not at all conspicuous. Flowering may occur throughout the year with the same plant producing several inflorescences; most flowers have been seen from April through November. The fruits develop rather quickly and are not often seen.

A very variable species.

Throughout most tropical and subtropical regions of the Western Hemisphere. In Panama, known chiefly from tropical moist forest in the Canal Zone, Bocas del Toro, and Panamá; known also from premontane wet forest in Chiriquí and Panamá (Cerro Campana).

Epidendrum coronatum R. & P., Syst. Veg. 242. 1798

E. moyobambae Kranzl.; *E. subpatens* Schlechter

Caespitose, pendent or ascending epiphyte, ca 80 cm long; pseudobulbs lacking; stem unbranched. Leaves elliptic-lanceolate to elliptic-ovate, acute, 6–16 cm long, 1.5–4 cm wide, coriaceous. Racemes terminal and pendent, to 40 cm long, long-pedunculate, the rachis longer than the peduncle, bearing few to many flowers; flowers greenish to yellowish or whitish; sepals mostly oblanceolate, 17–25 mm long, 5–9 mm wide; petals slightly smaller than sepals, of similar shape; lip broader than long, trilobate, the claw adnate to the column. Fruits not seen. *Croat 5462.*

Apparently rare, occurring in trees in the forest. Seasonal behavior uncertain. Collected once in flower in May.

Mexico to Venezuela, Brazil, Peru, and Ecuador; Trinidad. In Panama, known only from tropical moist forest in the Canal Zone and Veraguas.

Epidendrum difforme Jacq., Enum. Syst. Pl. Ins. Carib. 29. 1760

Caespitose or repent epiphyte, to 50 cm tall; pseudobulbs lacking; stems straight to flexuous, covered with leaf sheaths. Leaves usually ± oblong, blunt at apex and often emarginate, mostly 4–10(12) cm long and 0.7–3.5 cm wide. Inflorescences short, terminal, subumbellate racemes; flowers green or yellowish (especially in age), long-pedicellate, few to several; sepals 12–35 mm long; petals 7–30 mm long; both petals and sepals narrow; lip waxy, reniform, broader than long, 12–30 mm broad, the claw adnate to the column. Fruits ellipsoid, ca 3.5 cm long and 2 cm diam. *Croat 10106.*

Occasional, sometimes locally abundant; a variable species usually high in trees. Flowering to some extent all year, mostly in the early rainy season, from April to August, but especially in July and August. Mature dehiscing fruits are seen mostly in the dry season.

Pollinated by the moth *Amastus acona* in Ecuador (Dodson & Frymire, 1961).

KEY TO THE SPECIES OF EPIDENDRUM

Encyclia is included in this key because of possible confusion of the two genera.

Stems with true pseudobulbs:
- Pseudobulbs bearing 1 leaf:
  - Inflorescences borne from near base of pseudobulb; leaf blades not linear, less than 10 cm long ..... *Epidendrum rousseauae* Schlechter
  - Inflorescences borne at apex of pseudobulb:
    - Leaves linear, 4–12 cm long; flowers minute ..... *Epidendrum stangeanum* Reichb.f.
    - Leaves ligulate, more than 10 cm long; flowers more than 2 cm long ..... *Encyclia chimborazoensis* (Schlechter) Dressl.
- Pseudobulbs bearing 2 or more leaves:
  - Flowers less than 1 cm long, the lip ± trilobate; leaves less than 15 cm long and 2 cm wide ..... *Encyclia triptera* (Brongn.) Dressl. & Poll.
  - Flowers more than 2 cm long, the lip not trilobate; leaves usually more than 15 cm long and 2 cm wide ..... *Encyclia chacaoensis* (Reichb.f.) Dressl.

Stems lacking true pseudobulbs (although the stems sometimes thickened):
- Leaves equitant or semiequitant (folded along the midrib); inflorescences composed of 1 to several, ± sessile flowers in the upper leaf axils:
  - Plants forming dense mats, their stems appressed to tree, not more than 8 cm tall; sepals more more than 8 mm long ..... *Epidendrum schlechterianum* Ames
  - Plants erect, often more than 8 cm tall; sepals less than 8 mm long ..... *Epidendrum lockhartioides* Schlechter
- Leaves not equitant; inflorescences racemose (in *E. sculptum*, 2 terminal flowers):
  - Inflorescences long-pedunculate;
    - Flowers reddish or purplish:
      - Plants with long, adventitious roots near base; lip of the flowers markedly trilobate, the middle lobe smaller than the lateral lobes; plants rare ..... *Epidendrum radicans* Pav. ex Lindl.
      - Plants lacking long adventitious roots; lip of the flowers obscurely trilobate, the middle lobe larger than the lateral lobes; plants common ..... *Epidendrum imatophyllum* Lindl.
    - Flowers greenish to yellow or white:
      - Sepals less than 1 cm long; peduncle much longer than rachis of inflorescence; flowers brownish- to greenish-yellow ..... *Epidendrum anceps* Jacq.
      - Sepals more than 1.5 cm long; peduncle shorter than rachis of inflorescence; flowers greenish- to yellowish-white ..... *Epidendrum coronatum* R. & P.
  - Inflorescences not long-pedunculate:
    - Inflorescences of 2 terminal flowers subtended by spathaceous bracts ..... *Epidendrum sculptum* Reichb.f.
    - Inflorescences a raceme of more than 2 flowers:
      - Flowers white; sepals and petals more than 3.5 cm long, filiform to linear; plants common ..... *Epidendrum nocturnum* Jacq.
      - Flowers greenish to yellowish; sepals and petals less than 3.5 cm long:
        - Flowers in a short, many-flowered, subumbellate raceme; sepals and petals usually more than 1 cm long ..... *Epidendrum difforme* Jacq.
        - Flowers in a strict raceme dispersed along rachis; sepals and petals less than 1 cm long:
          - Sepals and petals less than 5 mm long; pedicel and ovary less than 1 cm long ..... *Epidendrum strobiliferum* Reichb.f.
          - Sepals and petals more than 5 mm long; pedicel and ovary more than 1.5 cm long ..... *Epidendrum rigidum* Jacq.

Throughout the New World tropics. In Panama, known from tropical moist forest in the Canal Zone, Veraguas (Coiba Island), Darién, and Panamá, from premontane wet forest in Chiriquí and Coclé, and from lower montane wet forest in Chiriquí.

Epidendrum imatophyllum Lindl., Gen. & Sp. Orch. Pl. 106. 1831

Erect epiphyte, usually 75–100 cm tall; pseudobulbs lacking, stems slender, somewhat weak. Leaves ± ligulate, mostly to 12(20) cm long and 1.5(3) cm wide, acute or obtuse at apex, articulate at apex of sheath. Flowers orchid to lavender or violet-purple (the lip more intense), to ca 3 cm wide, in corymbiform terminal racemes, subtended by linear-lanceolate bracts; peduncles 6–20 cm long; sepals and lateral petals subequal, 1–2 cm long, acuminate, slender at base; lip obscurely trilobate (the middle lobe largest), shorter than lateral petals, clawed at base, the claw adnate to the column, the outer margins lacerate-dentate; column with 2 mamillate calluses at apex, these continuous with lamellate calluses on lip.

Fig. 168. *Epidendrum imatophyllum*

Fig. 170. *Lycaste powellii*

Fig. 169. *Epidendrum nocturnum*

Fruits ellipsoid, ca 4 cm long, narrowly tapered to both ends, the ribs ± prominent. *Croat 8257.*

Occasional, in the canopy of the forest or on exposed branches along the shore. Flowering from January to July, chiefly in the dry season (February to April). The fruits develop quickly and may be present on a flowering raceme.

Often associated with ant nests and with *Aechmea tillandsioides* var. *kienastii* (22. Bromeliaceae). Similar to *E. radicans,* but lacking the adventitious roots on the stem characteristic of that species.

Mexico to Panama, Venezuela, the Guianas, Brazil, Peru, and Ecuador; Trinidad. In Panama, known from low elevations in tropical moist forest in the Canal Zone, Los Santos, Panamá, and Darién.

See Fig. 168.

Epidendrum lockhartioides Schlechter, Feddes Repert. Beih. 19:39. 1923

Densely caespitose epiphyte, to 15(25) cm tall; pseudobulbs lacking. Leaves laterally compressed, acute at apex, 1–3.5 cm long, the narrow base subequitant, ensheathing stem, the upper leaves crowded. Flowers green to brownish-yellow, solitary in axils of each of several uppermost leaves; sepals ± lanceolate, cucullate, 6–8 mm long, to 3 mm broad, keeled; petals linear, slightly arcuate, obtuse at apex, 4–7 mm long; lip clawed, the claw adnate to the column, the blade subrounded, 4–5 mm broad, often apiculate, the midvein thickened. Fruits not seen.

No specimens seen from BCI, but reported to occur by R. Dressler. Flowers elswhere in Panama at the beginning of the dry season (December to February).

Costa Rica and Panama. In Panama, known primarily from premontane wet forest in Coclé (El Valle) and Panamá (Cerro Azul and the Río Boqueron above Madden Lake); known also from tropical moist forest in the Canal Zone and from tropical wet forest in Panamá (Cerro Jefe).

Epidendrum nocturnum Jacq., Enum. Syst. Pl. Ins. Carib. 29. 1760

Caespitose epiphyte, 20–60(100) cm tall; pseudobulbs lacking; stem canelike, unbranched, often covered with leaf sheaths or becoming naked. Leaves mostly ligulate to elliptic-oblong, acute to obtuse at apex, 8–16 cm long, 1–3.5(6.5) cm wide, ± fleshy. Racemes terminal, few-flowered; peduncles short; flowers large, white, only 1 opening at a time; sepals alike, linear, 3.5–7(9) cm long, to 5 mm broad; petals smaller than sepals, 3–5(8) cm long, linear; lip prominently trilobate, to 6.5 cm long, clawed, the claw adnate to the column, the lateral lobes of lip acute, 1–4 cm long, the middle lobe subfiliform, 2–4 cm long, usually much longer than the lateral lobes. Fruits ellipsoid, usually to 5 cm long, narrowly tapered to apex, the old flower usually persisting, the ribs with prominent margins. *Croat 12619.*

Frequent in the forest trees and on branches along the shore. Flowering throughout most of the year, especially in the late rainy season and early dry season (November to January). Mature-sized fruits are common in February.

Throughout most tropical regions of the Western Hemisphere; also in Sierra Leone, Africa. In Panama, most common in tropical moist forest in the Canal Zone and Bocas del Toro; known also from premontane wet forest in Coclé (El Valle), Colón (Santa Rita Ridge), and Chiriquí.

See Fig. 169.

Epidendrum radicans Pav. ex Lindl., Gen. & Sp. Orch. Pl. 104. 1831

Terrestrial; pseudobulbs lacking; stems short or to 1 m, erect, pendent or sprawling, simple or branched, usually with long whitish roots opposite some of the leaf bases. Leaves ligulate to ovate, blunt at apex, 1.5–8(12) cm long, 0.6–2(3.5) cm wide, coriaceous. Inflorescences terminal, the racemes lax, subumbellate or paniculate, borne on long bracteate scapes; flowers variable in size and color, from red to white but usually brick-red or orange (Colombian and Venezuelan forms violet), 12–22 mm long, the lobes acute; lip suborbicular-cordate, trilobate (the middle lobe smallest), 7–17 mm long, the claw adnate to the column. Fruits oblong-elliptic, narrowly tapered at base. *Shattuck 768, Woodworth & Vestal 703.*

Not seen on the island recently; collected twice in 1932 on floating islands of vegetation along the shore. Elsewhere preferring open, sunny areas. Flowers throughout the dry season (January to April), rarely during the rainy season. The fruits develop quickly, and mature-sized fruits may be found on the same inflorescence with flowers.

The species is similar to *E. ibaguense* H.B.K., which is also terrestrial but roots only at the base; *E. radicans* is terrestrial and has roots forming all along the stem. The species may also be confused with *E. decipiens* Lindl., which is an epiphyte that has roots only near the base.

This species was reported to be visited by swallow-tailed skippers, *Papilio* sp., and also by the hummingbird *Amazalia* sp., believed by Dodson to be the legitimate pollinator (1962).

Mexico and Central America to southwestern Colombia. In Panama, known principally from premontane wet forest and tropical wet forest at higher elevations in Chiriquí, Coclé (El Valle), and Panamá (Cerro Campana); known also from tropical moist forest in the Canal Zone and Bocas del Toro.

Epidendrum rigidum Jacq., Enum. Syst. Pl. Ins. Carib. 29. 1760

Small epiphyte; pseudobulbs lacking; stem repent, unbranched, covered with amplexicaul leaf sheaths. Leaves linear to oblong-elliptic, obtuse to rounded at apex, emarginate to bilobed, 3–13 cm long, 0.5–2 cm wide, thick. Racemes terminal, 5–15 cm long, several-flowered, short-pedunculate; bracts to 1.5 cm long; flowers yellow to greenish; sepals oblong to narrowly ovate, mostly 5–9 mm long, 2–4 mm wide, the lateral ones sometimes obovate; petals ± obovate, oblique, narrower but about as long as sepals; lip cordate-orbicular, 4–6 mm long, about as broad as long, clawed, the claw adnate to the column, the

lateral margins revolute; ovary and pedicel together more than 1.5 cm long. Fruits oblong-ellipsoid to ellipsoid, 1.5–2.5(3) cm long, the old flower persisting at the apex. *Shattuck 345, 649.*

Rare; collected recently by R. Dressler. Elsewhere in Panama flowers from April to December in the middle to late rainy season, especially from September to December. Mature-sized fruits have been seen throughout the dry season.

Throughout most tropical and subtropical regions of the Western Hemisphere. In Panama, know principally from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Panamá, and Darién; known also from tropical wet forest at higher elevations in Panamá (Cerro Brewster).

Epidendrum rousseauae Schlechter, Beih. Bot. Centralbl. 36, abt. 2:407. 1918
E. laterale Rolfe

Small epiphyte, sometimes trailing; pseudobulbs slender, to 3.5 cm long, 1-leaved; stems simple or branched. Leaves ligulate to elliptic-oblong, 5–10 cm long, 1.5–3 cm wide, obtuse to somewhat rounded and mucronate at apex, thick. Racemes arising from base of pseudobulb, several-flowered, to 12 cm long; bracts small; flowers greenish; sepals narrowly lanceolate, acute, fleshy, ca 1.2 cm long; petals as long as sepals, linear; lip trilobate, ca 7 mm long, deeply cordate at base, clawed, the claw adnate to the column for the length of the column. Fruits not seen. *Shattuck 347.*

Not seen recently on the island but to be expected. Seasonal behavior not determined. *Shattuck 347* had fruits nearly mature in November.

Known only from Panama, principally from premontane wet forest in Chiriquí (Monte Lirio), Coclé (El Valle), and Panamá (headwaters of Río Corso); known also from tropical moist forest in the Canal Zone and adjacent Panamá.

Epidendrum schlechterianum Ames, Sched. Orch. 7:9, fig. 1. 1924

Densely caespitose, dwarf epiphyte, to 8 cm tall; pseudobulbs lacking; stems covered with overlapping leaf bases. Leaves ± equitant, linear-oblong, acute, 1–3 cm long, to 1 cm wide, fleshy. Inflorescences of 1 to few sessile flowers in terminal leaf axils; flowers pale greenish-brown tinged with pink; sepals usually ± lanceolate, 0.8–2 cm long, 2–4.5 mm wide, the lateral ones slightly shorter than dorsal one and connate at their base with the claw of the lip; petals similar to sepals except smaller; lip long-clawed, trilobate, 9–15 mm long, nearly as broad as long, the claw adnate to the column, the lateral lobes small, the terminal lobe obovate-cuneate, bilobed or deeply bifid. Fruits ± globular, ca 1 cm long, prominently 3-angled. *Croat 8199.*

Occasional, in the forest, usually on the upper surface of larger branches high in the canopy. Flowers in Panama principally during the early dry season (December to February). The fruits develop quickly; ones of mature size are seen frequently in February.

Mexico to Panama, Venezuela, Surinam, Brazil, and Peru; Jamaica. In Panama, known only from tropical moist forest in the vicinity of the Canal Zone and in Veraguas (Coiba Island). R. Dressler reports that he would expect it in most of the drier forests of Panama (pers. comm.).

Epidendrum sculptum Reichb.f., Bonplandia 2:89. 1854

Pendent or repent epiphyte, 10–50 cm long; pseudobulbs lacking; stems simple or branched, densely leaved, the old petiole bases persisting. Leaves oblong to lanceolate-oblong, obtuse to rounded and emarginate at apex, 2–6 cm long, 1–1.8 cm wide, thick. Inflorescences of 1–3 (usually 2) terminal flowers subtended by spathaceous bracts; flowers green to greenish-yellow, reportedly with a fetid odor; sepals oblong-lanceolate, 1–1.5 cm long, ca 3 mm wide; petals similar to sepals; lip about as long as sepals, clawed, lanceolate-ovate, acute, trilobate, the lateral lobes rounded and about half as long as the lanceolate middle lobe, the claw adnate to the column. Fruits ± ellipsoid, remaining enveloped by spathaceous bracts. *Shattuck 558.*

Not seen in recent years on the island. In Panama, flowers principally from the middle to late rainy season (September to November). The fruits are of mature size by the early dry season.

Known from Panama and the Guianas. In Panama, known principally from tropical moist forest in the Canal Zone and Panamá; known also from premontane wet forest in Colón (Río Indio de Fato, *Pittier 4265*).

Epidendrum stangeanum Reichb.f., Gard. Chron. n.s. 15:462. 1881

Small, repent or caespitose epiphyte, to 20 cm long, the rhizome slender, creeping; pseudobulbs 1.5–5 cm long, to 5 mm diam, 1-leaved. Leaf linear, often inrolled at margins, 4–12 cm long, to 3 mm wide. Raceme in leaf axil, several-flowered, shorter than the subtending leaf; flowers small, tan; sepals lanceolate, 5–7 mm long, 1.5–3 mm wide; lip clawed, deltoid to ovate-lanceolate, apiculate, ca 5 mm long, the claw adnate to the column. Fruits narrowly ellipsoid, ca 12 mm long and 4.5 mm wide, 6-ribbed, 3 stouter ribs alternate with the other 3. *Shattuck 454.*

Not seen in recent years on the island. On the basis of a few collections, it appears that this species flowers only in the late rainy season (October to December).

Known from Costa Rica and Panama. In Panama, known only from tropical moist forest in the Canal Zone.

Epidendrum strobiliferum Reichb.f., Ned. Kruidk. Arch. 4:333. 1859

Small, repent or caespitose epiphyte, to 20 cm long; pseudobulbs lacking; stems simple or branched, covered with dense, amplexicaul leaf sheaths. Leaves ligulate to linear-lanceolate, acute to obtuse and usually bilobed at apex, 0.8–4.5 cm long, 2–10 mm wide, thick. Racemes short, few-flowered, terminal; bracts to 8 mm long, cucullate, chartaceous; flowers small, yellowish or white; sepals

± lanceolate, 3.5–5 mm long, 1.2–2 mm wide, the dorsal one narrower; petals linear-oblanceolate, smaller than sepals; lip ovate-cordate, acute, to 3.5 mm long and 3 mm wide, adnate to base of the column. Fruits ellipsoid, ca 1 cm long, the old flowers persisting at the apex. *Shattuck 550.*

Not seen on the island in recent years. On the basis of few collections, it appears that the species flowers exclusively in the rainy season (August to December), especially from August to September, with the fruits maturing in the early dry season.

Florida and Mexico through Central America to Panama, Venezuela, the Guianas, Brazil, and Peru; Trinidad, West Indies. In Panama, known from tropical moist forest in the Canal Zone and Panamá.

EULOPHIA R. Br. ex Lindl.

Eulophia alta (L.) Fawc. & Rendle, Fl. Jam. 1:112, t. 22, figs. 4–8. 1910

Glabrous, rhizomatous, terrestrial herb, to 130 cm tall. Petioles tightly ensheathing stem; leaves appearing sessile, linear-lanceolate, gradually tapered to apex, to 80 cm or more long, 5.5–6 cm wide, the midrib prominently canaliculate in basal half of blade, whitish and prominently ridged on underside, the ridges diminishing by apical fourth of blade. Inflorescences long, stout, erect racemes 70–100 cm long, terminating leafless scapes produced directly from the rhizome; flowers olive or greenish-tan; sepals free, lanceolate to oblanceolate, acute, to 25 mm long and 8 mm wide; petals erect, oblong, obtuse, ± equal to sepals; lip trilobate, shaded with rose or purple, the middle lobe with numerous denticulate longitudinal veins. Fruits 3.5–4 cm long, ellipsoid, with 6 prominent ribs, the pedicel ca 1.5 cm long. *Croat 12809.*

Rare; known only from Rear #8 Lighthouse Clearing, where it usually persists after each cutting. Flowers during the middle to late rainy season and the earliest part of the dry season. Mature-sized fruits have been seen in the early dry season (December). Seeds are probably dispersed during the dry season.

Florida and Mexico to Peru and Brazil; West Indies; West Africa. In Panama, known from tropical moist forest in the Canal Zone, from premontane wet forest in Coclé (El Valle), and from tropical wet forest in Colón.

GONGORA R. & P.

Gongora quinquenervis R. & P., Syst. Veg. 227. 1798
G. maculata Lindl.

Epiphyte; pseudobulbs ovoid, 4.5–6.5 cm long, to 3.5 cm wide, dark brown, strongly ridged, enveloped at base by fibrous, imbricating bracts, bearing 2 or 3 terminal leaves. Leaves ± lance-elliptic, usually acuminate, plicate, 25–50 cm long, 5–12 cm wide, moderately thin. Racemes ± pendulous from base of pseudobulb, 30–60 cm long; flowers numerous (to 30), well spaced, grotesque, strongly fragrant, with all parts yellow and spotted or banded with reddish-brown, mostly membranaceous; pedicels slender, 2–3.5 cm long; dorsal sepal lanceolate, acuminate, to 1.8 cm long, free and erect, inserted about midway on the column, the lateral sepals strongly reflexed, obliquely ovate, acuminate, to 2.5 cm long, inserted on the column foot; petals slender, acuminate, to 8 mm long, inserted on column and fused at base to lateral sepals; lip fleshy, clawed, complexly bipartite, 1.5–2.5 cm long, with 2 slender, lateral, ± recurved projections from base and with 2 slender, erect, lateral antennae nearer the apex; column erect, ± arcuate, 1.5–2 cm long. Fruits not seen. *Dressler 2858.*

Apparently rare on BCI. Reportedly flowering irregularly more than once a year (*Powell 76*). Flowers principally in the dry season, but may flower in the early rainy season (to July) as well. The fruits apparently develop quickly and disperse their seeds chiefly in the dry season.

BCI plants are pollinated by the bee *Euglossa tridentata* Mourre, but have also attracted *E. cordata, E. townsendii, E. hemichlora,* and *E. cyanaspis* (Dressler, 1968a; Baker, 1963).

Mexico to Brazil and Peru. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Panamá, from premontane wet forest in Coclé (El Valle). Reported also from Colón (R. Dressler, pers. comm.).

Gongora tricolor (Lindl.) Reichb.f., Bonplandia 2:93. 1854
G. maculata Lindl. var. *tricolor* Lindl.

Epiphyte, similar to *G. quinquenervis* but the flowers more richly colored; the sepals rich yellow to orange, usually sparsely blotched with dark red or dark purple; the petals greenish-yellow, usually spotted with dark red; the lip very fleshy, its base (the hypochile) broader than in *G. quinquenervis,* the basal horns of the lip hemispheric and fleshy (thicker than those of *G. quinquenervis*).

Apparently rare on BCI; reported by Dressler, but no specimens seen from the island. More common than *G. quinquenervis* (*fide* R. Dressler, pers. comm.). Flowering pattern is apparently the same as that of *G. quinquenervis.* Dressler (1968a) reported it to flower during March and April.

Pollinated consistently by the bee *Euglossa ganura.* Visits are made in the morning until 11:00 A.M. (Dressler, 1966).

KEY TO THE SPECIES OF GONGORA

Hypochile when seen from above relatively narrow, the base with lateral ligular projections . . . . . *G. quinquenervis* R. & P.

Hypochile when seen from above relatively broad, the base auriculate or with short, lateral, fleshy, hemispheric horns . . . . . *G. tricolor* (Lindl.) Reichb.f.

KEY TO THE SPECIES OF HABENARIA

Petals entire; lip entire ..... *H. alata* Hook.f.
Petals bifid; lip trilobate:
Spur at base of lip less than 1.5 cm long; plants found in swampy places or on floating debris ..... *H. repens* Nutt.
Spur at base of lip more than 3 cm long; plants not found in swampy or aquatic habitats ..... *H. bicornis* Lindl.

Known from Panama and Peru. In Panama, apparently with the same range as *G. quinquenervis*. Dressler (1966) reported it to be common on the Atlantic slope in central Panama.

HABENARIA Willd.

Habenaria alata Hook.f., Exot. Fl. t. 169. 1826

Terrestrial, erect, 20–70 cm tall; pseudobulbs lacking. Leaves scattered along slender stems, linear-lanceolate, 6–14 cm long, 1–2 cm wide, much reduced at base and apex of stems. Inflorescences terminal, subracemose, 4–20 cm long; flowers dense, pale green; pedicels very short; sepals to 1 cm long, the dorsal sepal ovate to suborbicular, concave, to 7 mm wide, broader than the laterals, the lateral sepals ± lanceolate, acute to acuminate; petals ± entire, slightly smaller than the sepals, lanceolate, ± acute; lip ± lanceolate, 6–8 mm long, ca 2 mm broad; spur at base of lip recurved, subclavate, to 1.3 cm long. Fruits sharply ribbed to winged, ca 17 mm long and 6 mm wide, the lower fourth hidden by the persistent bract. *Kenoyer 249.*

Not seen in recent years on BCI. Flowers throughout the rainy season. The fruits are common in the late wet and early dry seasons.

Mexico to Colombia, Venezuela, and Bolivia; West Indies. In Panama, ecologically wide ranging; known from tropical moist forest in the Canal Zone and from lower montane wet forest in Chiriquí (Volcán).

Habenaria bicornis Lindl., Gen. & Sp. Orch. Pl. 309. 1835

Terrestrial, erect, to 65 cm tall; pseudobulbs lacking. Leaves scattered along slender stems, linear-lanceolate, 5–25 cm long. Racemes terminal, many-flowered, ca 8 cm long, bracteate; flowers green with white petals; sepals 6–10 mm long, ca 5 mm wide; petals bifid, the lobes unequal, to 9 mm long; lip trilobate, 7–12 mm long, the middle lobe shortest; spur at base of lip recurved, 4–5 cm long. Fruits narrowly ellipsoid, ca 2.5 cm long and 6 mm wide, prominently 6-ribbed.

No specimens seen for the island, but reported to occur by R. Dressler. Flowers in July, according to the label on *Powell 315*; flowering collections have also been made in September.

Panama and the West Indies. In Panama, known from tropical moist forest in the Canal Zone and Panamá.

Habenaria repens Nutt., Gen. N. Amer. Pl. 2:190. 1818

Terrestrial, ± aquatic, erect, to 1 m tall; pseudobulbs lacking. Leaves scattered along slender stems, ± linear-elliptic, to 20 cm long, reduced toward apex. Racemes terminal on stems, densely flowered, bracteate, 10–15 cm long; flowers light green; sepals 4–8 mm long; petals 4–9 mm long, bipartite, the lobes subequal; lip tripartite, 5–10 mm long, the middle lobe slightly shorter; spur at base of lip recurved, to 15 mm long. Fruits much like *H. alata* but perhaps more rounded at apex. *Bailey & Bailey 663.*

Not seen on the island in recent years; found on floating debris and in swampy places. Possibly flowering all year, but mostly in the late rainy and early dry seasons. Both flowering and fruiting individuals have been collected from the same area during February.

Scattered from southeastern United States to Brazil; Trinidad, Greater Antilles. In Panama, known only from tropical moist forest on BCI.

IONOPSIS Kunth

Ionopsis satyrioides (Sw.) Reichb.f., Ann. Bot. Syst. 6:683. 1863

Small epiphyte; pseudobulbs minute or lacking. Leaves ± linear, from a very short stem, narrowly acute at apex, mostly 3–8 cm long, 1–4 mm wide, about half as thick as wide, sulcate along one edge. Inflorescences arising from among the leaves, simple or sparsely branched, equaling or exceeding length of leaves, 3–10 cm long; peduncles slender, with several sheathing bracts 3–5 mm long; flowers ca 6 mm long; sepals brownish-cream to rose-purple, united for ca one-third their length, acute and ± recurved at apex, the midvein ± thickened on outside; petals white with purplish markings on veins, thinner than sepals, to 5.5 mm long and 1.8 mm wide; lip

KEY TO THE SPECIES OF IONOPSIS

Leaves less than 5 mm wide, almost as thick as wide; inflorescences less than 10 cm long ..... *I. satyrioides* (Sw.) Reichb.f.
Leaves 5–15 wide, considerably wider than thick; inflorescences 15–60 cm long ..... *I. utricularioides* (Sw.) Lindl.

± oblong, truncate, to 5.5 mm long and 2.5 mm wide, white with 2 purplish lines medially, with a yellow, bifurcate callus near base just above the short, terete claw. Fruits oblong-elliptic, the body ca 1.5 cm long and 1 mm wide, narrowly tapered at both ends, the basal stipe to 7 mm long. *Dressler s.n.*

Rare. Flowers mostly in March and April. Mature fruits have been seen in April.

Belize, Guatemala, Costa Rica, and Panama (possibly other parts of Central America as well) across northern South America to Venezuela and the Guianas; West Indies. In Panama, known only from tropical moist forest in the Canal Zone and Chiriquí (Concepción).

Ionopsis utricularioides (Sw.) Lindl., Coll. Bot. t. 39-A. 1825

Epiphyte; pseudobulbs minute or lacking; stems very short. Leaves linear-lanceolate, acute, 4–16 cm long, 5–15 mm wide, keeled on lower surface, ensheathing stem at base. Inflorescences paniculate, from leaf axils; scapes slender, erect to arching, 15–60 cm long; flowers several, mostly 6–7 mm long, diffuse, lavender or violet to white; sepals subequal, ± oblong-lanceolate, acute, the dorsal sepal free, concave, the laterals connate at the base and produced into a short, broad sac; petals subequal to dorsal sepal, elliptic-ovate; lip twice as long as sepals, deeply emarginate and bilobed, contracted at base into a fleshy claw, the claw adnate to the base of the short, stout column; anther terminal, caplike. Fruits ellipsoid, 2–2.5 cm long, moderately ribbed and thin-walled. *Croat 4679.*

Occasional, in the Laboratory Clearing. Flowers in the late dry season (March to May, especially April). The fruits mature in the rainy season (June to October).

Florida and Mexico along the Caribbean coast and along the eastern side of the Andes to Brazil and Paraguay; West Indies; Galápagos Islands. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién.

LEOCHILUS Knowl. & Westc.

Leochilus scriptus (Scheidw.) Reichb.f., Xenia Orch. 1:15, t. 6. 1854

Caespitose, erect epiphyte, 10–20 cm tall; pseudobulbs compressed, ellipsoid, 2–5 cm long, enveloped at base by several imbricating bracts. Leaves usually solitary from apex of pseudobulb, ligulate, shortly bifid at the apex, 6–14 cm long, 1–2.8 cm wide, short-petiolate. Racemes 1 or 2 from basal leaf axils, ± equaling leaves; flowers 1.5–2 cm diam, greenish-yellow with purplish-brown markings especially near center of each segment; sepals subequal, spreading, 8–12 mm long, 2.5–5 mm wide, the dorsal sepal concave, keeled; petals similar to dorsal sepal, lanceolate, acute; lip obovate-oblong, truncate, to 12 mm long and 7 mm wide, keeled on lower surface, thickened at base and adnate to the base of the column; column semiterete with 2 extended ligular arms below the stigma; anther terminal and caplike. Fruits narrowly ellipsoid, to ca 4 cm long, the body 2–2.2 cm long, 6-ribbed, 3 ribs obscure, the 3 alternate ribs very flattened. *Dressler 2900.*

Rare. Flowers in Panama chiefly in the late rainy and early dry seasons (November to February). The fruits probably develop quickly; mature fruits have been seen in February.

Guatemala to Panama. In Panama, known from tropical moist forest on both slopes of the Canal Zone and in Veraguas and Panamá.

LIPARIS L. C. Rich.

Liparis elata Lindl., Edward's Bot. Reg. 14, t. 1775. 1828

Terrestrial where humus abundant, or epiphytic, 15–40 cm tall; pseudobulbs inconspicuous, usually enveloped by leaves; stems short, becoming fleshy, sheathed with broad petiole bases. Leaves 3 or 4, rosulate, at apex of pseudobulb; blades ± elliptic, 5–30 cm long, 2.5–11 cm wide, plicate. Racemes terminal on stems, equaling or exceeding leaves; pedicels slender, 5–10 mm long; flowers light greenish-yellow with purplish-brown veins; sepals unequal, oblong to ovate, obtuse, 4–7 mm long, the lateral sepals arcuate; petals linear to linear-oblanceolate, obtuse, arcuate, smaller than sepals; lip ± obovate, truncate or emarginate and purplish-brown at apex, 4–5.5 mm long, with 2 tubercles at base. Fruits oblong-elliptic, ca 1 cm long. *Dressler 2864.*

Rare. Flowers mostly in the early rainy season. Fruits are seen throughout the dry season. The fruiting inflorescence sometimes persists on the old leafless stem until the next flowering.

Florida and Mexico to Peru and Brazil; West Indies. In Panama, known chiefly from premontane wet forest at middle elevations such as in Panamá (Cerro Campana); known also from tropical moist forest in the Canal Zone and Panamá.

LOCKHARTIA Hook.

Lockhartia acuta (Lindl.) Reichb.f., Bot. Zeitung (Berlin) 10:767. 1852

L. pallida Reichb.f.

Caespitose epiphyte; pseudobulbs lacking; stem flattened, unbranched, covered with equitant, distichously imbricating leaves. Blades acute, short, to 3 cm long. Flowers small, yellowish or white with a yellow lip, in 1–3 divaricately branched panicles to 8 cm long at or near apex; pedicels slender, subtended by small subcordate bracts; sepals and lateral petals subequal, ovate, ± rounded at apex, strongly concave, to ca 4 mm long; lip 4.7–6 mm long, somewhat expanded and bilobed at apex, fused to the short column near the base; column with lateral wings, the wings not surpassing apex; pollinia 2, pale yellow, teardrop-shaped. Fruits ± obovate, 6–10 mm long, pruinose, smooth, splitting into 3 valves. *Croat 8056.*

Common high in trees in the forest. Flowers in the dry season (December to April), especially in the early dry season, with the fruits maturing in the early rainy season.

KEY TO THE SPECIES OF LOCKHARTIA

Stems usually much more than 20 cm long; upper edge of the equitant leaf straight or slightly convex, in contact with the next higher leaf more than two-thirds of its length; inflorescences relatively large, spreading, divaricately branched panicles ..... *L. acuta* (Lindl.) Reichb.f.

Stems less than 20 cm long; upper edge of the equitant leaf usually concave, in contact with the next higher leaf less than one-third of its length; inflorescences short scapes of 1 flower ..... *L. pittieri* Schlechter

Inflorescences may appear successively with both flowering and fruiting inflorescences present on the same plant.

Panama across northern South America to Trinidad. In Panama, known from tropical moist forest in the Canal Zone and Panamá, apparently more frequently on the Pacific slope.

Lockhartia pittieri Schlechter, Feddes Repert. 12:216. 1913

Caespitose epiphyte; pseudobulbs lacking; stem flattened, unbranched, obscured by equitant, distichously imbricating leaves. Blades acute, 2–3.5 cm long. Inflorescences short, solitary, 1-flowered scapes from upper leaf axils; flowers yellow with an orange callus on inner surface of lip near base; sepals elliptic-lanceolate, acute, 4–5 mm long, with apiculate tips; petals broader than sepals, obtuse to acute; lip 7–8 mm long, ± convex and deeply emarginate, the margins raised, thickened, and papillose at apex with an erect, central spur. Fruits not seen.

No specimens seen for BCI, but reported by R. Dressler. Apparently flowers in the early dry season (*Powell 372*).

Belize to Panama. In Panama, known from tropical moist forest in the Canal Zone and Darién.

LYCASTE Lindl.

Lycaste powellii Schlechter, Feddes Repert. Beih. 17:65. 1922

Epiphyte (or elsewhere pseudoterrestrial, growing in sandy places, *fide Powell 15*); pseudobulbs elliptic-ovoid, laterally compressed, 3–6 cm long, smooth to ± ridged, bracteate at base, the uppermost bracts leaflike. Leaves 2 or 3, terminal on pseudobulb, ± lanceolate, acute to acuminate, 20–35 cm long, 3–3.5 cm wide, ultimately deciduous, ± plicate. Inflorescences 1–4, erect, 1-flowered, 5–15 cm long from base of pseudobulb before leaves have fallen; peduncles slender, with several sheathing bracts along their length and a solitary flower at apex; flowers relatively large, very fragrant; sepals usually pale green, 2.5–3 cm long, the apices strongly recurved, the laterals adnate to base of column; petals about equal to sepals, usually white with rose markings; lip trilobate, to 2.5 cm long, nearly as wide, colored like petals, the lateral lobes erect, the middle lobe broadly obtuse and somewhat reflexed; column 8–9 mm long, the undersurface conspicuously pubescent. Fruits not seen. *Dressler 2868.*

Rare, growing in wooded ravines (Allen (1949) in the *Flora of Panama*). Flowers in July.

The species is closely related to *L. brevispatha* Klotzsch ex Lindl., which is reported from higher elevations.

Known only from Panama, principally from premontane and tropical wet forests in Coclé (El Valle) and Panamá (Cerro Campana); known less frequently from tropical moist forest such as on BCI.

See Fig. 170.

MASDEVALLIA R. & P.

Masdevallia livingstoneana Reichb.f., Gard. Chron. ser. 2, 2:322. 1874

Caespitose epiphyte, 6–13 cm tall; pseudobulbs lacking. Leaves solitary on very short secondary stems; blades oblanceolate, 5–11 cm long. Inflorescences shorter to somewhat longer than leaves; flowers to 12 mm long, pale yellow or white with the throat violet-purple, solitary on peduncles from base of leaves, the fragrance strong, sweet; sepals 1.5–2 mm long, connate into a tube for half their length, the free part of dorsal sepal thickened, ligulate, to 12 mm long and 3 mm broad, arcuate-spreading, the lateral sepals similar to the dorsal sepal but slightly wider; petals and lip enclosed within calyx tube; petals 4–5 mm long with a single longitudinal callus from below middle to apex; lip ± oblong, 4–6 mm long. Fruits not seen. *Croat 9120.*

Occasional, in the forest usually high in trees on branches. Flowers from February to April.

Reported only from Panama; possibly also in Costa Rica. In Panama, known from tropical moist forest and premontane wet forest in the Canal Zone, Colón, and Panamá.

MAXILLARIA R. & P.

Maxillaria alba (Hook.) Lindl., Gen. & Sp. Orch. Pl. 143. 1832

Epiphyte with elongate, rhizomatous stems enveloped by closely imbricating, persistent bracts; pseudobulbs inserted at an acute angle to stem, ± overlapping, narrowly elliptic, flattened and 2-edged, 4–5 cm long, 1-leaved. Leaves ligulate, acute to bilobed at apex, conduplicate, 25–40 cm long, 1–2 cm wide. Flowers white to cream except for yellow on lip, solitary from axils of bracts of new growth, several open at once; pedicels 3–4 cm long, longer than bracts; sepals subequal, free, spreading, 2–2.5 cm long, to ca 5 mm wide, the laterals adnate to base of column; petals ca equal to sepals; lip obscurely trilobate, concave, slightly curved, yellow or white with yellow

KEY TO THE SPECIES OF MAXILLARIA

Leaves not borne on conspicuously thickened secondary stems (all but the leaves of the small, inconspicuous pseudobulb are actually foliaceous bracts); plants caespitose (lacking an elongate rhizome) ..... *M. crassifolia* (Lindl.) Reichb.f.
Leaves borne on conspicuously thickened secondary stems (i.e., pseudobulbs):
  Plants caespitose (growing in a flattened tuft); pseudobulbs all ± erect, among weathered bracts; scapes 1–4, 1-flowered, arising from among the pseudobulbs, 4–13 cm long, the bracts continuous along its length, mostly more than 1.5 cm long, scarcely if at all overlapping ..... *M. powellii* Schlechter
  Plants caulescent, erect, scandent, or pendent; pseudobulbs inserted at an oblique angle along an elongate, sometimes branching stem:
    Leaves very numerous, 1 per pseudobulb, mostly less than 4 cm long and 5 mm wide, ± triangular in cross section ..... *M. uncata* Lindl.
    Leaves much larger, not as above:
      Flowers ca 6 mm long, produced in dense clusters at base of pseudobulb on new growth, each flower enveloped by 2 glumaceous bracts; stem bracts closely spaced, ca 1.5 cm long or less; fruits globular, ca 5 mm long ..... *M. neglecta* (Schlechter) L. O. Wms.
      Flowers usually much larger, mostly more than 1 cm long, not densely clustered or enveloped by bracts; stem bracts usually longer than 1.5 cm (short in *M. friedrichsthalii*):
        Scapes closely bracteate throughout their length, usually several from base of mature pseudobulb; stem bracts mostly less than 1.5 cm long; leaves usually 2 or 3 (sometimes 4) per pseudobulb ..... *M. friedrichsthalii* Reichb.f.
        Scapes not bracteate (at least not toward apex), solitary from base of mature pseudobulb and/or from bract axils on flush of new growth; stem bracts mostly more than 1.5 cm long; leaves 1 or 2 per pseudobulb:
          Leaves usually 2 per pseudobulb; bracts of new growth unequally bilobed at apex; pseudobulbs often widely scattered along stem; flowers usually more than 2.5 cm long ..... *M. camaridii* Reichb.f.
          Leaves usually 1 per pseudobulb; bracts of new growth acute at apex; pseudobulbs usually closely positioned; flowers usually less than 2.5 cm long:
            Leaves usually less than 20 cm long; flowers usually less than 1.2 cm long ..... *M. variabilis* Lindl.
            Leaves usually more than 25 cm long; flowers usually more than 2 cm long ..... *M. alba* (Hook.) Lindl.

lobes, 1.2–1.5 cm long, ca 5 mm wide, contracted at base and articulated with foot of column. Fruit not seen. *Dressler 2951* (*F*).

Collected once in the forest. Flowers mostly in the rainy season, but flowering collections have also been made during the dry season.

Allen (1949) reported that flowers are produced more or less simultaneously, in contrast to most other species of *Maxillaria,* which produce flowers in succession.

Guatemala to Brazil; West Indies. In Panama, known from tropical moist forest on both slopes in the Canal Zone and in Panamá and Darién; known also from premontane wet forest in Colón (Santa Rita Ridge) and Chiriquí (Boquete).

Maxillaria camaridii Reichb.f., Hamburger Garten-Blumenzeitung 19:547. 1863
Camaridium ochroleucum Lindl.

Epiphyte with long, cylindrical, pendent stems covered with sheathing bracts; pseudobulbs inserted at an angle on the stem, 3–7 cm long, flattened and 2-edged. Leaves (1)2 at apex of pseudobulb, ± linear, shallowly and unequally bilobed at apex, 10–30 cm long, conduplicate. Flowers solitary on short peduncles, produced in successive pairs from bract axils on new growth, fragrant; sepals white, subequal, 2.5–3.5 cm long, the laterals adnate at base to base of column; petals white, nearly equaling sepals, widely spreading; lip white outside, yellow inside with purplish-brown, transverse streaks, trilobate, 10–12 mm long and wide, contracted at base and articulated with foot of column. Fruits not seen. *Shattuck 341, 346, 348.*

Not seen recently on BCI. Collected by Shattuck during November, but reportedly flowering in the dry season as well.

Allen (1949) in the *Flora of Panama* reported that each plant flowers three or four times during a season.

Guatemala to Panama and northeastern South America in the Guianas and Trinidad. In Panama, known from tropical moist forest in the Canal Zone and Panamá and from premontane wet forest west of the Canal Zone (El Valle in Coclé and Cerro Campana in Panamá).

Maxillaria crassifolia (Lindl.) Reichb.f., Bonplandia 2:16. 1854

Caespitose, erect epiphyte, 20–40 cm tall; pseudobulbs not obvious. Leaves linear-lanceolate, 1–3.8 cm wide, all but the leaf of the small, inconspicuous pseudobulb actually foliaceous bracts. Flowers solitary on very short scapes from upper bract axils; sepals subequal, spreading,

yellowish, lanceolate, acute, 1.5–2 cm long, the laterals adnate at base to foot of column; petals yellow, slightly smaller than sepals; lip obscurely trilobate, yellow with red spots to dark red, 12–14 mm long, concave, the lateral margins erect, contracted at base and articulated with foot of column. Fruits oblong, 2–3 cm long, ca 5 mm wide, closely ribbed.

No specimens seen for BCI, but reported by R. Dressler. Flowering collections have been made throughout much of the year, but in Panama mostly flowers in the rainy season with the fruits maturing in the early dry season.

Florida and Mexico to Brazil; Greater Antilles. In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién; reported also from an unknown locality in Chiriquí at 1,200 m elevation.

Maxillaria friedrichsthalii Reichb.f., Bot. Zeitung (Berlin) 10:858. 1852

Erect or pendent epiphyte; stems slender, covered by closely imbricating bracts; upper pair of bracts often foliaceous; pseudobulbs oblong-elliptic, rugose when dry, 1.5–5 cm long, inserted at an angle on the stem. Leaves 2 or 3 (sometimes 1 or 4) from apex of pseudobulb, ligulate, 4–18 cm long, to 1.5 cm wide, conduplicate and short-petiolate at base. Flowers solitary on 1 to several scapes from base of mature pseudobulb; scapes 2–4 cm long, bracteate; sepals and petals usually curved in the same direction; sepals subequal, linear-lanceolate, 1.5–3 cm long, greenish-yellow or greenish-lavender, the laterals adnate to base of column; petals 1–2.5 cm long, greenish-yellow, somewhat smaller than sepals; lip entire, linear-oblanceolate, 1–2.5 cm long, 3–6 mm wide, pale yellow-green, geniculate and ± S-shaped in side view, the lateral margins ± erect, dark maroon and thickened at apex, articulated with foot of column. Fruits ± oblong, narrowly tapered at apex, 2.5–3 cm long, ca 6 mm wide, bluntly 3-sided, slightly pruinose, the 3 ribs ca 1.5 mm wide, very thin-winged marginally, the old flower persisting. *Shattuck 453.*

Collected once on the island, but not seen in recent years. Flowers mostly in the early dry season, rarely in the rainy season. Apparently mature-sized fruits were seen undehisced in late July.

Grows clinging to the sides of trees in partial shade (*fide Powell 136*).

Mexico to Panama. In Panama, known chiefly from premontane moist forest on the Pacific slope in Chiriquí, Coclé, and Panamá at intermediate elevations; known also from tropical moist forest in the Canal Zone and Panamá.

Maxillaria neglecta (Schlechter) L. O. Wms., Ann. Missouri Bot. Gard. 29:348. 1942

Ornithidium anceps Reichb.f. non *M. anceps* A. & S.

Erect or pendulous epiphyte; stems frequently branching, covered by closely imbricating bracts; pseudobulbs variable, ligulate to suborbicular, 1.5–4.5 cm long, inserted at an acute angle on the stem, with 2 long bracts enveloping base. Leaves solitary from apex of pseudobulb, ligulate, 6–21 cm long, 1–2.5 cm wide, conduplicate and short-petiolate at base. Inflorescences many-flowered, produced in ± dense clusters from base of pseudobulbs; flowers small, solitary, usually enveloped in 2 glumaceous bracts borne on short scapes; sepals concave, ca 6 mm long, not spreading, yellow or white, the laterals broadly rhombic, oblique at apex, adnate at base to column; petals slightly shorter than sepals, colored similarly; lip yellow, geniculate in profile, ca 6 mm long, trilobate near apex, the lateral lobes erect. Fruits globose, ca 5 mm long, rugose, with 3 broad flat ridges. *Shattuck 544.*

Collected once on BCI; common elsewhere in Panama. Flowers throughout the rainy season. The fruits develop to full size by the early dry season, no doubt dehiscing during the dry season.

The vegetative habit is exceedingly variable, especially the shape and size of the pseudobulb.

Belize to Panama. In Panama, ecologically widespread; known primarily from higher elevations in premontane wet forest in Chiriquí and Panamá and from tropical wet forest in Colón and Los Santos; known also from tropical moist forest in the Canal Zone; possibly occurring in premontane rain forest and lower montane rain forest in Chiriquí.

Maxillaria powellii Schlechter, Feddes Repert. Beih. 17:70. 1922

Caespitose epiphyte; pseudobulbs elliptic-ovoid, 2–4 cm long, close, compressed, enclosed at base by papery bracts later weathering into fibers. Leaves solitary from apex of pseudobulb, ligulate, acute to bifid at apex, 15–40 cm long, 2–3 cm wide, conduplicate and petiolate at base. Inflorescences of 1–4 slender, 1-flowered, bracteate scapes 4–13 cm long from base of pseudobulb; bracts continuous along length of scape, mostly 1.5–2 cm long, scarcely if at all overlapping; sepals free, spreading, subequal, yellow or tan, 1.5–2 cm long, ± obtuse at apex, the laterals adnate at base to foot of column; petals 1.5–1.7 cm long, yellow or tan, obliquely ligulate, held ± erect on either side of the column; lip conspicuously trilobate at apex, ca 1.5 cm long, yellow or tan except the middle lobe sometimes reddish-brown, the lobes curved downward above the column. Fruits not seen. *Croat 12526a.*

Rare, in the forest. Flowers in the late rainy season and the early dry season (October to January), especially in the late rainy season.

According to Allen (1949) in the *Flora of Panama,* the species is doubtfully distinct from *M. ringens* Reichb.f.

Known only from Panama chiefly from premontane wet forest at intermediate elevations in Coclé and Panamá (west of the Canal Zone); known also from tropical moist forest in the vicinity of the Canal Zone.

Maxillaria uncata Lindl., Edward's Bot. Reg. 23, sub. t. 1986. 1837

Creeping or pendulous epiphyte; stems with many minute pseudobulbs ca 1 cm long enveloped at base by brown sheaths. Each pseudobulb with a single, thick,

sharp leaf, ± V-shaped in cross-section, mostly 2–4(8) cm long and 3–5(10) mm wide. Flowers usually solitary, 15–18 mm long, translucent with maroon or red stripes; dorsal sepal short, 7–9 mm long, equaling petals in length, the lateral sepals ca 1 cm long, oblique at base and adnate to foot of column to form a projection; the lip slender, extending from gibbous base, ± equaling the lateral sepals, the sides folded inward; column flat inside, rounded outside, bearing 4 small yellow pollinia at its apex, the apical hood entire, its front edge easily removed as a narrow rectangular strip bearing the pollinia with it. Capsules ca 1 cm long, with 3 boat-shaped valves, persisting after seeds are shed. *Croat 6744.*

Common in the forest, usually on tree branches high in the canopy. Flowers throughout the rainy season and the earliest part of the dry season, especially in the rainy season. The fruits mature quickly, but most are apparently mature during the dry season.

Mexico to Peru, Brazil, Venezuela, and the Guianas. In Panama, common from tropical moist forest in the Canal Zone, Colón, Veraguas, and Darién, from premontane wet forest on both slopes in the Canal Zone, Coclé, and Panamá, and from tropical wet forest in Coclé and Panamá.

Maxillaria variabilis Batem. ex Lindl., Edward's Bot. Reg. 23, sub. t. 1986. 1837

Erect or pendulous epiphyte; stems simple, bracteate, 5–30 cm long; pseudobulbs elliptic-oblong, 1.5–6 cm long, inserted at an angle on the stem. Leaves solitary from apex of pseudobulb, ligulate, shallowly bilobed at apex, 3–20 cm long, to 1.5 cm wide, conduplicate and petiolate at base. Flowers usually solitary on short scapes from axils of bracts of new growth or from base of pseudobulb, to 1.2 cm long, colored white, yellow marked with red, or entirely dark red; sepals subequal, ± lanceolate, 6–12 mm long, spreading, the laterals adnate at base to column; petals similar but slightly shorter than sepals; lip entire or obscurely trilobate, 6–12 mm long, half as wide, the lateral margins erect, the base articulated with foot of column. Fruits not seen.

No specimens seen from BCI, but reported by Dressler. Flowers principally in the dry season (especially early in the dry season), infrequently in the rainy season.

A vegetatively variable species. Reported by Ospina (1958) to be generally terrestrial in Colombia.

Mexico to Colombia, the Guianas. In Panama, ecologically wide ranging; known principally from premontane wet forest and lower montane wet forest in Chiriquí; known also from tropical moist forest in the Canal Zone and Panamá.

MORMODES Lindl.

Mormodes powellii Schlechter, Feddes Repert. Beih. 17:55. 1922

Dioecious epiphyte, often on rotting wood; pseudobulbs elongate, ± cylindrical, tapering gradually toward apex. Leaves several, scattered along stem, plicate, deciduous, the bases persistent, imbricating. Racemes arching, ca 30 cm long, produced from near base to middle of pseudobulb (often leafless when in flower); staminate and pistillate flowers similar; sepals and petals subequal, spreading, linear-lanceolate, acuminate, to 5 cm long, greenish to yellowish-brown to cream-colored; lip elliptic- to rhombic-ovate, with a short claw, the lateral margins often strongly recurved; column twisted to one side, pointed, with a slender apical bristle. Fruits not seen. *Croat 7794.*

Seen only in the epiphyte house, but reported for the island by Dressler. Flowers in the dry season, from December to March.

Reported by R. Dressler to be distinct from *M. colossus* Reichb.f., with which it was included in synonymy in the *Flora of Panama* (Allen, 1949). *Mormodes colossus* occurs in western Panama and Costa Rica and can be distinguished from *M. powellii* by having a much wider lip.

The species is pollinated by the bee *Euglossa tridentata* (Dressler, 1968a).

Known only from Panama, occurring in tropical moist forest in the Canal Zone and Colón and in premontane wet forest in Coclé (El Valle).

NOTYLIA Lindl.

All species of the genus are apparently pollinated by euglossine bees (Dressler, 1968a).

Notylia albida Klotzsch in Otto & Dietr., Allg. Gartenzeitung 19:281. 1851

N. panamensis Ames

Epiphyte; pseudobulbs ca 2 cm long and 1 cm wide, partially enveloped in papery imbricating bracts, the bracts soon weathering away. Petioles conduplicate, very short; blades solitary at apex of pseudobulb, oblong-lanceolate, obtuse and unequally bilobed at apex, to 15 cm long and 3.5 cm wide, coriaceous. Racemes pendulous, from base of current pseudobulb, densely flowered,

KEY TO THE SPECIES OF NOTYLIA

Column distinctly papillose ..... *N. pentachne* Reichb.f.
Column glabrous:
  Dorsal sepal broadly elliptic-oblanceolate, obtuse, ca 5 mm wide, distinctly broader than the lip ..... *N. albida* Klotzsch
  Dorsal sepal linear-lanceolate, subacute, 2 mm wide or less, distinctly narrower than the lip .... *N. barkeri* Lindl.

to 20 cm long; flowers white; pedicels slender, subtended by scarious, narrowly triangular, acuminate bracts; sepals subequal, the dorsal sepal broadly elliptic-oblanceolate, obtuse, concave, ca 7 mm long, 5 mm wide, the lateral sepals fused, the united segments linear-lanceolate, to 8 mm long, 2 mm wide; petals elliptic-lanceolate, acute, equaling sepals; lip ca 6 mm long, clawed, obliquely inserted at base of column, the blade sagittate, ca 3 mm wide, with a short-keeled callus; column slender, terete, ca 3 mm long. Fruits not seen. *Dressler 2908* (*US*).

Apparently rare. The Dressler collection was flowering in June.

The species is pollinated by the bee *Euglossa hemichlora* (Dressler, 1968a).

Panama and Colombia. In Panama, known from tropical moist forest in the Canal Zone, Colón (Achiote), and Darién.

Notylia barkeri Lindl., Edward's Bot. Reg. n.s. 1, Misc. 90. 1838

Small epiphyte, often with long, pendent roots; pseudobulbs oblong, to 2.5 cm long and 1 cm wide, enveloped at base by several imbricating bracts, the uppermost bracts foliaceous. Leaves solitary from apex of pseudobulb, ligulate, 8–18 cm long, 1.3–4 cm wide, conduplicate at base. Racemes 1 or 2, arching, 8–30 cm long (usually less than 15 cm long), from base of pseudobulb, many-flowered; flowers white; pedicels filiform, 2–6(10) mm long, subtended by minute bracts; sepals subequal, linear-lanceolate, ± spreading, the dorsal sepal free, 3–6 mm long, 1–2 mm wide, the laterals connate partway, 3–5 mm long, 1–2 mm wide together; petals 2.5–5 mm long, 1–1.5 mm wide; lip clawed and continuous with base of column, 3–5 mm long, 1–2 mm wide, the basal part with a distinct keeled callus; column terete, glabrous, 2–3 mm long. Fruits narrowly ellipsoid, ca 1.5 cm long, with low flat ribs.

No specimens seen for BCI, but reported by R. Dressler. Apparently flowers in the late dry season (March and April).

Flowers are pollinated by the bee *Euglossa* (Dressler, 1968a).

Mexico to Panama; apparently widespread ecologically, occurring from near sea level to 1,200 m. In Panama, known from tropical moist forest in the Canal Zone, from premontane moist forest in the Canal Zone (Balboa), and from premontane wet forest in Chiriquí and Veraguas.

Notylia pentachne Reichb.f., Bonplandia 2:90. 1854

Epiphyte, usually less than 15(25) cm high; pseudobulbs oblong, to 2.5 cm long, with foliaceous bracts at base, 1-leaved. Leaves oblong, to 20 cm long, 2–5 cm wide, tapered to short, conduplicate petiole. Flowers many, in 1 or 2 erect to pendulous racemes to 35 cm long (usually less than 25 cm long), from base of pseudobulb; pedicels slender, mostly 6–10 mm long; sepals green, 8–10 mm long, slender, recurved at apex, the lateral sepals connate for more than half their length; petals 7–8 mm long, slender, obliquely lanceolate, acuminate, whitish with a green or orange spot above base; lip white, narrowly deltoid above, with a basal claw; column slender, terete, densely papillose, 3–5 mm long; anther light green, ca 2.3 mm long; pollinia yellow on a long white appendage, sticky at apex. Fruits ± ellipsoid, to 4 cm long including beak, the beak tapered, prominent. *Croat 4745, 5708.*

Occasional, in the forest, usually rather high in trees. Flowers in the dry season, mostly from March to late May. The fruits develop quickly, and an old inflorescence may bear fruits during the late dry season while another inflorescence bears flowers.

Pollinated by the bee *Eulaema cingulata* (Dressler, 1968a).

Known only from Panama, principally from tropical moist forest in the Canal Zone, Veraguas (Santa Fé), and Darién.

ONCIDIUM Sw.

Oncidium ampliatum Lindl., Gen. & Sp. Orch. Pl. 202:1833

Epiphyte; pseudobulbs ovoid to orbicular, flattened or sometimes angular, 3–12 cm long, 3–9 cm wide, often purple-spotted, sometimes with large weathered bracts at base. Leaves 1–3 at apex of pseudobulb, narrowly oblanceolate to ligular, obtuse to subacute, 8–40 cm long, 3–12 cm wide, conduplicate and short-petiolate at base. Panicles 1 or 2, produced laterally from base of pseudobulb, much longer than leaves; flowers very flat, ca 2.5 cm diam; sepals subequal, 6–10 mm long, 3.5–5 mm wide, brownish-yellow, broader than sepals, 7–11 mm long, 5–9 mm wide, clawed at base, the blades suborbicular; lip trilobate, 1.5–2 cm long, the lateral lobes small, the center lobe deeply emarginate, 1.5–3 cm wide, the base of the lip with a fleshy, lumpy callus colored white with red spots, contracted into a short claw adnate to base of column; column 3–4 mm long, 3-winged at apex. Fruits not seen. *Croat 6746, Woodworth & Vestal 529, 706.*

Infrequent, in the forest and on stumps at the margin of the lake. According to Allen (1949), once common in the valley of the Río Chagres. Flowers usually in the early dry season (December to March), especially in February and March.

KEY TO THE SPECIES OF ONCIDIUM

Pseudobulbs conspicuous, compressed ..... *O. ampliatum* Lindl.
Pseudobulbs lacking, or rudimentary and inconspicuous ..... *O. stipitatum* Lindl.

Easily recognized by its more or less disk-shaped, often spotted pseudobulbs.

Guatemala to Venezuela, Trinidad, Peru, and Ecuador. In Panama, known principally from tropical moist forest in the Canal Zone; known also from tropical wet forest in Veraguas (on the Pacific slope near Bahía Honda).

Oncidium stipitatum Lindl. in Benth., Bot. Voy. Sulphur 172. 1846

Caespitose epiphyte; pseudobulbs lacking or 5–10 mm long, usually ensheathed in papery bracts, bearing a single leaf. Leaves terete, longitudinally grooved, 24–70 cm long, to 1 cm wide, becoming pendent and usually reddish-brown in age. Panicles solitary, many-flowered, from base of pseudobulb, ± equaling leaves; flowers variable in size, to 2.5 cm long; sepals and lateral petals subequal, clawed at base, yellow heavily marked with reddish brown; lip trilobate, fiddle-shaped, clawed, yellow, to 2 cm long, nearly as broad as long, the lateral lobes obovate-spatulate, with a short claw, separated from the broad bilobed middle lobe by a narrow isthmus; base of lip with a fleshy, toothed callus; column with lateral, fanlike wing. Fruits ± ellipsoid, tapered toward apex, to 2.5 cm long, with flat ridges. *Croat 8396.*

Occasional, along the margin of the lake, usually not in full sun. Flowers from January to April, especially in February and March. The fruits develop quickly and are dispersed usually by May (or as late as July).

Pollinated by a bee of the genus *Centris* (Dodson, 1965a).

Known only from Panama, principally in tropical moist forest in central Canal Zone, Colón, and Panamá; known also from premontane wet forest in Panamá (Cerro Campana).

See Fig. 171.

ORNITHOCEPHALUS Hook.

Ornithocephalus bicornis Lindl. in Benth., Bot. Voy. Sulphur 172. 1846

Small epiphyte; pseudobulbs lacking; stems very short, hidden by leaves. Leaves 5–12 cm long, flattened laterally, arranged in a suborbicular fan; blades oblong-lanceolate, obliquely acute, articulated to the conduplicate, imbricating, persistent base, the base to 3 cm long, obliquely acute at apex, resembling a pseudobulb. Racemes 1–17, from basal leaf axils, many-flowered, slender, equaling or exceeding leaf length; rachis densely erect-pubescent with short, simple or branched trichomes; flowers ca 4 mm diam, greenish; sepals suborbicular, concave, obtuse, glandular-puberulent outside, keeled medially, often tinged with yellow; petals as large as sepals, obovate, ca 2 mm diam, concave, thin, white toward apex, green at base, with a prominent ciliate keel; lip green, slender, strongly incurving, to 5.2 mm long and 1.2 mm wide, the base with a cushionlike callus and two papillate horns, the apex acute, white, held just above the ornate column; pollinia with a slender stipe extending down the column; stigma basal on column. Fruits ellipsoid, ca 5 mm long, densely pubescent with simple or branched trichomes. *Croat 8243.*

Occasional, in the forest. Flowers mostly in the dry season (December to April) or as late as July, with fruits developing quickly and commonly maturing in May.

Pollinated by the bee *Paratetrapedia calcarata* (Dodson, 1967a).

Mexico to Panama, Colombia, Venezuela, and Ecuador. In Panama, known from tropical moist forest in central Canal Zone, Veraguas, Panamá, and Darién.

Ornithocephalus powellii Schlechter, Feddes Repert. Beih. 17:88. 1922

Small, fan-shaped epiphyte; pseudobulbs lacking; stems short, hidden by leaves. Leaves grayish-green, few, obliquely ligulate, acute, often apiculate, 3–7 cm long, to 1.2 cm broad, articulate with a conduplicate base to 3 cm long and often oblique at apex. Racemes 1 or 2 from basal leaf axils, to 10 cm long, few-flowered; rachis laterally compressed, narrowly winged, subglabrous to puberulent with bracts to 7 mm long; flowers green, to ca 1.5 cm diam; sepals oblong-ovate, ca 4 mm long, keeled, the margins ciliate to serrulate; petals obovate-flabellate, to ca 6 mm long, often broader than long, round at apex, ciliate to serrulate; lip fiddle-shaped, to ca 1 cm long, the apex serrulate; disk with a fleshy, bilobed callus. Fruits not seen. *Croat 5487.*

Rare. Flowering records are scattered; apparently flowers intermittently in both the dry and rainy seasons.

Known only from Panama, from tropical moist forest in the Canal Zone and Panamá.

PALMORCHIS Rodr.

Palmorchis powellii (Ames) Schweinf. & Corr., Bot. Mus. Leafl. 8:119. 1940
Rolfea powellii Ames

Terrestrial, often caespitose, to 60 cm tall; stems slender, reedlike. Leaves few, scattered along stem, moderately thin, plicate; petioles to 8 cm long; blades ± elliptic, 15–30 cm long, 3–15 cm wide. Inflorescences usually

KEY TO THE SPECIES OF ORNITHOCEPHALUS

Rachis of inflorescence densely glandular-hispid; flowers generally less than 5 mm wide . . . . . *O. bicornis* Lindl.

Rachis of inflorescence glabrous or minutely puberulent; flowers generally 1 cm or more wide . . . . . *O. powellii* Schlechter

axillary, often borne at leafless nodes, racemose or paniculate, to 7 cm long, bracteate at base of flowers; bracts ovate, acute, 5–6 mm long; flowers white, 1.5–2 cm long; sepals and petals ± spatulate, obtuse, 3 mm wide; lip somewhat trilobate, about as long as but broader than sepals and petals, adnate to base of column; column ca 12 mm long. Fruits narrowly oblong, to 5 cm long, ca 5 mm wide, weakly ribbed. *Foster 2362.*

Rare on the island; seen recently in the older forest. Apparently flowers in the early rainy season (July and August). The fruits develop quickly, and the seeds may be dispersed in the rainy season.

The related *P. trilobulata* L. O. Wms. is found in tropical moist forest and in premontane wet forest in Coclé (El Valle) and Panamá (Chimán).

Apparently restricted to Panama, in tropical moist forest on BCI and in Panamá.

PERISTERIA Hook.

Peristeria elata Hook., Bot. Mag. 58, t. 3116. 1831
Holy Ghost, Dove orchid

Terrestrial, to 1.3 m tall; pseudobulbs ovoid, 4–12 cm long, 4–8 cm wide, enveloped at base by foliaceous bracts. Leaves 3–5 from apex of pseudobulb, deciduous; blades 30–100 cm long, 6–14 cm wide, plicate. Racemes solitary from base of pseudobulb, 80–130 cm tall, erect, few-flowered; flowers subglobose, fleshy, white, fragrant, opening 2–4 at a time from the base first; pedicels to 4 cm long; sepals subequal, 2.5–3 cm long, 2–3 cm wide, the laterals connate at base; petals 2–2.5 cm long, 1.5–2 cm wide; lip with lateral wings spotted red, articulated at base with the broad claw, thickened at base, with an apical crest; column ca 1 cm long. Fruits ellipsoid, 4–5.5 cm long, to 2 cm wide. *Shattuck 854.*

A plant of open areas, probably eliminated by succession. Flowers in the rainy season. Fruits in the dry season.

The national flower of the Republic of Panama, the species is highly favored by orchid growers, but has disappeared in some areas.

Pollinated by the bee *Euplusia concava* and also visited by *Euglossa* sp. (Dressler, 1968a).

Costa Rica to Colombia and Venezuela. In Panama, known from premontane moist forest and tropical moist forest in Panamá and from premontane wet forest at low to medium elevations in Colón, Coclé, and Panamá.

PLEUROTHALLIS R. Br.

Pleurothallis brighamii S. Wats., Proc. Amer. Acad. Arts 23:285. 1888
P. acrisepala Ames & Schweinf.

Caespitose epiphyte; pseudobulbs lacking; stems very short, each bearing a single leaf. Leaves ± oblanceolate, obtuse or acute, 1.5–9 cm long, the veins obscure except the midrib, the base ensheathed in slender, scarious bracts. Flowers 1 to few in terminal fascicles borne on slender peduncles usually above the leaves; peduncles usually persisting; sepals acute, maroon, fused at base, 7–9 mm long, the lateral sepals united to the middle or beyond; petals 2–3.5 mm long, solid maroon, the apex pointed; lip narrow, 2–4 mm long, 1–2 mm wide, lighter and papillate at apex, the margin ciliate, auriculate on both sides. Fruits ellipsoid, to 1 cm long, green or olive, tinged or striped with purple. *Croat 9787.*

Abundant in the forest, perhaps the most abundant orchid on the island; growing high or low in trees. Apparently flowers repeatedly throughout much of the year.

Guatemala to Panama. In Panama, known from tropical moist forest on both slopes of the Canal Zone and in Bocas del Toro, Colón, Panamá, and Darién.

Pleurothallis grobyi Batem. ex Lindl., Edward's Bot. Reg. 21, t. 1797. 1835
P. marginata Lindl.

Densely caespitose epiphyte; pseudobulbs lacking; stems very short, bearing a single leaf. Leaves oblanceolate to rarely suborbicular, obtuse to rounded and usually minutely emarginate at apex, attenuate to petiole, 1.5–7 cm long, 2–8 mm wide, drying bicolorous, the margin dark, thickened. Flowers pale yellow-green, few to several, in slender weak racemes 5–12 cm long, usually much exceeding leaf; both peduncles and petioles surrounded by dried sheaths; dorsal sepal 4–6(9) mm long, the lateral sepals weakly fused laterally, somewhat longer than dorsal sepal; petals erect, much shorter, hidden within sepals, marked with violet-purple; lip oblong, similar to lateral petals but longer; column white, equaling or exceeding petals, winged, the wings extending above anther in a point. Fruits not seen. *Croat 10800.*

Common high in trees on shaded, moss-laden branches. Apparently flowering repeatedly throughout the year.

KEY TO THE SPECIES OF PLEUROTHALLIS

Stems caespitose (tufted); leaves obtuse or at most acute at apex:
- Inflorescences fascicles borne at apex of long peduncles, of 1 to several flowers; peduncles often persisting; leaves 7 or 8 times longer than wide, ± concolorous ..... *P. brighamii* S. Wats.
- Inflorescences fragile racemes; peduncles not persisting; leaves usually less than 6 times longer than broad, bicolorous (at least when dried) ..... *P. grobyi* Lindl.

Stems elongate, erect or repent; leaves ± sharply pointed at apex:
- Inflorescences short, few-flowered fascicles, much shorter than the leaves; secondary stems to 6 cm long; leaves to 7 cm long ..... *P. trachychlamys* Schlechter
- Inflorescences few-flowered racemes, ca half as long as leaves; secondary stems to 19 cm long; leaves 6–16 cm long ..... *P. verecunda* Schlechter

Fig. 171. *Oncidium stipitatum*

Fig. 172.
Pleurothallis verecunda

Common throughout the New World tropics. In Panama, known principally from tropical moist forest on both slopes of the Canal Zone and in Panamá; known also from tropical wet forest in Colón (Río Indio and Portobelo).

Pleurothallis trachychlamys Schlechter, Feddes Repert. Beih. 17:23. 1922

Small repent epiphyte, to ca 11 cm high; pseudobulbs lacking; rhizome concealed in coarse sheaths, the sheaths bearing ± hispid trichomes; secondary stems to 6 cm long, covered with a scurfy sheath, each stem bearing a solitary leaf. Leaves narrowly elliptic to lanceolate, narrowly acute at both ends, 4.5–7 cm long, 0.4–1 cm wide. Flowers white, very short-lived, appearing in succession in short fascicles near the base of the upper leaf surface; sepals oblong-lanceolate, acute, 4–5 mm long, the lateral sepals united at base; petals lanceolate, to 4 mm long; lip oblong-oval, obtuse, to 2 mm long, with 2 erect lateral lobes near the middle and a small callus at the base, the apex recurved; column two-thirds as long as lip with the lateral margins raised. Fruits not seen.

No specimens seen for BCI, but reported to occur by R. Dressler. Known to flower in November.

Costa Rica to Venezuela and possibly Peru. In Panama, known from tropical moist forest in the Canal Zone and Panamá.

Pleurothallis verecunda Schlechter, Feddes Repert. Beih. 17:24. 1922

Erect or repent epiphyte, to ca 20 cm high; pseudobulbs lacking; secondary stems slender, 1-leaved, to 19 cm long, enveloped tightly at base by a scarious sheath, arising from a creeping, densely rooting rhizome. Leaves lanceolate-ligulate, acute to acuminate, narrowly acute at base, 6–16 cm long, 1–2.5 cm wide, thick; blade, secondary stem, and pedicels often violet-purple. Flowers few, in terminal racemes about half as long as leaves, yellow-green, all parts lightly or heavily marked with violet-purple especially near base; sepals narrowly pointed, 5.5–9 mm long, with a thick medial rib, persisting in fruit; petals oblong-oblanceolate, much shorter and enclosed within sepals, exceeding length of column; lip thick, ± oblong, 2.5–3.5 mm long, with 2 short erect teeth laterally below the middle. Fruits oblong, somewhat oblique, broadened toward apex, 2.5–3.5 cm long. *Croat 16200.*

Infrequent, in the forest and in *Citrus* (66. Rutaceae) trees at the Laboratory Clearing. Flowers principally in the rainy season but also in the late dry season (April to October). The fruits have been seen in January but also in mid-June.

Costa Rica and Panama, In Panama, known from tropical moist forest in the Canal Zone and tropical wet forest in Colón (Río Indio).

See Fig. 172.

POLYSTACHYA Hook.

Polystachya foliosa (Lindl.) Reichb.f., Ann. Bot. Syst. 6:640. 1863

P. cerea Lindl; *P. minor* Fawc. & Rendle

Caespitose epiphyte, 10–30(60) cm tall; stems short; pseudobulbs ovoid, enclosed in the leaf sheaths, with 2–5 leaves from apex. Leaves 3–15(25) cm long, 0.5–3 cm wide. Panicles terminal, 5–15(30) cm long; peduncles stout, with short racemose branches; rachis glabrous to sparsely puberulent; flowers yellow, maturing at base of raceme first, each subtended by a persistent bract; sepals 3–4.5 mm long, 1.5–3 mm wide; petals much smaller; lip 2.5–3.5 mm long, 2–3 mm wide, trilobate, the middle lobe largest, farinose (covered with a mealy powder); ovary glabrous. Fruits ellipsoid, ca 1 cm long, ridged. *Croat 6707.*

Frequent in the forest and on tree branches over the edge of the lake. Flowers chiefly in September and October. The fruits mature chiefly in the dry season (January to March).

Mexico through tropical South America; West Indies. In Panama, known from tropical moist forest chiefly on the Pacific slope of the Canal Zone and in Panamá and from premontane wet forest in Chiriquí (Lino) and Coclé.

Polystachya masayensis Reichb.f., Bonplandia 3:217. 1855

Tiny epiphyte, usually 3–10 cm tall; stems very short; pseudobulb inconspicuous, ovoid, usually enclosed in leaf sheaths, bearing 1–5 leaves at apex. Leaves mostly 2.5–8 cm long, 4–8 mm wide, acute to rounded at apex. Inflorescences terminal racemes, usually 1–2.5 cm long, shorter than the leaves; peduncles enclosed in leaf sheaths; rachis densely puberulent; flowers greenish-yellow, ca 3 mm long, each subtended by a persistent bract; dorsal sepal somewhat smaller than the laterals; petals slender; lip somewhat constricted at center, farinose, the apex acute; ovary puberulent. Fruits ellipsoid, ca 7 mm long, puberulent. *Croat 7370.*

Apparently uncommon, usually growing high in trees in the forest. Flowers from late November to March, perhaps over a longer span.

Mexico, Nicaragua, Costa Rica, and Panama. In Panama, known from tropical moist forest in the vicinity of the Canal Zone and from premontane wet forest in Colón, Chiriquí, and Coclé.

KEY TO THE SPECIES OF POLYSTACHYA

Ovary, fruit, and rachis usually glabrous; inflorescences branched many times in large plants; plants mostly more than 10 cm tall ..... *P. foliosa* (Lindl.) Reichb.f.

Ovary, fruit, and rachis usually pubescent (± puberulent); inflorescences usually unbranched, 1–2 cm long; plants usually less than 10 cm tall ..... *P. masayensis* Reichb.f.