JOURNAL
OF THE
ARNOLD ARBORETUM

HARVARD UNIVERSITY

C. E. WOOD, JR.
EDITOR

FRANCES M. JARRETT
ASST. EDITOR

LAZELLA SCHWARTEN
CIRCULATION

VOLUME XXXIX

CAMBRIDGE, MASS.
1958

Reprinted with the permission of the
Arnold Arboretum of Harvard University
KRAUS REPRINT CORPORATION
New York
1968

DATES OF ISSUE

No. 1 (pp. 1–100) issued January 10, 1958.
No. 2 (pp. 101–212) issued April 14, 1958.
No. 3 (pp. 213–378) issued July 14, 1958.
No. 4 (pp. 379–524) issued October 20, 1958.

Printed in U.S.A.

TABLE OF CONTENTS

With this issue, the Journal of the Arnold Arboretum becomes the responsibility of a new editor. It is with a deep sense of gratitude that I speak for the editorial board, the staff of the Arnold Arboretum and other contributors to these pages to express to DR. CLARENCE E. KOBUSKI *our appreciation for a job well done.*

After many years of careful attention to the time-consuming problems which beset an editor, Dr. Kobuski has asked to be relieved of this responsibility in order to devote more of his time to the herbarium and to his own research program. Dr. Kobuski ("K" to authors who have published in the Journal) has taken an active part in the publication of the Journal of the Arnold Arboretum for the past twenty-six years, except during the period of his war duty, and has served as Editor since 1949. His own high standards have been reflected in those of the Journal and provide a challenge for future editors.

Richard A. Howard
Director

JOURNAL

OF THE

ARNOLD ARBORETUM

VOL. XXXIX JANUARY 1958 NUMBER 1

STUDIES IN THE GENUS COCCOLOBA, V. THE GENUS IN HAITI AND THE DOMINICAN REPUBLIC

RICHARD A. HOWARD

IN VARIOUS LISTS of the flora of Hispaniola published by Lindau (the most recent monographer of the genus *Coccoloba*), Urban, Ekman, Barker and Dardeau (Flore d'Haiti 99–100. 1930) and Moscoso (Catalogus Florae Domingensis 168–171. 1943), forty-seven species and three forms of *Coccoloba* have been reported. Of these, thirty-two species and the three forms were considered to be endemic. Few of the species are either old or known only from the original collection or description. In general, the species are represented by several collections, the majority of which are the result of the meticulous collecting of Erik Ekman, who was encouraged by Ignatius Urban. There is no doubting Ekman's keen eye and inclusive memory for variations and locations. Again and again, his field notes indicate that he had seen the plant before and that it was the same as the earlier collection, or that a plant was different and "definitely not the same." Ekman's success in relocating old species or in collecting additional material was aided materially by his close co-operation with Urban. In many cases Urban directed Ekman to seek in a specific area which he designated from Berlin, or suggested that he look for a certain variation in an effort to recollect many of the older species. We are further indebted to them for retracing the routes of earlier botanists and for collecting sufficient new material to evaluate properly the older species. Ekman's collections were studied so promptly upon their receipt, that it appeared that the specimens were literally just received when Urban published a new name based on them. The rush to publish was continued after Urban's death by O. E. Schmidt who collaborated with Ekman, or rather, worked over his collections. Ekman's field notes indicate that he did not always agree with Schmidt and wished for more careful consideration of the entities involved.

Ekman recognized the general nature of the adventitious shoot in the genus *Coccoloba* and indicated in his field notes the variations from plant to plant and on single plants. Schmidt, in contrast, did not know the plants in the field and failed to appreciate Ekman's comments. As was indicated in an earlier study of the genus *Coccoloba* in Cuba (Jour. Arnold

Arb. 30: 388–424. 1949), Schmidt's failure to recognize adventitious shoots, the dioecious condition in the inflorescence and the nature of the pubescence led him to describe the two sexes of a single species under different names and to assign the adventitious shoots or the parent plants to different species, varieties or forms. Over a period of several years I have had the opportunity of spending several months collecting in the Dominican Republic and in Haiti.[1] During these collecting trips considerable emphasis was given to a field study of populations of the species of *Coccoloba*. I have made careful collections of young plants, mature plants, adventitious shoots and normal growth, as well as sun and shade foliage, to represent the range of leaf variation both on individual plants and in populations. Not all of the species reported from the island, or in fact, collected by Ekman, could be studied in the field. I believe, however, that the material which I have examined has made the conclusions drawn in this paper more reliable than the previously existing work.

I now recognize twenty-four species and four hybrid populations from Hispaniola. Fifteen species are regarded as restricted to the island. Three of the four hybrid populations are new but unnamed and, of these four hybrid populations, three are also to be considered endemic to Hispaniola, but may be expected on other islands. Of the fifteen endemic species, two (*Coccoloba fawcettii* and *C. ceibensis*) are regarded as representatives of probable hybrid populations. Two other species are questionably distinct from Cuban counterparts.

In addition to the fifteen endemic species, three (*Coccoloba costata*, *C. leonardii* and *C. wrightii*) are also known from Cuba but not from the Bahamas, Jamaica or Puerto Rico. Five species (*C. krugii, C. microstachya*, *C. pubescens*, *C. swartzii* and *C. venosa*) have ranges extending eastward throughout Puerto Rico to the Virgin Islands. Of these, *C. krugii* is also known from the Bahamas and from Jamaica and *C. swartzii* from Jamaica. *Coccoloba pubescens* and *C. venosa* have been reported from Jamaica but their occurrence there was questioned by me in an earlier paper (Jour. Arnold Arb. **38**: 105–106. 1957). However, they are well known in Puerto Rico and the Lesser Antilles. Only two species (*C. diversifolia* and *C. uvifera*) are regarded as widespread in the Caribbean area, but further study may place *C. swartzii* in the same category. Hispaniola is indeed a center of speciation in the genus, but clearly not to the extent recognized by earlier authors.

The following key to the species is artificial and, unfortunately, for a

---

[1] I am indebted to the trustees of the American Philosophical Society for a grant from the Penrose Fund which made one of these trips possible. I am also indebted to Mr. George Hamor of Hull's Cove, Maine, formerly of Barahona in the Dominican Republic, for his hospitality and assistance in the course of my field work. My appreciation is also gratefully expressed for the kindnesses and the co-operation given by many officials of the Dominican Republic; by the various officials of Compania Grenada of the United Fruit Company; by Dr. José de Js. Jiménez and Dr. M. Canela in services of value to this study. I am also grateful to the directors and curators of the herbaria cited in this paper for the long-term use of materials entrusted to their care when various aspects of this problem took extended time.

few species requires the use of complete material, including flowers and fruits. The majority of the species recognized are variable in vegetative characters, as an examination of the species descriptions will verify. The key given is applicable for all of the material which I have examined in fruiting condition and for most of the material when in flower. The key is not applicable in all cases to either sterile mature shoots or adventitious shoots. Abnormal variations on mature and adventitious shoots, such as fasciations, pathological anomalies and contortions have not been included in the key. Such specimens are common in herbaria and have been annotated, but are relatively infrequent in the field.

Many of the characteristics employed in the key should not be used in identification without considerable experience with the group. I have avoided the angles of departure of the primary veins which former monographers have used, but have used the prominence, curvature, bifurcations and reticulations of the primary and secondary veins individually or as patterns. I have introduced several new characters, such as the swelling of the nodes, the position of the base of the petiole in relation to the ocrea, the length of the pedicels in relation to the length of the ocreolae, the nature of the apex of the mature achene and the associated aspect of the lobes of the fruiting perianth. Morphological studies are needed on the bead-like swollen nodes which occur in a few species of *Coccoloba*. Swollen nodes are characteristic of the family Polygonaceae, but the exaggerated development of these in *Coccoloba* has not been investigated. The nodes are woody and extremely hard when dry. The pith in the swollen section is not enlarged. It is not clear whether the development of the nodal swelling is from the shortening of cambial initials or from a stimulated development of additional cells.

In most species of *Coccoloba* the petiole arises from the base of the ocrea. In a few species, the base of the petiole or the base of the abscission layer is a short distance above the base of the ocrea, as indicated both by vascular pattern and superficially by the color change between internodal stem tissue and the ocreal tissue. The relative position is readily determined in adventitious or vegetative shoots and can be seen on fertile specimens after the leaf has fallen. This characteristic has been checked in the field and appears to be a reliable one, since it shows no variation on individual plants or in populations.

In all but a very few species, the length of the pedicel is constant from the time the flower opens until the fruit is formed. The thickness of the pedicel varies, being much stouter when a fruit is developed than when the pistillate flowers do not form fruit. Staminate inflorescences show little thickening of the pedicels with age unless sterile fruits are produced.

The apex of the achene can be uniformly obtuse, acute, or constricted to form a rounded knob. When the last is the characteristic shape, the perianth in fruit consists of a fleshy hypanthium surrounding the body of the achene, the lobes of the perianth forming a crown around the knob. The latter condition has been referred to as "coronate." If the achene and the perianth are coronate, the perianth lobes may remain small and free, or may become fleshy and imbricated around the knob. Since the crown is prominent very early, this character can be used on immature fruiting specimens, as well as on fully mature fruit. The prominence of the vascular supply in the fruiting perianth has been mentioned in the species descriptions but has not been used in the key to the species. The number of vascular bundles indicated in dry fruits as ridges and grooves seems to be a reliable indicator for a particular species. This characteristic must be verified when the fruit is dry and is, therefore, difficult to check in the field. The bundles are not evident when the fruit is fresh; however, species which later will have prominent bundles in the hypanthium are generally less fleshy and, therefore, less edible when sampled in the field. Since most species of *Coccoloba* which I have eaten have had extremely astringent fresh fruits, there is no particular pleasure in checking for this characteristic.

The number of flowers at each locus or node of the inflorescence is related to the functional sex of the flower. In most species studied, the functionally pistillate flowers are borne singly while the functionally staminate flowers are in clusters of two to five flowers. The number of flowers has been given unjustifiable emphasis by Lindau, Urban and Schmidt. I do not feel this should be used. Another characteristic used by Lindau in his keys was the condition of exserted versus included stamens. This, too, proved to be associated with functional or pollen-producing stamens, in contrast to the included sterile, rudimentary or abortive stamens. I have been unable to find any characteristics of diagnostic significance in the flowers of *Coccoloba* as the genus occurs in the West Indies. The flowers are small and variations in the size and shape of the floral parts appear to me to be too insignificant to be of real value.

Specimens are cited with standard abbreviations given for the herbaria as cited in the third edition of Index Herbariorum. The provinces cited for locations in the Dominican Republic are those used on the Esso Standard Oil Company "Mapa de la Republica Dominicana" prepared by the General Drafting Company and copyrighted in 1955. Province boundaries on this most recent map vary considerably from earlier maps available. The provinces are listed in alphabetical order. For Haiti, five departments are recognized and listed in geographic order from northwest to southwest. Navassa Island, formerly a United States possession, has been turned over to the government of Haiti and is considered as associated with the Département du Sud.

The species are described following the key and are listed in alphabetical order.

KEY TO THE SPECIES OF COCCOLOBA IN HISPANIOLA

A. Perianth lobes exceeding the hypanthium in length, dominant in fruit; ocreolae increasing in size from flowering to fruiting condition; leaves chartaceous to membranaceous, rarely subcoriaceous.
  B. Leaves oblong-lanceolate to elliptic, longer than broad, apex acuminate. .... *C. venosa*.

BB. Leaves orbicular to reniform, as broad as long, apex rounded to emarginate.

  C. Leaves of normal shoots 3 × 3 to 9 × 9 cm. long and broad; petioles arising from the base of the ocreae; inflorescence rachis 5–7 cm. long. . . . . *C. leoganensis.*

  CC. Leaves of normal shoots 0.2 × 0.2 to 1.1 × 1.0 cm. long and broad; petioles arising from above the base of the ocreae; inflorescence rachis 0.4–1.0 cm. long. . . . . *C. subcordata.*

AA. Perianth lobes shorter than the hypanthium in fruit, imbricate or coronate; leaves generally coriaceous and not membranaceous.

  D. Leaves tipped with a spine or a cartilaginous point.

    E. Leaves cordate, the lower leaf surface with a conspicuous reticulum of veins. . . . . *C. fawcettii.*

    EE. Leaves ovate, oblong or elliptic, not cordate; lower leaf surface not conspicuously reticulate.

      F. Leaves oblong or elliptic.

        G. Primary veins 10–20 pairs, not raised on either surface and more or less uniform in strength; inflorescence rachis 1–4 cm. long; fruit rounded at the apex, not coronate, the base of the fruit attenuate but not sterile or corky; terminal spine of leaf 1 mm. long, sharp-pointed. . . . . *C. flavescens.*

        GG. Primary veins slightly elevated or evident below, 3–5 pairs; inflorescence rachis 5–15 cm. long; leaf blade terminated by a cartilaginous point, not sharp; fruit uncertain. *C. hotteana.*

      FF. Leaves ovate in general outline, broadest below the middle, venation evident and slightly raised on both surfaces; fruit coronate, the base sterile and corky.

        H. Primary veins generally 2–4 pairs, the lower two commonly separate from the others, the veins reaching to the margin before bifurcating and anastomosing; leaves generally 1–2 cm. long, uniformly acuminate from the middle to the apex. . . . . *C. incrassata.*

        HH. Primary veins generally 6–7 pairs, the lower two not noticeably separate from the others, the veins arcuate and bifurcating and anastomosing at a considerable distance from the margin; leaves generally 4–7 cm. long, the blade suddenly constricted above the middle and then acuminate to the apex. . . . . *C. fuertesii.*

  DD. Leaves not spine-tipped.

    I. Leaves with a conspicuous reticulum of raised veins and veinlets on the lower surface; perianth lobes imbricate in fruit, not coronate.

      J. Leaves of normal shoots 1–3 cm. long; inflorescence generally shorter than the leaves.

        K. Leaves of normal shoots as broad as or broader than long, apex rounded-truncate to emarginate. . . . . *C. picardae.*

        KK. Leaves of normal shoots longer than broad, apex apiculate to acuminate, rarely rounded but never subtruncate or emarginate. . . . . *C. pauciflora.*

JJ. Leaves of normal shoots larger, 6 × 4 to 50 × 80 cm. long and broad; inflorescence generally exceeding the leaves.

L. Leaves longer than broad; fruit ovoid.

M. Leaves rounded and generally asymmetrical at the base with one lobe usually overlapping the petiole, the blade commonly bullate between the veins. .... *C. ceibensis.*

MM. Leaves normally rounded and symmetrical at the base, occasionally cuneate, the blade not bullate. .... *C. wrightii.*

LL. Leaves generally as broad as or broader than long.

N. Fruit globose to ovoid; leaves generally pilose. *C. pubescens.*

NN. Fruit obovoid, narrowed to a stalk at the base; leaves at most puberulent. .... *C. uvifera* × *C. pubescens.*

II. Leaves without a conspicuous reticulum, primary veins alone conspicuous.

O. Flowers and fruits sessile or the pedicels short and not exceeding the ocreolae in fruiting condition; perianth lobes coronate in fruit.

P. Veins straight, not conspicuous, arcuate before bifurcating more or less equally and anastomosing near the margin; nodes swollen; petioles arising near the apex of the swollen nodes but from the base of the ocreae; leaves of normal shoots 3.5 × 5 to 7 × 4 cm. long and broad. .... *C. microstachya.*

PP. Veins arcuate ascending, the terminal dichotomies unequal; nodes not conspicuously swollen or bead-like.

Q. Petioles arising slightly above the base of the ocreae; fruits spindle-shaped, nearly twice as long as thick; leaf bases usually asymmetrical. .... *C. leonardii.*

QQ. Petioles arising from the base of the ocreae; fruit globular to ovate, scarcely longer than broad.

R. Leaves shiny when dry; fruit globular, 3 mm. diameter. .... *C. samanensis.*

RR. Leaves dull when dry.

S. Leaves of normal shoots obovate to obovate-elliptic, broadest above the middle, uniformly acute to rounded at the apex, not abruptly constricted; blade a dull brown when dry; fruit globular. .... *C. albicans.*

SS. Leaves of normal shoots ovate to elliptic, broadest below the middle, usually abruptly narrowed above the middle and acuminate to the tip; blade turning black on drying; fruit ovoid. .... *C. swartzii.*

OO. Flowers and fruits borne on pedicels which exceed the ocreolae in length.

T. Leaves of normal shoots generally orbicular and as broad as long or broader.

U. Branchlets with conspicuous swollen nodes, these often appearing moniliform.

V. Leaves drying black; petioles arising from above the base of the ocreae; branchlets ferruginously pubescent. .... *C. nodosa.*

VV. Leaves not turning black on drying; petioles arising from the base of the ocreae; branchlets pale puberulent. . . . . *C. buchii.*

UU. Branchlets terete, the nodes not conspicuously swollen.

W. Perianth lobes and achene coronate in fruit.

X. Inflorescence rachis 1–2.5 cm. long. . . . . *C. buchii.*

XX. Inflorescence rachis 10–20 cm. long. . . . . *C. costata.*

WW. Perianth lobes imbricate in fruit, the achene not coronate.

Y. Leaves 6 × 8 to 13 × 18 cm. long and broad or larger; venation not conspicuous; fruit obpyriform, 1.2–2 cm. long. . . . . *C. uvifera.*

YY. Leaves 1.1 × 1.2 to 2.5 × 2.5 cm. long and broad; fruit 3–4 mm. long.

Z. Inflorescence rachis 0.2–0.5 cm. long; branches generally appearing to be arranged in one plane; venation of leaves reticulate and conspicuous on both surfaces when dry; fruit round in cross section. . . . . *C. picardae.*

ZZ. Inflorescence rachis 5–8 cm. long; branches geniculate, not appearing to be in one plane; venation inconspicuous on both surfaces when dry; fruit strongly 3-angled in cross section. *C. krugii.*

TT. Leaves of normal shoots not orbicular, longer than broad.

a. Inflorescence rachis short, less than 3 cm. long.

b. Fruit coronate. . . . . *C. buchii.*

bb. Fruit not coronate, perianth lobes imbricate.

c. Leaves ovate, broadest below the middle, cordate at the base. . . . . *C. krugii.*

cc. Leaves obovate to obtriangular, broadest above the middle, narrowed or rounded at the base.

d. Leaves rounded-truncate to emarginate at the apex. . . . . *C. picardae.*

dd. Leaves normally apiculate to acuminate, rarely rounded but never subtruncate or emarginate at the apex. . . . . *C. pauciflora.*

aa. Inflorescence rachis normally 5–20 cm. long.

e. Flowering and fruiting pedicels short, exceeding the ocreolae but rarely twice as long.

f. Fruit sub-coronate at the apex; ocreae, petioles and rachises puberulent when young, the hairs generally persisting; leaves of normal shoots generally 7 × 5 cm. long and broad or larger; blades dark green when fresh and golden to dark brown when dry. . . . . . . *C. costata.*

ff. Fruit not coronate at the apex; ocreae, petioles and rachises glabrous; leaves of normal shoots generally

4 × 3 cm. long and broad or smaller; leaf blades pale greenish-tan in color when fresh or dry. . . . . . *C. krugii.*

ee. Flowering and fruiting pedicels conspicuous, two to several times the length of the ocreolae.

g. Perianth lobes and achene sub-coronate when mature; primary veins of leaves conspicuous and with secondary venation forming an elevated and conspicuous reticulum on both surfaces when dry. . . . . *C. wrightii.*

gg. Perianth lobes imbricate, the achene rounded at the apex, not sub-coronate; primary veins evident, secondary venation inconspicuous, not elevated and reticulated on the lower surface.

h. All parts glabrous. . . . . *C. diversifolia.*

hh. Ocreae, petioles and inflorescence rachises puberulent or pubescent at least when young. *C. hotteana.*

Coccoloba albicans Ekman in Schmidt, Fedde Rep. Spec. Nov. 27: 103. 1929.

Small, medium or large tree (fide Ekman); branches terete, striate or canaliculate, light gray, glabrous; ocreae 6–8 mm. long, stiff, glabrous, cleft at the apex, frequently splitting at maturity and appearing as two ovate-lanceolate acuminate stipules; leaves of normal shoots with petioles 4–6 mm. long, glabrous, arising from the base of the ocreae; blades obovate to obovate-elliptic, 4 × 2.5, 5 × 4, to 5.5 × 3.5 cm. long and broad, coriaceous, glabrous, the apex rounded, rarely bluntly apiculate, the base rounded, the margin slightly revolute; midrib and primary veins impressed above, prominent below, the primary veins 6–8 pairs, arcuate, anastomosing conspicuously near the margins, the ultimate venation evident below but not above; leaves of adventitious or fast-growing shoots with ocreae 1–1.5 cm. long, the petioles 1–1.2 cm. long, the blades obovate-elliptic to elliptic-lanceolate, rarely ovate-elliptic, 6.5 × 5, 8.5 × 6, to 9.5 × 5 cm. long and broad, otherwise the same; inflorescences single or aggregated as 3 or 4 racemes, terminal or terminal on axillary shoots, to 13 cm. long, the basal ocreae to 1 cm. long, the rachis angular, glabrous; flowers sessile, the staminate flowers 1–3 at each locus, the pistillate flowers 1 at each locus, the bracts about 0.5 mm. long, ocreolae membranaceous, 1–1.5 mm. long, expanding and splitting after flowering; hypanthium to 1 mm. long, the perianth lobes ovate to suborbicular, 1.8 × 2.0 mm. long and broad, the functional stamens 1–1.5 mm. long, the rudimentary stamens less than 0.5 mm. long, the fertile pistil 2.5 mm. long, the ovary triangular, the rudimentary pistil about 0.5 mm. long; fruit sessile, ovoid to globose, 5 mm. long, 4.5–5 mm. in diameter, the perianth lobes slightly coronate, the achene light tan in color.

DISTRIBUTION: Endemic to Haiti.

Haiti. DEPT. DU SUD: Massif de la Hotte, Les Roseaux, Nan-Patates, *Ekman H-10693* (s-lectotype, US); Les Roseaux between Nan-Patates and Alnette, *Ek-*

man H-10720 (B, S); Massif de la Hotte, Morne Rochelois, Miragoâne at Quaert-Chemis, *Ekman H-9206* (S), *H-7936* (A, S, US); Miragoâne on trail to Morne Rochelois, *Eyerdam 515* (F, GH, NY, US), *519* (A, F, GH, NY, US).

It is not clear to me whether Schmidt or Ekman compiled the original description of *Coccoloba albicans*. Although the species was published by Schmidt, he gives credit to Ekman for the taxon as a new entity. Various herbarium sheets bear labels indicating as author either Ekman or Ekman and Schmidt. In any case, leaves from fast-growing shoots and those from shoots of normal growth have been combined in the description, with a resulting lack of clarity. The description above distinguishes between the branches which are mature and those which are terminal shoots or adventitious branches. Among the specimens cited are both flowering and sterile adventitious shoots.

The original publication cites *Ekman H-10693* as the type. However, the collection *10720* in the Berlin herbarium bears the annotation "typus" in Urban's handwriting, while the Stockholm specimen of the same number has a printed label indicating that is the type. A specimen of the number published as the type is not in the Berlin herbarium and I have chosen to select the Stockholm specimen of *Ekman H-10693* as a lectotype. This is the correct number as published and is better material than is the second collection cited in the original description and labeled as the type.

Two collections, *Ekman H-7936* and *H-9206*, were originally labeled "*Coccoloba albicans* Ekman, forma." These are the smaller-leaved mature branches, while the collection *Ekman 10720* labeled "typus" by Schmidt consists primarily of adventitious shoots.

The collections cited in the original publication are from staminate plants. The collection *Ekman H-7936* labeled "forma" bears fruit. Pistillate flowers are seen on the *Eyerdam* collections. In the original description Schmidt refers to the punctations on the lower leaf surface. These are blocked stomata and their adjacent cells which dry darker than other areas of the lower mesophyll.

Coccoloba buchii Schmidt, Ark. Bot. **20A**(15): 32. 1926; Fedde Rep. Spec. Nov. **24**: 75. 1927.

Coccoloba revoluta Leonard, Jour. Wash. Acad. Sci. **17**: 66. 1927.
Coccoloba tortuensis Ekman & Schmidt, Ark. Bot. **20A**(15): 32. 1926.
Coccoloba ciferriana Ekman, Bull. Estac. Bot. Moca, Ser. B, **17**: 10. 1927 (nomen).

Small tree with numerous spreading branches; branches terete, puberulent to pilose, the nodes slightly tumid; ocreae membranaceous, 3–7 mm. long, oblique to nearly bilobed at the apex, puberulent to pilose; leaves of normal shoots with petioles 3–4 mm. long, puberulent to pilose, at least on the adaxial surface, arising from the bases of the ocreae, the blades ovate to elliptic-orbicular or reniform to obovate-elliptic, 2 × 1.5, 3 × 2.5 cm., thin, coriaceous, puberulent above, glabrous below, the apex rounded or obtuse, the base subcordate, rounded or occasionally narrowed, the margin entire, recurved; midrib prominent on both surfaces, the primary veins 5 or 6 pairs, straight or slightly arcuate, strongly recurved and anastomosing near the margin, the secondary venation minutely reticulate above, coarsely reticulate below; leaves of adventitious shoots with petioles 4–5 mm. long, the blades elliptic, elliptic-lanceolate to ovate-lanceolate, 4.5 × 3, 8.5 × 3 to 11.5 × 4.5 cm. long and broad; inflorescences terminal on short lateral shoots 1–2.5 cm. long, the rachis puberulent at the base or on the lower portion, becoming glabrate; staminate flowers 1–3 at each locus, pistillate flowers borne singly at each locus, the bracts and ocreolae membranaceous, to 1 mm. long, the ocreolae tightly cylindrical around the pedicels, the hypanthium less than 1 mm. long, the perianth lobes ovate, 1 mm. in diameter, the fertile stamens to 1 mm. long; fruiting pedicels 1–1.5 mm. long, glabrous, the fruit ovoid, 5 mm. long, 4 mm. in diameter, the base rounded, the perianth lobes subcoronate, the achene brown.

LOCAL NAME: *Papelite* (H).

DISTRIBUTION: Endemic to Hispaniola.

Dominican Republic. PROV. INDEPENDENCIA: near Puerto Escondido, *Howard 12150* (GH). PROV. LIBERTADOR: between Restauración and Banica, *Howard 12554* (GH). PROV. MONTE CRISTI: El Morro, *Ekman 13140* (A, S, US, number designated by Ekman and Schmidt as type of *Coccoloba ciferriana*), *Howard 12533* (GH), *Howard 12535* (GH), *Jiménez 1370* (GH). PROV. PUERTO PLATA: Arroyo Francés, *Ekman 14399* (S, US). PROV. SAMANÁ: Los Haitises, Boca del Infierno, *Ekman 15439a* (S), *15439b* (S, US), *15439c* (S), *15439d* (S). PROV. SANTIAGO: Las Lagunas at Arroyo Arrenquillo, *Ekman 16078* (S).

Haiti. DEPT. DU NORD OUEST: Moustique Mts., Bassin Bleu, *E.C. & G.M. Leonard 15235* (NY, US), Port de Paix, *Ekman H-3646* (B, S, US), Presqu'ile du Nord-Ouest, Port de Paix, Haut Moustique, *Ekman H-3647* (S), Isle de la Tortue, La Vallée, Morne Barranca, *Ekman H-4107* (B-type of *C. tortuensis*, S, US), *H-4308* (B, S). DEPT. DU NORD: St. Michel de l'Atalaye, *E.C. Leonard 8499* (B, GH, US-type of *C. revoluta*), *7244* (NY, US), Massif du Nord, Gros Morne, Morne Chabre, *Ekman H-5024* (S), Massif du Nord, Gros Morne, Morne Bonpère, *Ekman H-4951* (S-type of *C. buchii*).

Ekman in his publication entitled "Excursion Botanica al Nord-Oeste de la Republica Dominicana" (Estacion Agronomica de Moca, Ser. B. 17: 9–10. 1930) refers to a new and distinct species of *Coccoloba* on the top of El Morro near Monte Cristi. He comments that this is dedicated to his amiable companion of the trip, Dr. R. Ciferri. His field label for this specimen (*Ekman 13140*) reads "C. Ciferriana Ekman." Later collections from neighboring areas, e.g., *Ekman 14399*, from Arroyo Francés near Puerto Plata, and *Ekman 16078*, Arroyo Arrenquillo near Santiago, all bear field labels reading, "*C. Ciferriana* Ekman and Schmidt." By 1932, however, Schmidt had changed his opinion of this material and all the sheets cited above bear his annotation labels reading "*Coccoloba Buchii.*"

A study of these plants in the field reveals that both *Coccoloba buchii* as interpreted by Schmidt and *C. ciferriana* as interpreted by Ekman are present on the top of El Morro. Careful analyses of these populations were made in the field and reveal a continuous variation in a series in the shape of the leaves from sterile and fertile plants and from normal leaves to leaves of adventitious shoots. The type specimens chosen for these species (and for *C. revoluta*) represent extremes of the variation. It is more satisfactory to consider the entire range of variation as delimiting the species and to apply the oldest name, *C. buchii,* to the population. *Coccoloba revoluta* Leonard represents an extreme development of pubescence.

The assignment to this species of plants from the Samaná Peninsula in eastern Hispaniola extends the range of the species to the eastward, in violation of Ekman's concepts of species distribution in Hispaniola. Ekman's field label for his collection *15439* is preserved in the Stockholm herbarium. He believed that this plant from the Bocas del Infierno in Samaná was a new species having affinities with *C. flavescens.* He commented, "The plants made, however, the impression of something new. The leaves of the saplings are larger than those of mature plants, otherwise similar." To this Ekman added "a,b,c,d, different stages, a — mature, d — sapling." All of these specimens are sterile and *Ekman 15439a,* described by Ekman as a mature shrub, has smaller ovate-elliptic leaves 4.5 × 3 to 3.5 × 2 cm. long and broad. Specimens *15439 c & d* are obviously from faster-growing leader or adventitious shoots. The leaves of these are lanceolate-ovate to 7.5 × 2 cm. long and broad to elliptic-ovate 10 × 4 cm. long and broad. It seems best to recognize this as a normal variation, although a troublesome one from the taxonomic point of view.

Howard 12554 is tentatively referred to this species. The flowers were either past or else the inflorescence had aborted in the dry period. Leaves of the adventitious shoots are larger, thicker and more prominently veined than in the remainder of the specimens seen in the field or cited above.

Coccoloba tortuensis was based on *Ekman H-4107* and *H-4308,* the former being selected by Schmidt as the type. It was described at the same time as *C. buchii* and both species were based on incomplete or sterile material. In subsequent papers Schmidt referred additional specimens to *C. buchii* and expanded his definition of this species. It is my feeling that *C. tortuensis* should be referred to the synonomy of *C. buchii.* Originally Schmidt distinguished between *C. buchii* and *C. tortuensis* on the basis of the length of the ocrea, the size of the leaf and thickness of the nodes and the leaf shape. In all characters considered, *C. tortuensis* is sufficiently similar to *C. buchii* to be referred to it. The leaf shape is slightly different and the pubescence on young parts heavier, but these are within the range of expected variation.

Coccoloba buchii is similar in general appearance to *C. praecox* of Cuba, especially in sterile condition. The two species can be distinguished on the basis of the more tumid nodes, the longer inflorescences, the larger leaves and petioles of *C. praecox.*

Coccoloba krugii is also similar to *C. buchii*, but the former can be distinguished by the more cordate-ovate leaves, the angular rachis of the inflorescence and the angular fruits.

Coccoloba ceibensis Schmidt, Fedde Rep. Spec. Nov. 32: 81. 1933.

Shrub or small tree; branches terete, striate, puberulent, the nodes swollen; ocreae 1–1.5 cm. long, uniformly membranaceous, ferruginous puberulent, bilobed and acute at the apex; leaves with petioles 5–7 mm. long, puberulent, attached at the bases of the ocreae; blades broadly elliptic, to ovate-elliptic or obovate-elliptic, 7 × 5, 10 × 8.5, 12 × 10 cm. long and broad, coriaceous, slightly bullate especially between the veins, the apex rounded to apiculate, the base rounded, the margin recurved; midrib slightly impressed but sharply keeled above, prominent below; primary veins 6–8 pairs, arcuate and anastomosing near the margin, impressed above and conspicuous below, the ultimate venation also conspicuous below, the lower leaf surface sparsely short pilose-pubescent, the upper surface glabrous and pitted; inflorescences terminal, 8–11.5 cm. long, the basal ocreae to 1.5 cm. long, puberulent, the rachis angular, puberulent; flowering material not known; fruiting racemes with broadly triangular bracts to 1 mm. long, the ocreolae 1–1.2 mm. long, the fruiting pedicels 1–1.5 mm. long; fruit ovoid, 6 mm. long and 4 mm. diameter, the perianth lobes half the length of the fruit, imbricate, the achene tan to brown, shining.

DISTRIBUTION: Endemic to Hispaniola.

Dominican Republic. PROV. TRUJILLO: Llano Costero, Cuenca at La Ceiba, *Ekman H-13344* (B-type, S); Llano Costero, El Manielito, *Ekman H-14281* (S); Bayaguana at Loma Managuá, *Ekman H-11108* (S).

Material of *Coccoloba ceibensis* has not been recollected in satisfactory condition and the species is known only from the type collection. The two additional Ekman collections cited above are referred here but with some question. *Ekman H-11108* was collected in sterile condition in January, 1929. The second collection, *Ekman H-14281*, was collected in February, 1930, and Ekman states on his field notes, "collected before sterile." Schmidt noted this comment with his initials and a question mark. The second collection is fragmentary, consisting of two small branchlets, in quality unlike the material Ekman generally prepared. It bears a staminate inflorescence. Schmidt referred this specimen to *C. scrobiculata*, a species which I have referred to *C. wrightii*. Schmidt compared this species with *C. pubescens*, as well as with *C. fawcettii*, which I have suggested represents the hybrid of *C. pubescens* and *C. fuertesii*.

Coccoloba ceibensis appears to me to be a hybrid of *C. pubescens* and probably *C. samanensis*, although the latter species has not been reported from the same area. The strong venation of the leaves and the shape of the fruit with the imbricated lobes of the perianth are similar to *C. pubescens*. The suggested parentage of *C. samanensis* is based on the short fruiting pedicels surrounded by membranaceous ocreolae, as well as the texture and aspect of the upper leaf surface. Although I spent some time collecting in the area where Ekman found these plants, I was unable to locate additional material near stands of *C. pubescens.* Ekman reported on the field label of the type specimen that the plant was "not common."

Coccoloba costata Wr. ex Sauvalle, Fl. Cub. 139. 1868; Lindau, Engl. Bot. Jahrb. 13: 155. 1890, Symb. Antill. 1: 225. 1899; Schmidt, Fedde Rep. Spec. Nov. 27: 105. 1929; Howard, Jour. Arnold Arb. **30**: 145. 1949, **38**: 235. 1957.

Coccoloba eggersiana Lindau, Engl. Bot. Jahrb. **13**: 153. 1890.
Coccoloba verruculosa Lindau, Engl. Bot. Jahrb. **13**: 154. 1890.
Coccoloba rupicola Urban, Symb. Antill. **6**: 10. 1909.
Coccoloba sp. Urban, Symb. Antill. **4**: 656. 1911.
Coccolobis costata Brit. & Wils. Sci. Surv. P. R. **5**: 270. 1924.
Coccoloba helwigii Schmidt, Fedde Rep. Spec. Nov. **27**: 104. 1929.
Coccoloba samuelssonii Ekman & Schmidt, Fedde Rep. Spec. Nov. **27**: 105. 1929.

Small tree of shrubby growth or tree to 30 feet tall; branches stout with a ferruginous to golden pubescence, this often persisting only in protected spots or at the apex; ocreae membranaceous 4–6 mm. long, ferruginous-puberulent to subglabrous; leaves of normal shoots with petioles 8–10 mm. long, stout, lightly puberulent, arising from the bases of the ocreae; blades generally ovate to elliptic, less commonly suborbicular to obovate-orbicular, 2.5 × 2.2, 5 × 5, 7 × 5, 11 × 8, to 18 × 12 cm. long and broad, coriaceous, usually golden, shining above, dull brown below, sparsely pitted above and below, often showing anomalous peltate or variously shaped resinous stomatal excretions which may be black and are abundant when the leaf is young, scattered and few in mature leaves, otherwise glabrous; apex obtuse or rounded, the base generally slightly and unequally cordate to narrowly and unequally decurrent on the petiole; midrib and veins impressed above, prominent below, the primary veins 5–7 pairs, arcuate, anastomosing; leaves of adventitious shoots to 35 × 22 cm. long and broad on petioles to 1.5 cm. long; inflorescence terminal, rachis puberulent, 15–20 cm. long, the staminate flowers in clusters of 2–4, the pistillate flowers solitary on pedicels 0.5 mm. long, the bracts ovate, 0.5 mm. long, the ocreolae membranaceous, 0.5 mm. long, the hypanthium 0.5 mm. long, the perianth lobes 0.5–1 mm. long and broad, the fertile stamens 1 mm. long; fruiting pedicels to 1.5 mm. long, the fruit globose to 6 mm. long, 5 mm. thick, the perianth lobes coronate.

DISTRIBUTION: Cuba, Hispaniola, Puerto Rico.

Dominican Republic. PROV. BARAHONA: Palo Mino to Montasse on trail to Polo, *Howard 12070* (GH), *12233* (GH); Mt. Laho, La Cueva to Placer Bonito, *Howard 12272* (A, GH). PROV. BENEFACTOR: San Juan, Loma La Vieja near Lemba, *Ekman H-13448* (S,US); Rio Arriba del Norte, *Howard 8843* (GH). PROV. LA VEGA: Banao, Firme del Banilejo, *Ekman H-16460* (S, US). PROV.

PUERTO PLATA: La Rosa, *Eggers 1762* (B-type of *C. verruculosa*, K, M, NBV); Sosúa, *Ekman H-14459* (S); Puerto Plata, *Eggers 2731* (B-type of *C. eggersiana*, GH, M), *Ekman H-14401* (A, S). PROV. TRUJILLO: Villa Altagracia, *Ekman H-11231* (S).

Haiti. DEPT. DU NORD OUEST: Bombardopolis, *EC & GM Leonard 13509* (NY, US). DEPT. DU NORD: Massif du Nord, Le Borgne, edge of Estere Savate, *Ekman H-4855* (B-type of *C. samuelssonii*, S, US); Massif du Nord, Gros Morne, Morne Bonpère, *Ekman H-4944* (S, US), *H-8523* (B-type of *C. helwigii*, S); Massif du Nord, Hinche, Bois Charles, *Ekman H-6077* (S, US); Massif du Nord, Bayeux, Morne Brigand, *Ekman H-2855* (B, S, US); Massif du Nord, St. Louis du Nord, Morne Baron, *Ekman H-4684* (S); Massif du Nord, St. Louis du Nord, between Baron and Rio Jean-Claire, *Ekman H-3904* (S). DEPT DE L'OUEST: Massif des Matheux, l'Archaie, Lully to Caye-Nicolas, *Ekman H-9287* (A, S, US); Massif des Cahos, Las Caobas, Belladère, *Ekman H-5589* (B, S); Ile de la Gonave, *Ekman H-8721* (S).

In a treatment of the genus *Coccoloba* as it occurs in Puerto Rico (Jour. Arnold Arb. **38**: 235–237. 1957), I discussed the morphological variation of *Coccoloba costata* and extended the recognized range of this species from Cuba alone to Hispaniola and Puerto Rico. A number of species from Hispaniola formerly considered distinct and endemic were reduced to the synonymy of this taxon. These included *C. samuelssonii*, considered distinct on the shape of the leaf base and the texture and shine of the leaf blade; *C. helwigii*, supposedly distinct in having orbicular leaves with minute punctations, the latter proving to be blocked stomata and resinous excretions from the stomata; and *C. verruculosa* which Lindau distinguished from *C. costata* on the matter of pubescence as well as the number and length of flowering pedicels. Still another Hispaniolan endemic species, *C. eggersiana*, must be included in this species and reduced to the synonymy of *C. costata*. In his key Lindau distinguishes *C. eggersiana* from *C. verruculosa* by the size of the leaves and the thickness of the inflorescence rachis. *Coccoloba eggersiana* is also distinguished from *C. costata* in the same key on the absence of pubescence on the inflorescence rachis. The abundance of material cited above demonstrates numerous intermediates on all characters and the type collection of *C. samuelssonii* (*Ekman H-4855*) shows clearly the range of variation from material matching the type of *C. costata* to shoots comparable to the type specimens of *C. eggersiana*.

The following series of specimens from near Puerto Plata and from the Province of Samaná are referred to *Coccoloba costata*, but with some question: PROV. PUERTO PLATA: Sosúa, coral reef at Forma, *Ekman H-14460* (S, US). PROV. SAMANÁ: San Lorenzo Bay, *Abbott 2237* (B, GH, NY, US); *2245* (US); Samaná, Laguna, *Ekman H-15096* (S, US); Los Haitises, Cueva de Cal, *Ekman H-15573* (S); Samaná, Laguna, Loma Zaramagua, *Ekman H-15249*; Los Haitises, Cayo de los Cueros, *Ekman H-15516* (S).

Each of these collections differs in some aspect from the expected range of variation now recognized for *Coccoloba costata*. Two collections, *Ek-*

man 14460 and *15096*, from Puerto Plata and Samaná respectively, have normal shoots with leaves similar to the type specimen of *C. eggersiana* and are clearly confluent with the range and variation of *C. costata.* The adventitious shoots of these same plants which are mounted on herbarium sheets are oblong, varying from 7.5 × 3 to 14 × 4.5 cm. long and wide. This leaf shape has not been found on adventitious shoots of *C. costata* in other sections of its range. *Ekman 15249* and *15573* from the Samaná peninsula and the two Abbott collections from the same area appear to be vigorous shoots, possibly adventitious in origin, but with small oblong leaves 6 × 2 to 9 × 2.5 cm. long and wide. All of these collections bear staminate inflorescences. *Ekman 15573* bears field notes indicating that the plant is "very common in the Haitises." It also has unripe fruits which are too small to permit the determination of either the fertility of the fruits or their possible similarity to those of *C. costata.* Finally, *Ekman H-15516* from Los Haitises bears a staminate inflorescence and unripe fruits which appear to be comparable to those of the Ekman collection just mentioned. This plant, Ekman notes on his field label, is "rare" in the same area. The leaves of collection *H-15516* are ovate-lanceolate to lanceolate-oblong. While the leaf base is similar to that expected in *C. costata,* the general aspect of this specimen suggests a relationship to *C. diversifolia.* It is possible that further collections may reveal a hybrid population of *C. diversifolia* and *C. costata* in the Samaná area, particularly inland on the limestone mountains.

Coccoloba costata Wr. ex Sauv. × **Coccoloba uvifera** L., hybr. nov.

Shrub or small tree (acc. Ekman), branches terete, striate; persistent bases of ocreae 4–5 mm. long, the membranaceous portions unknown; puberulent; leaves with stout petioles, 5–6 mm. long, puberulent, attached at the base of the ocreae; blade orbicular to elliptic, 7 × 6, 10 × 10, 10.5 × 9 cm. long and broad, coriaceous, the apex rounded, the base rounded to slightly cordate, one basal lobe larger than the other, one or both slightly overlapping the petiole, the margin slightly revolute; midrib conspicuous on both surfaces, the veins 6 pairs, slightly conspicuous on both surfaces, the lower three close together; inflorescence terminal; immature, to 8 cm. long with a shorter basal branch, the rachis puberulent; flowers immature; fruit not known.

Dominican Republic. PROV. PUERTO PLATA: Puerto Plata, cliffs facing the sea at Arroyo Francés, *Ekman H-14402* (A, S).

Schmidt referred this collection to *Coccoloba verruculosa* with a question. In the general appearance of the leaves, this plant resembles *C. uvifera.* The similarity is accentuated by the nature of the leaf base and the branching habit of the inflorescence. The similarity to *C. costata* is found in the texture, the venation and the color of the leaf blades. Both *C. uvifera* and *C. costata* are found at Arroyo Francés and it is apparent that this single collection represents a hybrid of these two species.

Coccoloba diversifolia Jacq. Enum. Pl. 19. 1760; Hist. Stirp. Amer. 114, pl. 76. 1763.

Coccoloba cubensis Meisner, DC. Prodr. **14**: 162. 1857.
Coccoloba laurifolia Lindau, Engl. Bot. Jahrb. **13**: 158. 1891, and all recent authors, not Jacquin.
Coccoloba longifolia Schmidt, Fedde Rep. Spec. Nov. **24**: 73. 1927, not Fischer ex Lind.

Shrub or tree to 23 feet tall; branches terete, often geniculate by limited growth, glabrous, the nodes rarely slightly swollen; ocreae coriaceous in the persistent lower portion, membranaceous and deciduous above, 3–5 mm. long; leaves of normal shoots with petioles 7–10 mm. long, glabrous, arising from the base of the ocreae; blades ovate, oval, oblong, elliptic, lanceolate or obovate, variable on one branch, 4 × 3.5, 7 × 5.5, 8 × 4.5, 12 × 8 cm. long and broad, coriaceous, often shining above, dull beneath, glabrous, the apex rounded, obtuse, acute or acuminate, the base cuneate, rounded or subcordate, the margin entire; midrib and primary veins slightly prominent above, the secondary venation reticulate on both surfaces, the primary veins 3–7 pairs, arcuate, anastomosing before reaching the margin; leaves of adventitious shoots on petioles 1–2.5 cm. long, with blades of varying shapes 17 × 8, 24 × 13, to 32 × 12.5 cm. long and wide; leaves of windswept specimens often much smaller than those of normal shoots with blades 2 × 1.3 to 3 × 2 cm. long and broad; inflorescence terminal 4.5–18 cm. long, rachis glabrous, the flowers on pedicels 2–4 mm. long, the staminate flowers 2–4 at each locus, the pistillate flowers borne singly at each locus, the bracts ovate, less than 0.5 mm. long, the ocreolae membranaceous, less than 0.5 mm. long, the hypanthium 1 mm. long, the perianth lobes ovate to oblong, 2–3 mm. long, 1–2 mm. broad, the functional stamens 1 mm. long, the sterile stamens rudimentary; fruiting pedicels 3–4.5 mm. long, the fruit globose to obpyriform, 10 × 7, 12 × 8, 13 × 8 mm. long and in diameter, the apex rounded, the perianth lobes imbricate and appressed.

COMMON NAMES: *Maivisse* (H), *raisin marron* (H), *resinier* (H), *uva cimarrona*, *uvero* (DR), *uvilla* (DR), *zamon maron* (H).

DISTRIBUTION: Florida, Bahamas, Greater and Lesser Antilles.

Dominican Republic. PROV. LA ALTAGRACIA: La Romana, *Taylor 384* (NY, US). PROV. AZUA: Azua, *Rose, Fitch & Russell 3934* (NY, US), *4415* (NY, US). PROV. BARAHONA: Beata Island, *Howard 12361* (GH), Palo Mino to Montasse near Polo, *Howard 12096* (GH), Barahona, *Fuertes 1104* (F, GH, MO, NY, S, US). PROV. BENEFACTOR: Rio Arriba, *R.A. & E.S. Howard 8976* (GH). PROV. MONTE CRISTI: El Morro, *Howard 12536* (GH), *12538* (GH), *12531* (GH), *Moscoso 158* (SD); Santiago Rodriguez, Moncièn, *Valeur 254* (A, F, MICH, MO, NY, S, US). PROV. PUERTO PLATA: Sosúa, *Jiménez 1676* (GH); Savana de Guainamoca, *Eggers 2558* (B, NY, US). PROV. SAMANÁ: Lajana, *Abbott 1297* (US). PROV. SAN PEDRO DE MACORIS: San Pedro de Macoris, *Rose, Fitch & Russell 4444* (US). PROV. SANTIAGO: Angostura, *Jiménez 1824* (A). PROV. TRUJILLO: Jaina, *Faris 113* (US). DISTRICTO DE SANTO DOMINGO: Ciudad Trujillo, *Schiffino 138* (G). San

Gabriel Island, *Miller 1022* (US). Puerto Escondido, *Howard 12139* (GH), *12145* (GH). LOCALITY UNCERTAIN OR NOT INDICATED: *Wright, Parry & Brummel 477* (G, US); Lopez, *Eggers 3387* (NY, US); Rio Verde, *Eggers 2325* (M); *Sharff 4* (F), *17a* (F); *Jaeger 313* (NY); *Sessé & Mociño 5428* (F), *948* (F).

Haiti. DEPT. DU NORD OUEST: Tortue Island, La Vallée, *EC & GM Leonard 11288* (MICH, GH, US); Mole St. Nicolas, *EC & GM Leonard 13367* (US). DEPT. DU NORD: Bayeux near Port Margot, *Nash 287* (F, NY). DEPT. DE L'ARTIBONITE: Ennery, *Leonard 8909* (GH, NY, US), *9527* (US); Petit Rivière de l'Artibonite, *Picarda 1580* (B); St. Michel de l'Atalaye, *Leonard 7483* (MO, US), *7426* (US); La Brande to Mt. Blanche, *Nash & Taylor 1649* (NY). DEPT. DU SUD: Ile Grande Cayemitte, *Eyerdam 318* (F, GH, US); Navassa Island, *Rehder 12* (A, NY, US), *Ekman 10800* (S), *Proctor 15478* (A, IJ); Jeremie, *Picarda 1314* (B); Massif de l'Hotte, Trouin, *Ekman 5944* (A, S); Miragoâne, *Prince Paul 1313* (M). DEPT. DE L'OUEST: Gonave Island (Anse Galette), *Leonard 3265* (B, NY, US), *3261* (US); Port au Paix, La Coup River, *EC & GM Leonard 11138* (MO, NY, US); between Passe Aubert & Passe Chance aulme, *Ekman 3819* (S, US); Jean Rabel, *EC & GM Leonard 12704* (A, US); Fond Parisienne, *Holdridge 1822* (GH, US); Morne Hospital, *Buch 1839* (B); Petionville, *Picarda 1410* (B).

This species is more common in Hispaniola than the few specimens cited above would indicate. In many areas *Coccoloba diversifolia* is in general use as a fence row tree, although I could never determine whether the plants were started as seeds or as cuttings.

The general misapplication of the names *Coccoloba diversifolia* and *C. laurifolia* by nearly all recent authors and their proper application has been discussed in an earlier paper (Jour. Arnold Arb. 30: 422–424. 1949).

Coccoloba fawcettii Schmidt, Fedde Rep. Spec. Nov. 24: 76. 1927.

Small tree (fide Ekman); branches tortuous, the nodes conspicuously swollen, the youngest parts densely golden-pubescent; ocreae 3–5 mm. long, membranaceous, pubescent, truncate or slightly bilobed at the apex; petioles 2–3 mm. long, pubescent, arising at the bases of the ocreae; blades cordate, 3.5 × 3, 4 × 4, 8 × 6 cm. long and broad, rigid and thin, papery in texture, the apex acute or obtuse, slightly apiculate, the base cordate, the margin entire, slightly undulate; midrib slightly prominent above, conspicuous below, primary veins 3–5 pairs, arcuate and anastomosing at the margin, scarcely impressed above, prominent beneath, the secondary venation prominent and reticulate below, the upper surface full and glabrous, the lower surface sparsely short pubescent; inflorescence terminal 1.8–3 cm. long, the rachis puberulent, the bracts triangular to 1.2 mm. long, spreading, the ocreolae membranaceous, to 1.2 mm. long, the pedicels shorter than the ocreolae; staminate flowers unknown, the pistillate flowers 1, rarely 2, at each locus, the hypanthium less than 0.5 mm. long, the perianth lobes broadly ovate, 1.5–2 mm. wide and 1.0–1.5 mm. long, the stamens rudimentary, less than 0.5 mm. long, the ovary ellipsoidal, 1.5 mm. long, sharply 3-angled; fruit not known.

DISTRIBUTION: Endemic to the Dominican Republic. Known only from the type collection.

Dominican Republic. PROV. BARAHONA: Mare-à-chat, *Ekman H-6948* (B-type, S).

While the Berlin specimen of this collection has old inflorescences from which the flowers have fallen, the Stockholm specimen still retains a few open flowers. Schmidt states in the original description that the flowers and fruit are unknown. It is obvious that the Berlin specimen is the holotype. The staminate flowers and fruits are still unknown, but the pistillate flowers are described above.

The Berlin specimen consists of two fragments, one obviously from a mature shoot with inflorescences and the other from a more vigorously growing sterile shoot. The larger leaf size given in the description refers to leaves on the latter shoot. Truly adventitious shoots are not known.

In his original description Schmidt compared *Coccoloba fawcettii* with *C. pubescens* and *C. fuertesii.* It seems probable to me that *C. fawcettii* is a natural hybrid between these two species, both of which occur in the area where *C. fawcettii* was collected. Schmidt refers to the leaves of *C. pubescens* as being many times larger, yet some leaves of mature shoots in that species scarcely exceed those of the larger leaves on the type specimen of *C. fawcettii.* I was unable to find any plants of this species on a trip to the type location. Ekman stated in his field notes that the plant was "rare" and seen "only here." As a hybrid, *C. fawcettii* would derive the pubescence and reticulation from *C. pubescens* and the leaf shape and the swollen nodes from *C. fuertesii.*

Coccoloba flavescens Jacq. Hist. Stirp. Amer. 115. tab. 75. 1763.

Coccoloba pungens Urban, Symb. Antill. **5**: 335. 1907; **8**: 195. 1920.

Shrub, often with many trunks, to small tree with single trunk reaching 15 feet in height; bark gray, the youngest branches tan, slightly puberulent, geniculate, the nodes commonly swollen; ocreae membranaceous except at the base, to 3 mm. long, the base cartilaginous, ring-like, the petioles arising from this ring-like base, often appearing terminal due to geniculation of the stem; leaves of normal shoots with petioles 2–5 mm. long, puberulent to glabrous, the blades elliptic, ovate-elliptic or lanceolate-elliptic, 1.6 × 1.2, 3.6 × 1.8, 4.0 × 1.6, to 5.6 × 2.2 cm. long and broad, rigid, flat or slightly umbonate, the apex acute, mucronate, the cartilaginous mucro to 1 mm. long, sharp and stiff, the base rounded to slightly cordate, the margin entire; venation not evident in fresh condition, only slightly evident when dry, the veins 10–20 pairs, equally developed; leaves of adventitious shoots similar in shape, 6.0 × 3.2 to 7.8 × 3.1 cm. long and wide; inflorescence terminal, 2–2.5 cm. long, the rachis glabrous, the bracts to 1 mm. long, slightly erose at the apex, the ocreolae less than 1 mm. long, the flowering pedicels short, those of the staminate flowers less than 1 mm. long, deciduous or rarely persisting and elongating slightly; staminate flowers borne singly at each locus, the hypanthium short, about 0.5 mm. long, the lobes 5 or 6, ovate, 2–3 mm. long, 1.5–2.5

mm. wide, the filaments 1–1.5 mm. long, the pistil rudiment to 2 mm. long; female flowers not seen; fruiting inflorescence stout, 1–4 cm. long, often strongly angled, the peduncles decurrent on the axis; fruit bright red, 4–5 mm. diameter, 6–9 mm. long, broadest at the middle, the apex rounded, the base slightly pedicellate, the perianth segments free to the middle, imbricate over the achene, strongly lined but the vascular bundles not evident.

DISTRIBUTION: Endemic to Hispaniola.

Dominican Republic. PROV. BARAHONA: Barahona, *Fuertes 543* (F, GH, MO, NY, S, US); Las Salinas, *Howard 12059* (GH), *12062* (GH). PROV. INDEPENDENCIA: Lake Enriquillo to Puerto Escondido, *Howard 12132* (GH); Puerto Escondido to Rancho Viejo, *Howard 12132* (GH).

Haiti. DEPT. DU NORD: Massif du Nord, Gros Morne, Morne Bonpère, *Ekman H-4939* (S). DEPT. DE L'ARTIBONITE: Gonaives to La Hotte Rochée, *Nash & Taylor 1560* (NY). DEPT. DE L'OUEST: Fond Parisien, Étang Saumatre, *Leonard 10138* (NY, US); Massif des Matheux, Croix des Bouquets, Morne à Cabrits, *Ekman H-989* (S, US). DEPT. UNCERTAIN: Cape Francois, *Ehrenberg s.n.* (B, NY); Poste Coudau, *Buch 1024* (B-type of *C. pungens*).

This is a distinctive species apparently restricted to the dry areas at low elevation. Three leaf forms were seen in the field. The normal leaves were found on the much-branched and geniculate branches. Much smaller leaves were seen occasionally on fasciated lateral branches which are borne on wand-like shoots; see *Ekman H-3499*. Slightly larger than normal leaves are found on shoots of less compact habit, having longer internodes and these are considered to be adventitious shoots. All three habits and leaf sizes are commonly found on one plant. The leaves are rigid even when fresh and the short but sharp mucro is very much in evidence when collecting this species. The leaves when fresh have the characteristic grayish-green color dominant in arid regions of the West Indies.

The fruits of *C. flavescens* are distinctive in shape and in the nature of the perianth in fruit. The fine striations on the lobes of the fruiting perianth seem to be characteristic of this species. Much larger fruits are associated with *Ekman 989*. These appear to be teratological and gall-infested. The few fruits opened were devoid of seed.

Coccoloba fuertesii Urban, Symb. Antill. 7: 210. 1912.

Coccoloba taylori Urban, Fedde Rep. Spec. Nov. 13: 446. 1914; Symb. Antill. 8: 196. 1920; Ark. Bot. 20A(15): 29. 1926.
Coccoloba barkeri Ekman & Schmidt, Fedde Rep. Spec. Nov. 27: 104. 1929.

Tree to 40 feet; diameter at breast height ten inches, bark rough, in characteristic 1-inch squares; branches terete, the nodes swollen, glabrous or at most papillose; ocreae to 5 mm., membranaceous above, this part lobed to the base on one side, often flaring, thick and persistent below; leaves of normal shoots with petioles 2–6 mm. long, papillose, arising above the base; blades ovate to ovate-triangular, less frequently ovate-lanceolate, elliptic or obovate, 2.5 × 2, 4 × 3, 5 × 4, 5 × 5.2, 6.5 × 4.5 to 7 × 3.7 cm. long and wide, generally broadest above the middle, coriaceous, entire, glabrous, the apex short- to long-acuminate, mucronate, the ultimate apex generally spine-tipped, the cartilaginous spine 0.5–2 mm. long, at times rounded to emarginate or almost bilobed through failure of the midrib to develop, the base cuneate to rounded, rarely acute or subtruncate, the margin entire; veins 5–10 pairs, subequal, prominently reticulate on both surfaces when dry, the veins arcuate, approaching but distinct from the cartilaginous margin of the leaf; leaves of adventitious shoots borne above the base of the ocreae 1–1.5 cm. long but occasionally to 3.4 cm. long, on petioles 1 cm. long, the blades broadly ovate to ovate-triangular to elliptic or ovate-lanceolate or elliptic-lanceolate, 8.2 × 6.2 to 16.5 × 9 cm. long and wide, often asymmetrical, the apex acute, acuminate, obtuse or rounded, the terminal spine present or absent, the base truncate, subtruncate or rounded; inflorescences equalling or surpassing the leaves, 2.5–6.5 cm. long, terminal, 1–4 at each locus; flowers sessile or on pedicels not exceeding 1 mm.; staminate flowers 1–4 at each locus, the pistillate flowers 1 at each locus, the bracts broadly ovate, 0.5 mm. long and wide, the ocreolae membranaceous, flaring, 0.5 mm. long; hypanthium to 1 mm. long, the perianth lobes oblong to ovate-orbicular, 1–1.3 mm. long and wide, the functional stamens to 1 mm. long, the sterile stamens with rudimentary anthers; functional pistil to 3 mm. long, the sterile pistil rudimentary; fruit red when mature, oblong or ovate, fleshy, 6–9 mm. long, 3–5 mm. in diameter, the hypanthium red in fruit, the perianth lobes coronate, 1–2 mm. long; fruit with a corky or woody sub-hemispherical sterile base, this often marked with a horizontal constriction and frequently attenuate below; achene brown or tan.

DISTRIBUTION: Endemic to Hispaniola.

Dominican Republic. DIST. DE SANTO DOMINGO: Santo Domingo on road to Puerto Plata, *Wright, Parry and Brummel 474* (GH, US). PROV. BARAHONA: Barahona, *Fuertes 716* (B-type), Palo Mino to Montasse on trail to Polo, *Howard 12065* (GH), Cañada Maluca, *Howard 12196* (GH). PROV. MONTE CRISTI: Restauración, *Ekman H-6250* (S). PROV. PUERTO PLATA: Sosúa at La Goleta, *Ekman H-14529* (S, US). PROV. SAMANÁ: Samaná, Pan de Azucar, *Ekman H-15181* (S), Punta Arena, *Ekman H-14788* (S), Los Haitises near La Llanada, *Ekman H-15452* (S). PROV. TRUJILLO: Villa Altagracia, *Ekman H-11238* (A, S, US).

Haiti: DEPT. DU NORD OUEST: Massif du Nord, Port de Paix, Haut Piton, *Ekman H-4633* (B, S, US); Moustique Mts., Bassin Bleu, *E.C. & G.M. Leonard 14985* (US), *14986* (US), *15021* (A, GH, NY, US); Presqu'ile du Nord, Port de Paix, Haut Moustique, *Ekman H-3639* (S); Jean Rabel, *E.C. & G.M. Leonard 13635* (A, GH, NY, US). DEPT. DU NORD: Massif du Nord, Morne Belance, *Ekman H-4911* (S); Massif du Nord, Bayeux, Morne Brigand, *Ekman H-2854* (S, US). DEPT. DE L'ARTIBONITE: Massif du Nord, Gros Morne, Morne Chabre, *Ekman H-5015* (S), Massif du Nord, Morne Bonpère, *Ekman H-4952* (A, S, US); La Brante to Morne Belance, *Taylor 1674* (B-type of *C. taylori*, NY); Ennery, *Ekman H-2468* (B). DEPT. DU SUD: Tiburon, Morne Sentier, *Ekman H-10597* (B, S, US); Morne Rochelois, Charlier, *Ekman H-9037* (A, S); Grand Cayemite, *Eyerdam 304* (A, F, GH, MO, NY, US), *Ekman H-8927* (S, US), Miragoane, Petit-Rivière des Nippes, *Eyerdam 398* (A, F, GH, NY, US). DEPT. DE L'OUEST: Massif de la Selle, Leogane near Citronniers, *Ekman H-6464* (B-type of *C. barkeri*, S, US); Massif de la Hotte, Jacmel at Savanette, *Ekman H-7081* (S, US).

The full variation in leaf size, shape and texture and the development of the terminal spine in this species must be seen in the field to be appreciated. One of my collections (*Howard 12065*) is represented by a series of twelve sheets taken from a single tree. This tree was 40 feet tall and 10 inches in diameter at breast height. Adventitious shoots developed in profusion from the trunk and from along the first main branch. The range of variation on the upper branches of the tree was significant, but this was exceeded by the variation on individual and different adventitious shoots. In general the leaves of the adventitious shoots were 2 to 3 times the size of the leaves on normal shoots. A second collection (*Howard 12196*) was made from a plant which consisted of a cluster of 14 trunks, the smallest less than an inch in diameter and the largest 8 inches and 20 feet tall. The original tree had been felled, but the stump remnant was still present. The smaller adventitious shoots produced the expected large leaves typical of such shoot systems, but the larger trunks retained only a few large leaves, while the majority were of the size range characteristic of the mature shoots. Other collections which show variations, apparently on single plants, are *Ekman H-7081* and *H-14788*.

Urban recognized the affinity of *Coccoloba taylori* with *C. fuertesii*, but distinguished between them on the basis of petiole length and the shape of the leaves. The material which Urban studied consisted of a fast-growing, probably adventitious, shoot (the type of *C. fuertesii*), and two gnarled branches of a mature tree (the type of *C. taylori*). Comparable variation can be found very readily on one tree.

Coccoloba barkeri is based on a specimen of mature growth with inflorescences to 9 cm. long, these being 1–4 in number. Urban's distinction of *C. barkeri* from *C. taylori* on the basis of inflorescence length was made by comparing the longest inflorescence of the type specimen of *C. barkeri* with the average, if not the shortest, inflorescence of *C. taylori*. Recent collections demonstrate that *C. barkeri* is to be included with *C. taylori* in the species *C. fuertesii*.

Much of the material cited has been determined by others as *Coccoloba retusa* or *C. diversifolia*. *Coccoloba retusa*, a Cuban species, differs in having thinner textured leaves, less tumid nodes and more conspicuously pedicellate flowers and fruits. Leaves of *C. retusa* also lack the spiny tip found in *C. fuertesii*, but perhaps the most significant difference is the absence in *C. fuertesii* of the solid basal section of the fruits of *C. retusa*. The two species are very similar and perhaps eventually *C. fuertesii* should be considered a geographical variety of *C. retusa*. *Coccoloba diversifolia* of recent authors is now known as *C. swartzii* and is clearly distinct as to the shape of the fruit, the leaf venation and margin and the lack of any development of pedicels.

Coccoloba fuertesii is similar to *C. incrassata* and the relationship of these two species requires further study of the populations in the field.

Coccoloba hotteana Schmidt, Ark. Bot. **20A**(15): 31. 1926.

A shrub or depauperate tree to 5 feet tall; branches slender, terete, the nodes not enlarged; ocreae 5–6 mm. long, obliquely truncate at the apex, more or less bilobed, short ferruginous-pubescent; leaves of normal shoots with petioles 3–4 mm. long, ferruginous-short-pubescent, inserted at the base of the ocreae; blades elliptic, rarely ovate-elliptic or narrowly obovate, 3 × 1.8, 4 × 2.5, 4.5 × 2 cm. long and broad, thin coriaceous, the apex narrowed and generally abruptly acuminate and slightly apiculate, the base rounded or narrowed, the margin entire, slightly revolute; midrib lighter in color, slightly conspicuous above, prominent below, primary veins 4 or 5 pairs, evident on both surfaces, slightly arcuate to the margins then anastomosing parallel to the margin, the stomata depressed and appearing as punctations on both surfaces; leaves of adventitious shoots lanceolate-elliptic, rounded or narrowed at the base, acute at the apex or apiculate, to 8 × 3 cm. long and broad; inflorescence terminal 5–15 cm. long, glabrous to sparsely puberulent, the bracts ovate or triangular, to 0.5 mm. long, the ocreolae membranaceous, 0.5–1 mm. long, the pedicels about 1 mm. long; staminate flowers 1–4 per locus, the pistillate flowers borne singly at each locus, the hypanthium 1–1.5 mm. long, the perianth lobes ovate to suborbicular to 2 mm. long and wide, the fertile stamens 1.5–2 mm. long, the sterile stamens rudimentary, the sterile pistil rudimentary, the fertil pistil 1–1.5 mm. long; fruit subglobose, 6 mm. in diameter, the fruiting perianth lobes imbricate, the achene dark brown, smooth.

DISTRIBUTION: Endemic to Haiti.

Haiti. DEPT. DU SUD: Anse-à-Veau, *Ekman H-5399* (B-holotype, S, US); Ile Grande Cayemitte, *Ekman H-8954* (S), *Eyerdam 285* (A, F, GH, NY, US).

The type collection of this species represented by herbarium specimens from Berlin, Stockholm and the U.S. National Museum comprises nine plant fragments. Normally Erik Ekman collected material of good quality and a single specimen fills an herbarium sheet. It would be interesting to know what happened to this material. The nine specimens of plant material represent sterile mature growth, possible adventitious growth, staminate, flower-bearing branches, pistillate flower-bearing branches and fruiting twigs. One fruit is attached to an inflorescence which appears to be from a staminate plant. Additional fruits in the packet on this sheet are hollow and sterile. The type specimen from the Berlin herbarium consists of three fragments, one pistillate flowering axis, one fruiting axis and one sterile branchlet. In the packet on this sheet are three fruits on which both Schmidt and I have based our descriptions. If the fruit belongs with the specimen, its characteristics are of value in recognizing this species, but I question the authenticity of this fruit.

Coccoloba hotteana appears to be a distinct species. At the present it is known only from a coral reef west of Anse-à-Veau and from Ile Grande Cayemitte. Additional material is much desired. The species can be recognized by the shape and venation of the leaf, the apiculate apex to the leaves and the pubescence on the ocreae and inflorescence rachis.

Ekman did not approve of Schmidt's choice of name for this species, for La Hotte is a mountain range, while *C. hotteana* is known only from low coral reefs at sea level. He comments in the field notes of a second collection, "The specific name is misleading in a way. 'Hotteana' ought to be reserved for mountain plants."

Coccoloba hotteana Schmidt × **C. uvifera** L., hybr. nov.

Shrub (acc. to Ekman); branches terete, striate and canaliculate, puberulent to short pubescent; ocreae to 1 cm. long, strongly bilobed at the apex, puberulent, persistent; leaves of normal shoots with petioles 3–6 mm. long, stout, puberulent, arising from the bases of the ocreae; blades broadly elliptic to obovate-elliptic or orbicular, 6 × 4 to 7 × 6 cm. long and broad, coriaceous, the apex rounded to short apiculate, the base rounded, usually slightly asymmetrical, the margin flat; midrib conspicuous on both surfaces, the primary veins 5 or 6 pairs, conspicuous on both surfaces, the ultimate venation reticulate and conspicuous when dry, the upper surface glabrous, the lower surface puberulent and densely punctate-dotted with blocked stomata, the midrib and veins puberulent; leaves of adventitious shoots similar, to 10 × 8 cm. long and broad; inflorescence terminal, 10 to 25 cm. long, the rachis angular, puberulent, the bracts broadly ovate to 1 mm. long, the ocreolae 1 mm. long; pedicels 2–2.5 mm. long.

Haiti. DEPT. DU SUD: Ile Grande Cayemitte, northern coast in the Côtes de Fer, *Ekman H-8950* (B, S), *Eyerdam 303* (A, F, GH, MO, NY, US).

This hybrid is represented by collections of Ekman and Eyerdam numbered separately but made when these men were travelling together, on the same date and obviously from the same plant. This material in some respects resembles hybrids of *Coccoloba uvifera* and *C. costata* recognized from the vicinity of Puerto Plata and some specimens (e.g., *Eggers 1762*, the type of *C. verruculosa*) assigned to *C. costata* as a species. It seems distinct from these and appears to be derived from the parentage of *C. uvifera* and *C. hotteana*, both of which occur on Ile Grande Cayemitte. The leaf shape, particularly the nature of the leaf apex and the venation, appears to be derived from *C. hotteana*. The texture of the leaf, the nature of the inflorescence and the shape of the sterile fruits are those of *C. uvifera*. The inflorescences are old in the specimens cited above and a few fruits have been retained in packets. The flowering pedicels are borne, 3–5 at each node, on the inflorescence rachis, a character usually associated with staminate plants. As has been pointed out (Jour. Arnold Arb.

30: 390. 1949.), staminate plants of *Coccoloba uvifera* often form fruits which are of full size and normal shape but hollow or with aborted seeds or embryos. The fruits associated with the cited specimens resemble those of *C. uvifera*, not *C. hotteana*. They are obovoid, to 1.5 cm. long and 1 cm. in diameter. The fruits are strongly narrowed at the base and rounded at the apex with imbricated perianth lobes. The achene is dark brown and smooth but hollow or with a very small seed and is obviously infertile.

Coccoloba incrassata Urban, Symb. Antill. 7: 208. 1912.

Coccoloba mansfeldii Schmidt, Ark. Bot. **20A**(15): 29. 1926; Fedde Rep. Spec. Nov. **27**: 103. 1929.

Shrub 10 feet tall to densely branched tree 20 feet tall; branches compact or geniculate, the lateral branches with short internodes often appearing as short shoots, the nodes conspicuously swollen, the branches often appearing moniliform, papillose to puberulent; ocreae membranaceous above, 1–2 mm. long, glabrous; leaves of normal shoots with petioles 1 mm. long, glabrous, inserted above the bases of the ocreae, the blades ovate-triangular, 1 × 0.7, to 1.7 × 1.1 cm. long and wide, thick coriaceous, glabrous, the stomata and subsidiary cells clear, appearing as translucent dots, the apex attenuate to a spinose mucro, the spine about 1 mm. long, the base rounded to subtruncate; midrib cartilaginous, conspicuous on both surfaces, the veins anastomosing, conspicuous on both surfaces, 2 pairs of veins near the base of the blade separated from the upper pairs of veins, the veins reaching the margin without becoming arcuate, then fusing with the cartilaginous ring at the margin; leaves of adventitious shoots with petioles 4 mm. long, the blades lanceolate to lanceolate-ovate or elliptic-lanceolate 2.5 × 1.4 to 3 × 1 cm. long and wide, acuminate and pointed or narrowed to a rounded apex, base rounded to triangular, the adventitious stems densely pilose to completely glabrous; inflorescence terminal, shorter than the leaves or reduced to an almost sessile 1–4-flowered cluster; bracts and ocreolae minute, less than 0.5 mm. long, the pedicels approximately 1 mm. long; staminate flowers 1 or 2 per locus, occasionally 1–4 on adventitious flowering shoots, the pistillate flowers borne singly at each locus on the inflorescence; hypanthium to 1 mm. long, the perianth lobes 1 mm. long and 0.7 mm. wide, the fertile stamens to 1 mm. long, the fertile pistil 2 mm. long; fruit 5 mm. long and 3 mm. diameter, narrowed to a corky sterile base, coronate at the apex, on pedicels 1 mm. long.

DISTRIBUTION: Endemic to Hispaniola.

Dominican Republic. PROV. AZUA: *Wright, Parry & Brummel 476* (GH, US). PROV. SAMANÁ: Los Haitises, La Marachita, *Ekman 15531* (A, S, US).

Haiti. DEPT. DU NORD OUEST: Pendu, *Buch 1269* (B–type, NY); Môle St. Nicolas, *E.C. & G.M. Leonard 13356* (MO, US); Bombardopolis, *E.C. & G.M. Leonard 13428* (A, GH, NY, US); Bombardopolis road south of Môle George, *E.C. & G.M.*

Leonard 13421 (MICH, US); Presqu'ile du Nord Ouest, Môle St. Nicolas at Pap-à-foux, *Ekman H-4487* (S, US); Presqu'ile du Nord, Port de Paix, Haut Moustique, *Ekman H-3648* (A, B, S, US). DEPT. DE L'ARTIBONITE: Ennery, *Leonard 8861* (US); Massif du Nord, Ennery, *Ekman H-2468* (S, US); Trois Rivières near Gros Morne, *E.C. & G.M. Leonard 9893* (GH, MO, US); Mt. La Cidre, near St. Michel de l'Atalaye, *Leonard 7397* (NY, US). DEPT. DE L'OUEST: Massif de la Selle, Anses à Pitres, *Ekman H-6688* (S); Massif de la Selle, group Crete-à-Piquants, Port-au-Prince, Morne Aux-Fourques, *Ekman H-5921* (B-type of *C. Mansfeldii*, S); Massif des Matheux, l'Arcahaie, *Ekman H-9330* (B, S).

The presently accepted distinctions between *Coccoloba incrassata* and *C. fuertesii* are not entirely satisfactory. *Coccoloba incrassata* was based on a Buch collection from dry hillslopes at moderate elevation near Pendu. Urban compared the species with *C. armata* of Cuba which is clearly distinct in the manner of branching as well as in the shape and venation of the leaves. *Coccoloba mansfeldii*, described by Schmidt, was based on a sterile collection made by Ekman and is clearly a fast-growing shoot of *C. incrassata.* It is possible to assemble an almost complete series of specimens to show the transitions from the very small-leaved form typical of *C. incrassata* to the larger leaves of *C. fuertesii.* In almost every character selected, these two species tend to be closely associated. Nevertheless I am hesitant to merge the two without further field study of this complex. On a field label associated with his collection *H-4911* which was assigned by Schmidt to *C. retusa,* Ekman writes, "evidently the same as n. ——— and n. ———. Resembles *C. retusa* Griseb. but is of course different, being in fact related with *C. incrassata* through a series of intermediate species." Few taxonomists split species finer than did Ekman and Schmidt; nevertheless it is interesting that Ekman felt he had seen and collected intermediate "species" between the two, although he never filled in the collecting numbers on his field label. For the present I distinguish *C. incrassata* on the basis of smaller leaves with fewer veins and with two pairs of these diverging near the base of the blade. The venation in specimens of *C. fuertesii* also differs from that of *C. incrassata,* in which the primary veins run straight to the margin before curving and fusing with the cartilaginous leaf margin. In *C. fuertesii* the veins divide or arch before reaching the margin, forming a network free from the cartilaginous margin. A parallel set of characters has been used to distinguish *C. retusa* and *C. northropiae* in Cuba and the Bahamas. Additional field study will be required to determine the value or validity of this distinction. The close association of *C. fuertesii* and *C. incrassata* is also indicated by the fruits, each possessing the sterile corky base to the achene. Only a few fruiting collections of *C. incrassata* are known, but in these the fruit appears to be smaller and the sterile base less differentiated than that of *C. fuertesii.*

Coccoloba krugii Lindau, Engl. Bot. Jahrb. **13**: 145. 1890; Symb. Antill. 1: 222. 1899; Howard, Jour. Arnold Arb. **37**: 337. 1956.

Coccoloba børgesenii Schmidt, Fedde Rep. Spec. Nov. **24**: 75. 1927.

Coccoloba børgesenii forma *ovato-lanceolata* Schmidt, Fedde Rep. Spec. Nov. **24**: 76. 1927.

Shrub or small tree to 19 feet tall; branches terete, glabrous, slightly geniculate and nodose; ocreae membranaceous; persistent, 3–5 mm. long; leaves of normal shoots with petioles 5–6 mm. long, corky at the base, arising from the bases of the ocreae; blades ovate to suborbicular, 2 × 1.8, 4 × 3.5, 5 × 4 cm. long and broad, thin-coriaceous, glabrous or rarely with a few hairs near the attachment of the petiole, the apex obtuse or rounded, the base cordate or rounded, the margin flat or recurved; midrib flat above, slightly prominent below, the primary veins 4–6 pairs, straight, bifurcating and anastomosing near the margin, flat on both surfaces, the secondary venation minutely reticulate below, smooth above; leaves of adventitious shoots with petioles 1 cm. long, the blades cordate or elliptic to 7 × 6 cm. long and broad; inflorescence terminal 5–8 cm. long, the rachis glabrous, the staminate flowers 1–3 per node, the pistillate flowers borne singly, the bracts broadly ovate, membranaceous, 1 mm. long; ocreolae membranaceous, flaring to 1 mm. long; pedicels wanting or shorter than the ocreolae, the hypanthium 1 mm. long, the perianth lobes ovate, to 2 mm. long, the filaments of fertile stamens 1.5 mm. long; fruit ovoid or angularly fusiform, strongly triangular in cross section, 4–5 mm. long, 3–3.5 mm. in diameter, the perianth lobes appressed, about half the length of the fruit.

DISTRIBUTION: The Bahamas, Hispaniola, Jamaica, Puerto Rico, Anagada, Antigua, Barbuda, St. Martin.

Dominican Republic. PROV. MONTE CRISTI: El Morro, *Ekman 13143* (S), *R.A. & E.S. Howard 12532* (GH), *12534* (GH), *Jiménez 1356* (A).

Haiti. DEPT. DU NORD OUEST: Isle Tortue, Morne Barranca, *Ekman 4314* (B-type of *C. børgesenii*, S, US); Port au Paix, Vallée des Trois Rivières, *Ekman 3588* (B-type of *C. børgesenii* forma *ovato-lanceolata*, S, US); Port au Paix, *E.C. & G.M. Leonard 15252* (A, GH, S, US).

Coccoloba krugii resembles *C. praecox* of Cuba and *C. buchii* of Hispaniola. It can be distinguished from these species by the angular rachis of the inflorescence and the angularity of the fruit.

Coccoloba børgesenii was described by Schmidt as having a puberulent rachis to the inflorescence. This "puberulence" appears to be a mixture of fungal hyphae, crystals of mercuric chloride and fibers of pressing material. *Coccoloba børgesenii* forma *ovato-lanceolata* is based on a specimen representing the adventitious shoots of this species.

Coccoloba krugii Lind. × **Coccoloba uvifera** L.; Howard, Jour. Arnold Arb. **38**: 216, 217. 1957.

Coccoloba scandens Ekman, Bull. Estac. Bot. Moca, Ser. B. **17**: 14. 1927, nomen.

Shrub of 6 feet or small tree with habit of *Coccoloba uvifera*; young branches terete, striate, puberulent to pubescent; ocreae membranaceous, oblique and slightly flaring at the apex, 1–1.5 cm. long, puberulent to pubescent; leaves of normal shoots on petioles 7–10 mm. long, the blades ovate to ovate-elliptic, 6 × 3, 8 × 6, 11 × 8 cm. long and broad, the apex obtuse to broadly rounded, rarely acuminate with an obtuse point, the base oblique, cordate to rounded, one basal lobe often overlapping the petiole; midrib and veins prominent below, sub-prominent above when dry, the ultimate venation reticulate, the primary veins 6 or 7, arcuate and anastomosing near the margin, 2 or 3 veins close to the base of the blade; leaves of adventitious shoots on petioles 7–10 mm. long, the blades ovate, ovate- elliptic or rarely ovate-lanceolate, 14 × 8 to 29 × 18 cm. long and broad; inflorescence simple, terminal, to 20 cm. long, the rachis slender, puberulent becoming glabrate; bracts broad, triangular-ovate, puberulent, the ocreolae membranaceous, to 1 mm. long, puberulent, the pedicels shorter than the ocreolae; staminate flowers 2–4 per locus, the pistillate flowers solitary at the nodes, the hypanthium to 1 mm. long, the perianth lobes orbicular, 1.5–2 mm. long and broad, the filaments of fertile stamens 2 mm. long; pedicels in fruit equalling to twice as long as the ocreolae, the fruit fusiform to fusiform-ovoid, 11 mm. long, 8 mm. in diameter, the perianth lobes not coronate.

DISTRIBUTION: Puerto Rico, Virgin Islands, Hispaniola.

Dominican Republic. PROV. MONTE CRISTI: Los Siete Hermanos, *Howard 12524* (GH), *12525* (GH), *12526* (GH), *12527* (GH), *12528* (GH), *12529* (GH); *Ekman H-13164* (S, US).

Haiti. DEPT. DU NORD OUEST: Tortue Island, La Vallée, *E.C. & G.M. Leonard 15352* (US), *11320* (A, NY, US); Boucan-Guepes, *Ekman H-9732* (S, US); Mare-Rocher, *Ekman H-4122* (S, US); Môle St. Nicolas, *E.C. & G.M. Leonard 13183* (MO, US), Port de Paix, *E.C. & G.M. Leonard 11180* (NY, US), *Ekman H-3935* (S).

This hybrid was recognized and described originally in relation to material from Puerto Rico and the Virgin Islands. Subsequent study of these troublesome populations and of the several series of collections cited above have shown additional and isolated occurrences of this hybrid in Hispaniola.

Ekman first discovered one population in 1925 on Ile de la Tortue and suggested in his field notes that it was a new species related to *Coccoloba uvifera*. A few days later he encountered it again along the sea coast west of Saline Michel near Port de Paix and indicated in his field notes that while sterile it was not the same as the Tortue plant and that it was "not *C. uvifera*, by no means." Schmidt annotated these specimens as *C. verruculosa* Lindau; Leonard, who collected in the same areas, also found the plant and used the same species identification. In 1929 Ekman visited Monte Grande in the Los Siete Hermanos island group off Monte Cristi and collected the plant there. In his field notes he identified the plant as *C. verruculosa* again, but comments, "I am beginning to feel suspicious about this. It is altogether too widely distributed and common to have escaped notice of the old collectors; e.g., Jacquin. How about

C. leoganensis?" In a brief published report of this last island trip Ekman refers to the occurrence of "*Coccoloba scandens*" on Monte Grande. *Coccoloba scandens* is published without description and, in any case, is a later homonym of *Coccoloba scandens* Benth., also a nomen nudum. The epithet "scandens" however was particularly appropriate, for several of the plants seen on Monte Grande had scrambling branches. As was true with populations of this hybrid in Puerto Rico and the Virgin Islands, there is a considerable range of variation between plants, accentuated in some cases by the normal variation between adventitious and juvenile shoots and those of more mature plants.

Coccoloba krugii, one of the suggested parents of this hybrid, is present on Tortue Island, Môle St. Nicolas and near Port de Paix where the hybrid has been collected. It was not found on any of Los Siete Hermanos, but occurs on El Morro near Monte Cristi. *Coccoloba uvifera* has been found in all locations where the hybrid occurs.

Coccoloba leoganensis Jacq. Enum. 19. 1760; Hist. Stirp. 113. pl. 178, f. 33. 1763; Pl. Amer. Pict. t. 60, f. 30, 1780.

Coccoloba rotundifolia Meisn. DC. Prodr. **14:** 154. 1857.
Coccoloba uvifera var. *leoganensis* Willd. Sp. Pl. **2:** 457. 1799.

Small tree to 20 feet tall, d.b.h. 6 inches; branches generally tortuous, striate, minutely pubescent, the nodes slightly swollen; ocreae 6 mm. long, membranaceous, minutely puberulent, obliquely truncate, light gray-green; leaves of normal shoots with petioles 7–15 mm. long, puberulent, swollen at the base, arising from the bases of the ocreae; blades orbicular, 3 × 3, 5 × 6, 7.5 × 8 to 9 × 9 cm. long and broad, subcoriaceous, glabrous above, glabrate below or with pubescence in axils of veins or along the midrib, the apex rounded, emarginate or obtusely short acuminate, the base shallowly cordate, the margin entire but generally slightly undulate; midrib and primary veins evident above and only slightly conspicuous below, the primary veins 5–7 pairs, the secondary venation evident but not conspicuous; fast-growing shoots not seen; adventitious shoots from trunk of tree slow-growing, tortuous and flattened, the leaf-bearing branches terete; leaves with petioles 2–3 mm. long, the blades similar in shape to those of normal branches 0.4 × 0.4 to 1.2 × 1.5 cm. long and broad; inflorescences terminal, 5–7 cm. long, the basal ocreae to 1 cm. long, the rachises puberulent, densely flowered, commonly thin to tenuous in flowering condition becoming thick in fruiting condition; staminate flowers 1–3 at each locus, the pistillate flowers generally borne singly at each locus, the bracts ovate, to 1.5 mm. long, the ocreolae 1–1.5 mm. long, membranaceous, puberulent; pedicels 1.5–2.0 mm. long, puberulent, articulated at the base and dehiscent after flowering, the flowers articulated, the hypanthium 1 mm. long, commonly narrowed to the pedicel, the perianth lobes broadly orbicular, 2–3 mm. long and broad, the functional stamens 1–1.5 mm. long, the fertile pistil 2.5 mm. long, the sterile stamens and pistils abortive, to 0.5 mm. long; fruit ovoid, 4.5 mm. long, 3.5 mm. in diameter, narrowed at the base, the fruiting perianth red in color, the lobes tightly imbricate, longer than the hypanthium; achenes obtusely 3-angled, greenish brown.

LOCAL NAMES: *Uvero* (DR), *uvilla* (DR).

DISTRIBUTION: Endemic to Hispaniola.

Dominican Republic. DISTRICTO DE SANTO DOMINGO: Ciudad Trujillo, *Schiffino 164* (GH). PROV. BARAHONA: Along the Rio Yaque, *Fuertes 188* (BM, C, EDIN, F, GH, K, M, MO, NY, S, US). PROV. INDEPENDENCIA: Puerto Escondido, *Howard 12185* (GH). PROV. LA VEGA: Cuesta de Piedra, *Eggers 2376* (BM, GH, K, M, NY, US). PROV. LIBERTADOR: Between Restauración and Bánica, *Howard 12555* (GH). PROV. MONTE CRISTI: Copey, *Howard 12522* (GH); Villa Isabela, *Howard 12521* (GH). PROV. SANTIAGO: Santiago to Quinigua, *Eggers 2429* (A, B, C, US); Sabaneta, *Jiménez 1737* (GH). PROV. TRUJILLO-VALDEZ: Bani, *Howard 12045* (GH), *12048* (GH).

Haiti. DEPT. DU NORD OUEST: Port de Paix, Vallée des Trois-Rivières, *Ekman H-3991* (S, US); Bassin Bleu, *E.C. & G.M. Leonard 14603* (A, NY, US), *14782* (US); Cabaret, Baie des Moustiques, *E.C. & G.M. Leonard 11820* (MICH, US), *12051* (A, GH, K, MO, NY, US); Jean Rabel, *E.C. & G.M. Leonard 12071* (GH, US). DEPT. DE L'ARTIBONITE: Gonaives, *Buch 654* (B); Gonaives to La Hotte Roche, *Nash & Taylor 1586* (NY); Gonaives to La Branle, *Nash & Taylor 1592* (NY, US). DEPT. DE L'OUEST: Between Port-au-Prince and Léogane, *Jacquin s.n.* (BM-holotype); Port-au-Prince, *Ekman H-2110* (S); Montagnes du Trou d'Eau, Morne à Cabrits, *Ekman H-990* (A, S, US); Ile de la Gonave, Pte. à Raquette, *Eyerdam 54* (A, F, GH, MO, NY, US); Petit Gonave Island, *Leonard 5233* (NY, US). DEPT. NOT KNOWN: Cape Francois, *Ehrenberg s.n.* (B, G-type of *C. rotundifolia*, NY).

Jacquin's descriptions of *Coccoloba leoganensis* are brief and the illustration cited above is of a single leaf which lacks any distinctive characteristics. All authors since Jacquin have referred *C. leoganensis* to the synonymy of *C. uvifera*. Willdenow established *C. leoganensis* as a variety of *C. uvifera* and Meisner accepted this placement, but with a query. Mr. Dandy, of the British Museum, kindly determined for me that the Jacquin specimen was there and verified the similarity to *C. rotundifolia*. I have since had the opportunity of seeing the material myself and it seems that at last the elusive name "*leoganensis*" can be properly placed. It certainly did not seem reasonable to me that Jacquin could not distinguish *C. uvifera* from other species.

The species *Coccoloba rotundifolia* Meisner was compared originally by the author with *C. leoganensis* and distinguished on the basis of smaller leaves. While Meisner did have a specimen from the smaller end of the range in size, his material can easily be matched with the more abundant specimens cited above.

Coccoloba leoganensis is a distinctive species both as living plants and as herbarium specimens. The habit of the plant, a low, densely branched and rounded or flat-topped tree is striking. When in full flower the plants seen attract thousands of bees, so that collecting specimens becomes almost too competitive. In this species alone among those known from the Greater Antilles, the pedicels absciss immediately after flowering in the staminate inflorescences, and, if fertilization has not been effected, in the pistillate. A staminate inflorescence may have a few fully mature flowers at the apex and be naked and pitted below where flowers had been. This is particularly noticeable in fresh condition.

The fruits are described here for the first time. They are bright red in color and astringent, without any pleasant taste. The fruit is constricted at the base to a short stalk. The fleshy perianth lobes surround the achene tightly with only three lobes visible on the surface. The bracts and ocreolae enlarge slightly in fruit. This combination of characters would place the present species in the section *Campderia* of Lindau's classification. In total aspect the fruiting inflorescence resembles that of *Coccoloba nivea*, currently the only other West Indian species in this section.

Considerable individual variation in the amount of pubescence on the lower leaf surface was also noticed in living specimens in the field. The majority of mature leaves had a small amount of pubescence in the axils of the lateral veins on the lower leaf surface and additional pubescence along the midrib. On other plants the leaves were entirely glabrous below.

Perhaps the most unusual feature of *Coccoloba leoganensis* is the size of the leaves produced by lateral and adventitious shoots. Root sprouts and lateral stem sprouts were found on a number of trees near Bani in the Dominican Republic. This was the largest stand of *C. leoganensis* seen and here the species was the dominant tree in the dry thorn-shrub region at kilometer 80. The sprouts produced near the base of the trunk and on the trunk of these trees were short, compacted and contorted, in contrast to the normal elongate, fast-growing trunk sprouts of other species. In addition, the leaves are exceedingly small, ranging in size from 4 × 4 mm. to 12 × 15 mm. on petioles 2-3 mm. long. The leaves of these sprouts were generally orbicular and rounded at the apex, although some were ovate and obtuse at the apex. These sprouts all resembled *C. subcordata*. Careful attention was required to determine that these were parts of the plant of *C. leoganensis*. Even now, in dealing with the herbarium specimens, it has been necessary to recheck field notebooks to make certain that this point had been determined in the field and that the labels were not in error. Several of Leonard's collections (*12071*, *11820* and *14603*) posed the same problem, although they had leaves grading to a larger size. In all of these collections, the petioles arise from the base of the ocreae, as in *C. leoganensis*, and not from the apex of of the ocreae, as in *C. subcordata*. *Coccoloba subcordata* has an entirely distinct habit in the field and has short inflorescences, but in sterile herbarium specimens that two may well be confused. This is the only species of *Coccoloba* so far encountered in which the leaves of the sprout shoots are smaller instead of larger than the leaves of mature branches.

Coccoloba leonardii Howard, Jour. Arnold Arb. **30**: 419. 1949.

Tree to 30 feet tall; branches terete, the nodes only slightly tumid, glabrous; ocreae subcoriaceous, the persistent part 3 mm. long, glabrous; leaves of normal shoots with petioles 8–11 mm. long, glabrous, arising about 0.5 mm. above the bases of the ocreae, the blade ovate, 6.5 × 4, 8 × 5.5 to 11 × 7 cm. long and broad, coriaceous, the apex rounded to acute, the base rounded to slightly cordate, unequal, usually slightly decurrent on the petiole, the margin entire, flat; midrib not conspicuous above, the primary veins 5–7 pairs, ascending, arcuate, anastomosing near the margin, the ultimate venation reticulate, leaf surface glabrous, drying to a chestnut brown or ash color, the blocked stomata as seen on the lower surface brown in color; leaves of adventitious or fast-growing shoots elliptic, rounded or apiculate at the apex, often strongly cordate at the base, not larger than leaves of normal shoots in material seen; inflorescences terminal, 5.5–10 cm. long in fruit; staminate flowers 2–4 at each locus, the pistillate flowers solitary at each locus, the bracts 0.5 mm. long, the ocreolae about 1 mm. long, the pedicels short, less than 0.5 mm. long in fruit; hypanthium 0.5–1 mm. long, the perianth lobes 1.5 mm. long and broad, the fertile stamens 1 mm. long, the fertile pistil 2 mm. long, the sterile stamens and pistil rudimentary, less than 0.5 mm. long; fruit broadly fusiform, 10–11 mm. long, 5–7 mm. broad, the perianth lobes slightly coronate, these 1 mm. long, many-ribbed, drying black above and reddish brown below, the achene elongate, dark brown and shiny.

DISTRIBUTION: Haiti and Cuba.

Haiti. DEPT. DU NORD OUEST: Tortue Island, Basse Terre, *E.C. & G.M. Leonard 12466* (A-holotype, MO, NY, US), La Vallée, *E.C. & G.M. Leonard 11335* (MICH, US), *11381* (A, GH, K, US), *11421* (NY, US), *11423* (G, US); Pte. Petite Bois, *Ekman 4150* (S), Saline Michel near Port au Paix, *Ekman 3931* (S). DEPT. DU NORD: Morne la Vigie, Cap Haitien, *Ekman 2706* (S, US); Bayeux, *Nash 293* (F, NY). DEPT. DU SUD: Navassa Island, *Ekman 10843* (S, US).

Coccoloba microstachya Willd. Sp. Pl. **2**: 459. 1800; Lindau, Engl. Bot. Jahrb. **13**: 146. 1890; Howard, Jour. Arnold Arb. **37**: 332. 1956, **38**: 217. 1957.

Coccoloba klotzschiana Meisn. DC. Prodr. **14**: 155. 1856.
Coccoloba obtusifolia Lindau, Symb. Antill. **1**: 22. 1899, not Jacquin.

Shrub or tree to 20 feet tall; branches terete, the nodes tumid, pubescent or with hair primordia, the bark gray to tan in color; ocreae membranaceous, cylindrical, pubescent, 4 mm. long; leaves of normal shoots with petioles 3–6 mm. long, pubescent, arising from the bases of the ocreae; blades variable in size and shape, ovate, ovate-lanceolate, oblong or elliptic, 3.5 × 1.5, 4 × 2, 5.5 × 3.5 to 7 × 4 cm. long and broad, thin-coriaceous, usually turning black on drying, the apex acute, acuminate, rounded or emarginate, the base narrowed, rounded or slightly cordate, the margin entire; midrib and vein evident but not conspicuous above, prominent below, primary veins 7–9 pairs, all glabrous above, pilose or glabrate below rarely persistently and densely pubescent; leaves of adventitious shoots on petioles to 7 mm. long with blades ovate-lanceolate to oblong, reaching 12 × 2.5 or 17 × 4 cm. long and broad, these generally more pubescent than leaves of mature shoots; inflorescence terminal, 5–10 cm. long, the rachis usually pubescent, tenuous, often geniculate, commonly recurved; staminate flowers 2 at each locus, the pistillate flowers solitary at each locus, the bracts broadly ovate, to 0.5 mm. long, puberulent, the ocreolae membranaceous, puberulent, to 0.5 mm. long, erect on the staminate plants, generally appressed or flattened on the pistillate, the pedicels shorter than the ocreolae or lacking, the hypanthium less than 1 mm. long, the perianth lobes 1–1.5 mm. long and 1 mm. wide; fruit sessile, generally ovate with distinctly coronate perianth lobes, to 6 mm. long and 4 mm. in diameter.

DISTRIBUTION: Dominican Republic, Puerto Rico, St. Thomas, St. Jan, Tortola, Virgin Gorda, Anguilla and St. Croix.

Dominican Republic. PROV. ALTAGRACIA: La Romana, *Ekman H-12098* (S, US). PROV. MONTE CRISTI: summit of El Morro, *Howard 12537* (GH). PROV. PUERTO PLATA: Puerto Plata, at La Boca, *Ekman H-14381* (A, S, US); Puerto Plata at Arroyo Francés, *Ekman H-14400* (S, US); between Puerto Plata and Maimon, *Eggers 2674* (B, M). PROV. SAMANÁ: Cabo Samaná, *Ekman H-14905* (S); Santa Barbara de Samaná, *Ekman H-15322* (B, S).

The variation in the size and shape of leaves and the amount of pubescence on plants of this species has been discussed in earlier papers in relation to *Coccoloba swartzii.* The few specimens from the Dominican Republic cited above represent nearly the extremes of variation. Most unusual is the shape of the leaves of adventitious shoots in several specimens. These are oblong — nearly linear-oblong — in shape. A similar variation also occurs in *C. costata* on the adventitious shoots of plants from the Samaná peninsula and from the eastern end of the island of Hispaniola.

Coccoloba nodosa Lindau, Engl. Bot. Jahrb. 13: 147. 1890.

Uvifera nodosa Ktze. Rev. Gen. 2: 561. 1891.

Small tree or bush 10–15 feet tall; branches of mature plant conspicuously nodose with short internodes, the branchlets often moniliform where leafless, sparsely short pubescent with golden to chestnut hairs; ocreae membranaceous, 3 mm. long, the apex acute, short pubescent; leaves of normal shoots with petioles 2 mm. long, puberulent, arising from the bases of the ocreae, the blades obreniform, orbicular or oblate, 0.5 × 0.9, 1 × 2 to 2 × 2.5 cm. long and broad, coriaceous, generally drying black, sparsely short pubescent on both surfaces becoming glabrate, the apex broadly and shallowly emarginate or truncate, the base cuneate or rounded, the margin entire and flat, the blade flat; primary veins 3–5 pairs, mostly straight to the margin, then bifid and anastomosing, the venation evident above but slightly prominent below; adventitious shoots with nodes slightly swollen but not bead-like, the internodes striate, all densely ferruginous short-pilose, the ocreae 6–8 mm. long, deeply bilobed at the apex, membranaceous and deciduous above, chestnut-colored and pubescent, persistent below, this portion gray-green in color, the leaves with petioles 2–4 mm. long, densely gray pilose, arising from the bases of the ocreae, the blades cordate to ovate, to 6.5 cm. long and 5 cm. broad, the apex acute to obtuse, the base cordate to truncate, the margin undulate, the lateral branches of such shoots producing normal-sized leaves; inflorescence terminal 4–10 mm. long, puberulent to glabrous, the bracts triangular, membranaceous, to 1 mm. long, the ocreolae membranaceous, less than 1 mm. long; staminate flowers 1–3 at each locus, the pedicels 1 mm. long, the hypanthium 0.5 mm. long, the perianth lobes broadly ovate to orbicular, 1–1.5 mm. in diameter, the stamens 1–1.2 mm. long, the pistil rudimentary, less than 0.5 mm. long; pistillate flowers and fruit not known.

DISTRIBUTION: Endemic to the Dominican Republic.

Dominican Republic. DISTRICTO DE SANTO DOMINGO: Llano Costero, El Manielito, *Ekman H-11289* (A, S, US); Llanura de Santo Domingo at Las Rosas, *Ekman H-5804* (S); La Yuca, *Jiménez 3401* (A); on road from Santo Domingo City (Ciudad Trujillo) to Puerto Plata, *Wright, Parry and Brummel 475* (GH, NY, US). Without specific location: *Bertero 928* (B-type, M), *R. Schomburgk 65* (B).

Until recently I had considered the sterile collection *Ekman 5809* to represent the adventitious shoot condition of this species. Several months ago Dr. José Jiménez of the Dominican Republic sent for identification a small specimen of *Coccoloba* which I assigned to this species. Since I had not been able to locate plants of this species during several visits to the Dominican Republic, I asked Dr. Jiménez to obtain additional material to show all possible leaf variation in this plant. Such specimens were collected for me by Professor Marcano of the Instituto Botanico "Rafael M. Moscoso" and were forwarded by Dr. Jiménez. I am indebted to both gentlemen for the material essential to a better understanding of leaf variation in *Coccoloba nodosa.* Unfortunately, the plants under observation have not flowered and hence several details of the description remain uncompleted.

Coccoloba nodosa may eventually include *C. picardae.* When Urban described the latter species he disinguished between them on the basis of the swollen nodes and obtriangular leaves of *C. nodosa.* He also noted that the flowers are in multiples in *C. nodosa.* This aggregation of flowers or pedicels is usually found in the staminate flowers, while the pistillate flowers are borne singly at each locus on the rachis. On the basis of normal shoots the leaves of *C. nodosa* and *C. picardae* are similar; however, until pistillate flowers and fruits are obtained for *C. nodosa* and adventitious shoots for *C. picardae,* the species should be kept distinct. *Coccoloba* *nodosa* has been collected at lower elevations while *C. picardae* has been found only at elevations above 5000 feet.

Coccoloba pauciflora Urban, Symb. Antill. 7: 209. 1912.

Coccoloba neurophylla Urban, Fedde Rep. Spec. Nov. **19**: 1. 1923; Ark. Bot. **20A**(15): 30. 1926.
Coccoloba mornicola Urban, Fedde Rep. Spec. Nov. **13**: 446. 1914; Ark. Bot. **20A**(15): 30. 1926.
Coccoloba fulgens Leonard, Jour. Wash. Acad. Sci. **17**: 66. 1927.
Coccoloba nalgensis Schmidt, Fedde Rep. Spec. Nov. **32**: 80. 1933.

Shrub or tree to 28 feet tall; branches terete, the nodes not swollen, short ferruginous pubescent, almost pilose or becoming glabrous, the hair bases and the often resinous stomatal excretions frequently resembling peltate scales; ocreae membranaceous, 3–8 mm. long on normal shoots, oblique at the apex, ferruginous pubescent; leaves of normal shoots with petioles 2–10 mm. long, generally pilose at least on the adaxial surface, arising at the bases of the ocreae, the blades obovate to obovate-elliptic, 1.5 × 0.8, 2 × 1.4, 3 × 1.5, 4 × 2 to 5 × 3 cm. long and wide, subcoriaceous, glabrous or with conspicuous or inconspicuous stomatal excretions, the apex rounded to shortly and abruptly acuminate, occasionally truncate, often asymmetrical, the base cuneate; primary veins 3–5 pairs, prominent on both surfaces when dry; adventitious shoots terete, the ocreae to 1.5 cm. long, conspicuously ferruginous pilose or puberulent, the leaves with petioles 1.3–1.7 cm. long, the blades ovate-elliptic to ovate-lanceolate and 17 × 9 or 14.5 × 8 cm. long and broad, these broadly cuneate to acute at the base, broadest below the middle and acuminate at the apex, or blades obovate to obovate-lanceolate to 14 × 7 cm. long and wide, these broadest above the middle, cuneate at the base and acute at the apex; inflorescences terminal on axillary shoots of varying lengths and ages, the youngest often appearing as axillary clusters of flowers, the axis 2–3 rarely 4 cm. long, densely ferruginous pilose or puberulent at the base or, when young, soon becoming glabrate, the bracts broadly triangular, puberulent, the ocreolae 0.5–0.75, rarely 1 mm. long, tubular and not spreading; pedicels 1 mm. long in flower, those bearing staminate flowers increasing to 2 mm. long before or after abscission of flowers; staminate flowers in clusters of 2–3, the pistillate flowers borne singly at each locus; hypanthium 0.5–0.75 mm. long, the perianth lobes orbicular, 1–1.5 mm. long and broad, the functional stamens 1.2–1.4 mm. long, the sterile stamens less than 1 mm. long, the functional pistil 2 mm. long, the abortive pistils less than 0.5 mm. long; fruit brilliant to dull red when fresh, reddish brown when dry, ovoid to pyriform 6–7 mm. long, 4–5 mm. in diameter, slightly coronate at the apex, the fruiting hypanthium extending above the middle, the lobes of the perianth imbricate and covering the achene at the apex; achene chestnut-brown.

DISTRIBUTION: Endemic to Hispaniola.

Dominican Republic. PROV. BARAHONA: El Aguacate to crest on road to

Pedernales, *Howard 12572* (GH), *12586* (GH); La Tierra Fria, *Howard 12210* (A); Polo, *Howard 12239* (GH). PROV. LA VEGA: Constanza, *Türckheim 2955* (B-lectotype, M, NY). PROV. SAMANÁ: Samaná, Laguna, Los Bañaderos Prietos, *Ekman H-15135* (S, US). PROV. SAN RAFAEL: Loma Nalga de Maco, *Ekman H-6322* (B-holotype of *C. nalgensis*, S, US). PROV. SANTIAGO RODRIGUEZ: Monción, *Ekman H-12085* (B, S, US).

Haiti. DEPT. DU NORD OUEST: Massif du Nord, Port de Paix, Haut Piton, *Ekman H-3697* (B, S, US); Bassin Bleu, Morne Haut Piton, *E.C. & G.M. Leonard 15043* (A, GH, US), *15046* (MO, NY, US), *15064* (US). DEPT. DU NORD: Massif du Nord, Bayeux, Morne Brigand, *Ekman H-2853* (S, US). DEPT. DE L'ARTIBONITE: Ennery, Puilboreau Pass, *Leonard 9145* (B, GH, NY, US-type of *C. fulgens*); Massif du Nord, Gros Morne, Morne Belance, *Buch 811* (B-type of *C. mornicola*), *Ekman H-4910* (S). DEPT. DU SUD: Massif de la Hotte, Nouvelle Touraine, *Ekman H-1657* (A, S). DEPT. DE L'OUEST: Massif de la Selle, Morne Tranchant near Godet, *Ekman H-1953* (S); Massif de la Selle, Petionville, *Ekman H-1657* (US); Massif des Matheux, Grand-Bois, Cornillon, *Ekman H-5686* (S, US); Massif de la Hotte, Petit Goave, road to Morne Calumette, *Ekman H-7304* (S); Fond Verettes, *Leonard 5347* (B-type of *C. neurophylla*, US).

To the present, *Coccoloba pauciflora* has been represented only by the original collection of Türckheim; *Coccoloba nalgensis*, also, is known from the type collection alone and the several collections cited above, assigned indiscriminately to either *C. mornicola* or *C. neurophylla*. Both *Coccoloba mornicola* and *Coccoloba neurophylla* were described on sterile material and in each case Urban published a note adding to the description when additional material became known. Unfortunately, the additional material has been staminate in the case of *C. mornicola* and pistillate in the case of *C. neurophylla*. Here again arises the necessity of combining names and species based on the erroneous idea that the flowers are perfect. The study of a considerable number of plants and populations of this species in the Dominican Republic has allowed me to describe the range of variation found in the leaves, pubescence and inflorescence of this species.

Coccoloba pauciflora was so named for the short inflorescence axis and the few flowers produced. The nature of the leaf margin was also a characteristic which Urban used in describing the plant. It is possible to find short inflorescences at the top of many plants where the inflorescences terminate axillary branches. At a lower level in the tree, however, the lateral branches, which are little more than short shoots, have elongated slightly and the inflorescence produced is longer.

Leaf variation is considerable, both within a population and on the same plant, as to size, texture and apex. The shape of the leaf apex is related either to the development of the midrib or to its failure to develop at the apex. Three conditions are found on different plants, or on the same tree on one branch, or on different branches: (1) the midrib can be uniformly developed to the apex, in which case the tip of the blade is acuminate; (2) the midrib may apparently fail to develop at the apex of the blade, in which case this area is vascularized by the upper pair of primary veins; or (3) a remnant of the midrib may be present or absent. In this situation the apex of the leaf is obtuse or rounded.

In the third condition observed, the midrib fails to develop to the tip of the blade and one of the upper pair of primary veins dominates the other. In this case the leaf apex is asymmetrical. Examples of the three types of leaf apices on one plant are found in the collections of *Ekman H-2853, H-1657* and *Howard 12586*, the latter collected especially for this purpose.

The smaller range of leaf variation in this species is represented by the specimen *Ekman H-6322* which Schmidt selected as the type of his *Coccoloba nalgensis*. The herbarium sheets of this collection bear an unpublished specific name based on the province of Azua where, it is said, this collection was made. Loma Nalgo de Maco, as now known, is in San Rafael Province. While Schmidt describes the leaves as 1–2 cm. long and 0.8–1.2 cm. wide, the majority of the leaves on the three examples of this number are at the smaller end of the range given. Several more recent collections (e.g., *Ekman H-12805* and *Howard 12572*) are intermediate between the type collection of *C. nalgensis* and the majority of the specimens cited above. One collection (*Howard 12572*) consists of several specimens from a single tree made to show a full range of variation from the smallest leaf and shortest inflorescence to the larger ones more typical of the expanded species concept here employed. Unfortunately, this single tree did not have any adventitious shoots. Plants of this series approach *C. picardae* in form and it is possible that additional collections will demonstrate that *C. picardae* should be included in this species, in which case *C. picardae*, the earlier name, must be used.

Several excellent examples of plants with well developed adventitious shoots were found in the mountains around Barahona. One of these (*Howard 12239*) was a 25-foot tree in full flower. Several of the lateral branches possessed side shoots with normal leaf size and shape (obovate with a rounded apex 3 cm. long and 1.5 cm. wide), while the apex of the branch had longer internodes and larger leaves, some of these reaching a length of 10 cm. and a width of 4 cm. Strict adventitious shoots arising from the base of this tree were wand-like with long internodes and obovate leaves 14 cm. long and 7 cm. wide above the middle. A second plant in the same general area was growing on a steep hillside and at an angle. The tree was sterile but the apex of the plant had branches with obovate leaves averaging 3.7 cm. long and 1.7 cm. wide with acute to acuminate apices. From the trunk of this plant were developed numerous adventitious shoots, these all arising vertically and at an angle to the tree. The leaves on these adventitious shoots were ovate-elliptic to ovate-lanceolate and broadest at or slightly below the middle. The leaves ranged to 17 cm. long and 9 cm. wide. They were broadly cuneate to acute at the base and acuminate at the apex. The contrast between the normal foliage and that of the adventitious shoots was startling when seen in the field and was almost unbelievable when the herbarium specimens were studied in the laboratory.

An Ekman collection from the Samaná peninsula is referred here. Although it is sterile and represents an adventitious shoot, it matches the material of *Howard 12239*. Schmidt studied this collection and referred to it as "*C. subtruncata* forma." Neither *C. pauciflora* nor "*C. subtruncata*" have been reported from the Samaná peninsula.

Coccoloba picardae Urban, Symb. Antill. **5**: 336. 1907.

Shrub to tree of 30 feet; branches terete, the nodes not swollen, short ferruginous-pubescent becoming glaborous, the branchlets often arranged in one plane; ocreae short, 1–2 mm. long, ferruginous-pubescent; leaves of normal shoots with petioles 1.5–2 mm. long, almost villose pubescent on the adaxial side, arising from the bases of the ocreae; blades orbicular to obtriangular, 1.1 × 1.2, 1.6 × 1.2, 1.7 × 1.7 to 2.5 × 2.5 cm. long and broad, coriaceous, stiff and rigid even when fresh, stomatal excretions evident on the lower surface, the apex rounded, subtruncate to submarginate, often asymmetrical, the base rounded, to subtruncate or narrowed and nearly cuneate, the primary veins 3–4 pairs, the venation reticulate and conspicuous on both surfaces when dry; adventitious shoots or leaves not known; inflorescences terminal on lateral short branches, often appearing capitate, the rachis 2–5 mm. long, the bracts broadly triangular 0.5–1 mm. long, the ocreolae to 1 mm. long, the pedicels 0.5–1.4 mm. long; staminate flowers 1–2 per locus, the pistillate flowers 1 at each locus, the hypanthium to 0.5 mm. long, the perianth lobes suborbicular 1.2–1.4 mm. long and broad, the fertile stamens 1–1.5 mm. long, the sterile stamens 0.5 mm. long, the functional pistil 1.5 mm. long, the pistillate rudiment less than 0.5 mm. long; fruit ovoid, 3–4 mm. long, 2–3 mm. broad, the hypanthium shorter than the lobes in fruit, the achene not coronate.

DISTRIBUTION: Endemic to Hispaniola.

Dominican Republic. PROV. BARAHONA: Crest of ridge between El Aguacate and Pedernales, *Howard 12594* (GH).

Haiti. DEPT. DE L'OUEST: Massif de la Selle, Petionville on top of Morne Tranchant, *Ekman H-1163* (S, US), *Picarda 784* (B-holotype), *Buch 1614* (B), *1663* (B), *Leonard 4385* (GH, NY, US); Guimbi Galata, Morne des Commissaires, *Holdridge 1280* (GH, NY, US).

This species is very similar to the small-leaved variation of *Coccoloba pauciflora* and may eventually prove to be part of the same complex. For the present, the two species can be distinguished on the basis of the very short inflorescences, the leaves broader than long, the non-coronate fruit and the single-plane branching of *C. picardae*.

Coccoloba pubescens L. Syst. Nat. ed. 10. 1007. 1759; Hooker, Bot. Mag. t. 3166. 1832; Fawcett & Rendle, Jour. Bot. **51**: 123. 1913; Howard, Jour. Arnold Arb. **38**: 227. 1957.

Scortea arbor Americana, amplissimis foliis, aversaparte nervis extantibus hirsutie ferruginea refertis; Plukenet, Phytographia t. 222, f. 8. 1691.

Coccoloba rubescens L. Sp. Pl. ed. 2. 523. 1762.

Coccoloba grandifolia Jacq. Enum. 19. 1760.
Coccolobis pubescens Sandwith, Jour. Bot. **78**: 98. 1940.
Coccolobis antiguensis Sandwith, Jour. Bot. **78**: 98. 1940.

Mature tree to 40 feet tall, d.b.h. 12 inches, much branched above a well defined trunk; branches terete, swollen at the nodes, the lenticels not conspicuous, tomentose to pilose; the ocreae to 1 cm. long, generally completely deciduous, pubescent; leaves of completely mature plants varying considerably in size and shape, the petioles 3–6 mm. long, inserted below the ocreae, densely short pubescent, the blades broadly orbicular to orbicular-ovate, 4 × 6, 7.5 × 10 cm. long and broad, grading into size of leaves of adventitious shoots, rugose or bullate, the apex rounded, the base cordate, the basal lobes rounded and only rarely approximate, sparsely pubescent above to glabrate, densely to sparsely pubescent below or glabrate, the margin undulate, the venation of 5 pairs of primary veins, arcuate to the margin, strongly anastomosing, slightly impressed above, conspicuous and reticulate below; adventitious shoots generally strict and sparsely branched, to 30 feet tall, the branches stout, terete, slightly swollen at nodes, strongly grooved or striate, the ocreae 2 cm. long, membranaceous and evanescent above, coriaceous and persistent below, the petioles stout 1–2 cm. long, densely tawny pubescent, the blades large, generally orbicular except for the terminal leaf, frequently broader than long, 30 × 40, 50 × 80 cm. long and broad, coriaceous, rugose or bullate when mature, thin and plane when young, the apex rounded, the base rounded to cordate, the basal lobes commonly encircling the stem, the terminal leaf commonly rhombic, longer than broad when mature, densely tomentose, the veins slightly impressed above, all venation conspicuous and reticulate below, the midrib and secondary veins persistent-pubescent above, the others sparsely pubescent when young, becoming glabrate above, the veins and leaf surface pubescent or becoming glabrate below, the margin irregular, commonly undulate; inflorescences terminal, often stout, the basal ocreae to 7 mm. long, membranaceous, the peduncle to 1.5 cm. long, the rachis minutely and often densely puberulent, 10–18 cm. long on mature shoots, to 45 cm. long on adventitious shoots, the bracts broadly ovate, about 1 mm. long, puberulent, the ocreolae membranaceous, spreading, 1 mm. long, minutely puberulent or glabrate; staminate flowers 2–4 per locus, the pistillate flowers 1–3 per locus, the pedicels 2–3 mm. long, the hypanthium 0.5–1 mm. long, the perianth lobes broadly orbicular, 1.5 mm. long, 2 mm. wide, puberulent, the fertile stamens 2.5 mm. long, the sterile stamens rudimentary, 0.5–1 mm. long, the fertile pistil glabrous or rarely slightly puberulent on the ovary, the sterile pistils glabrous, rudimentary, 0.5–1.5 mm. long; fruit globose to ovoid, 5–6 mm. long and 4–5 mm. in diameter, the fruiting perianth imbricate at the apex, not coronate, the fruiting hypanthium with conspicuous vascular bundles; achene sub-globose, dark brown, shining, slightly triradiate at the apex, the fruiting pedicels puberulent, 3–4 mm. long.

LOCAL NAME: *Gamelle* (H), *Hojancha* (DR).

DISTRIBUTION: Hispaniola, Puerto Rico, Barbuda, Antigua, Montserrat, Nevis, Guadeloupe, Dominica, Martinique, St. Lucia.

Dominican Republic. DIST. DE SANTO DOMINGO: Ciudad Trujillo, *Schiffino 137* (GH); Cuenca, *R.A & E.S. Howard 9884* (A). PROV. BARAHONA: El Caiman, between Enriquillo and El Can, *Howard 12187* (GH); Beata Island, *Howard 12352* (GH); Mare-à-Chat, *Ekman H-6947* (S, US). PROV. ESPAILLAT: Moca, *Eggers 2559* (B, GH, M, NY, US). PROV. INDEPENDENCIA: Between Puerto Escondido and Rancho Viejo, *Howard 12143* (GH). PROV. LIBERTADOR: Between Restauración and Bánica, *Howard 12569* (GH). PROV. PUERTO PLATA: Hoja Anchas, *Jiménez 2088* (A). PROV. SAMANÁ: Pilón de Azúcar, *Abbott 401* (US). LOCALITY UNCERTAIN: *Prince Paul s.n.* (M).

Haiti. DEPT. DU NORD QUEST: Bassin Bleu, *E.C. & G.M. Leonard 15199* (A, US); Môle St. Nicolas, *Ekman H-4489* (S). DEPT. DU NORD: Between Pignon and Hinche, *Holdridge 1272* (GH, US); Ranquitte, *Christ 2090* (B). DEPT. DE L'ARTIBONITE: St. Michel de l'Atalaye, *Leonard 7296* (NY, US); Hinche, *Ekman H-6142* (A, S, US). DEPT. DU SUD: Massif de la Hotte, Morne Rochelois, Charlier, *Ekman H-9035* (B, S), *H-9086* (S); Miragoane, *Eyerdam 396* (GH, NY, US); Port-à-Piment, *Ekman H-336* (S); Camp Perrin, *Ekman H-249* (S). DEPT. DE L'QUEST: Petit Gonave Island, *Leonard 5242* (S); montagnes du Trou d'Eau, Fond-des-Oranges, *Ekman H-2312* (S).

The variation in leaf shape and size in specimens of *Coccoloba pubescens* encountered in the herbarium and as seen in the field has been discussed in a previous paper (Howard, Jour. Arnold Arb. **38**: 229–231. 1957). These variations contrast the adventitious and juvenile shoot systems from those of mature trees. A greater proportion of the specimens cited above represents mature plants than would a comparable number of specimens from other islands. A similar observation was made in the field; i.e., the number of individuals of this species represented by mature plants was greater in Hispaniola than on other islands where the species seemed almost typified by the adventitious shoot condition of very large leaves. In most of Haiti and western Dominican Republic the plants of *Coccoloba pubescens* grew relatively unmolested. In eastern Hispaniola and on the other islands of the Antilles, mature or undisturbed specimens were rarely encountered and second-growth habit seemed most abundant. A population of this species near Cuenca was visited first in 1946 and at two five-year intervals since, but the plants, though larger and with some now in flower, retain the characteristic adventitious leaves.

One known hybrid of *Coccoloba pubescens* with *C. uvifera* is described in this paper and I have suggested the possible hybrid condition and origin of *C. fawcettii* and *C. ceibensis*, with *C. pubescens* as one of the parents of each.

Coccoloba samanensis Schmidt, Fedde Rep. Spec. Nov. 32: 81. 1933.

Small to medium-sized tree (fide Ekman); branches terete, lightly striate, puberulent, the nodes slightly swollen; ocreae 6–10 mm. long, membranaceous glistening, puberulent to glabrous; leaves of normal shoots with petioles 6–8 mm. long, puberulent with shining hairs, 6–8 mm. long, inserted at the bases of the ocreae; blades ovate to elliptic, rarely orbicular-ovate, 5 × 4, 7.5 × 5 to 7.5 × 8 cm. long and broad, coriaceous, apex obtuse, short and abruptly acuminate or rarely subtruncate, the base obtuse to slightly cordate, the margin entire, slightly revolute, the midrib impressed above, prominent below; the primary veins 6 or 7 pairs, inconspicuous above, prominent below, the ultimate venation minutely reticulate; leaves of adventitious shoots with petioles 1.4 cm. long, similar to those of normal shoots in shape, to 12 × 10 cm. long and broad; inflorescences terminal, 8–18 cm. long, the rachis glabrous, lightly puberulent to short pilose, the bracts broadly ovate, to 1 mm. long, the ocreolae membranaceous, flaring, 2- or 3-lobed, to 1 mm. long, puberulent; staminate flowers not known, the pistillate flowers on pedicels shorter than the ocreolae, the hypanthium 0.5 mm. long, the perianth lobes obovate to elliptic, 1.2 mm. long, puberulent, the stamens abortive, about 0.5 mm. long, the ovary to 1.5 mm. long; fruit ovate with conspicuous coronate perianth lobes, 3 mm. long and 3 mm in diameter, the vascular bundles conspicuously developed, the achene globular, smooth, tan in color.

DISTRIBUTION: Endemic to Hispaniola.

Dominican Republic. PROV. SAMANÁ: Los Haitises, Boca del Infierno, *Ekman H-15392* (S); Samaná, slopes of Pan de Azúcar, *Ekman H-15175* (A, B-type, S, US), *H-15095* (S); Samaná, Laguna, Los Bañaderos Prietos, *Ekman H-15125* (S).

This species is poorly known and is represented in large part by sterile material. The collection *Ekman H-15392* has a very few fruits in a packet and two other specimens possess a few flowers. In general appearance this species is similar to *Coccoloba costata*, although in the details of smaller fruits, the coronate perianth lobes and the sessile flowers, it is distinct from *C. costata*, as well as from other species of Hispaniola. This is one of the few species of *Coccoloba* with the leaves shiny on the upper surfaces when dry. The coloration of the vein pattern is conspicuous when dry, giving the impression of a minute network or reticulum.

Coccoloba subcordata (DC.) Lindau, Engl. Bot. Jahrb. **13**: 131. 1890; Symb. Antill. 7: 209. 1912.

Erythroxylon subcordatum DC. Prodr. 1: 575. 1824.

Low shrub to 6 feet tall with numerous arching branches, these branching in one plane, the short-shoots conspicuously developed, the branchlets terete, ferruginous pubescent, the nodes not enlarged; ocreae 2–5 mm. long, membranaceous, of uniform texture, obliquely truncate to slightly bilobed at the apex, appressed, minutely puberulent; leaves of normal shoots with petioles 1.5–2.5 mm. long, puberulent, arising from the upper portion of the ocreae, the blades broadly suborbicular to ovate, 2 × 2, 4 × 4, 11 × 10 mm. long and broad, subcoriaceous, glabrous above, glabrate below, rarely puberulent on the veins, commonly shining on both surfaces and slightly paler in color below, the apex rounded to emarginate, the base rounded to rounded-cordate, the margin entire, often slightly undulate, primary veins 3–5 pairs, occasionally clustered near the base, the veins forking and anastomosing near the margin, reticulate, only slightly prominent on both surfaces when dry; inflorescences terminal on lateral branches or short-shoots, 4–10 mm. long, the rachis puberulent or glabrate, the bracts short triangular to 0.5 mm. long, the ocreolae membranaceous, flaring at the apex, to 1 mm. long; pedicels solitary or rarely 2 in the axil of each bract, to 2 mm. long at maturity, the hypanthium tapering from the apex of the pedicel, about 0.5 mm. long, the lobes ovate, about 1 mm. long and broad; fertile stamens 1–1.5 mm. long, the filaments slightly united at the base, the sterile stamens aborted or rudimentary, less than 0.5 mm. long, the functional ovary strongly 3-angled; fruit broadly ovoid, broadest below the middle, 4 mm. long, 3–3.5 mm. in diameter, the fleshy perianth bright red, the perianth lobes ½–⅔ the length of the fruit, strongly imbricated, the achene pale tan in color.

DISTRIBUTION: Endemic to Hispaniola.

Dominican Republic. PROV. BARAHONA: Las Salinas, *Fuertes 822* (F, GH, US), *Howard 12060* (GH); Beata Island, *Howard 12488* (GH). PROV. BENEFACTOR: San Juan, Loma de Jayaco, *Ekman H-13471* (S, US). PROV. INDEPENDENCIA: Between Lake Enriquillo and Puerto Escondido, *Howard 12130* (G). PROV. NOT KNOWN: *Bertero s.n.* (B, G-type of *Erythroxylon subcordatum*, GH-photos, M).

Haiti. DEPT. DU NORD OUEST: Jean Rabel, *E.C. & G.M. Leonard 12761* (A, GH, NY, US); Presqu'ile du Nord-Ouest, Baie de Henne, *Ekman H-4536* (S, US). DEPT. DE L'ARTIBONITE: Gonaives, *Leonard 10058* (GH, NY, US). DEPT. DE L'OUEST: Cul de Sac east of Gautier, *Holdridge 1241* (GH, US), *1166* (GH, US); Fond Parisien, Étang Saumatre, *Leonard 4056* (C, GH, NY, US); Montagnes du Trou d'Eau, Morne à Cabrits, *Ekman H-1023* (A, S); Massif des Matheux, Magasin Carriès, *Ekman H-3302* (A, S, US).

The habit of this plant in the field is strikingly different from all other species of *Coccoloba* which I have encountered. The plant occurs as a low shrub in arid regions, especially in thorn-shrub zones. There is no single trunk to the plant, but numerous branches arise in a cluster and each branch-system arches. The lateral branches from the shoots are all arranged on two sides of the stem so that the aspect of the plant is of flattened leafy shoots.

There were no signs of damage to these plants seen in the field. Although the habit of the plant suggested that it consisted of adventitious shoots, no evidence of a central trunk was found. While all growth was slow on the plant, a few branches showed signs of more vigorously growing twigs. These possessed slightly longer internodes and leaves around 1 cm. in diameter. This relatively small-sized leaf blade was in contrast to the even smaller leaves of the rest of the plant. The secondary branches are characteristically short shoots of extremely slow growth with compacted nodes and no internodal regions.

The sterile herbarium specimens of *Coccoloba subcordata* are difficult to distinguish from the adventitious shoots of *C. leoganensis*. The flattened branches and the short shoots, as well as the petiole arising from the apex of the ocrea, enable one to distinguish this species from the adventitious shoots of *C. leoganensis* either in the field or in the herbarium, however.

The similarity in appearance of these two species is disturbing. *Coccoloba subcordata* was originally described by De Candolle as a questionable species of *Erythroxylon* and was based on a Bertero specimen. Martius (Abhdl. Bayr. Acad. 3: 303. 1841) suggested the correct affinity for the plant and Lindau transferred the species, publishing the new combination. Interestingly enough, several of the specimens cited above had been incorrectly referred to the genus *Erythroxylon*.

Coccoloba swartzii Meisner, DC. Prodr. **14**: 159. 1856; Lindau, Engl. Bot. Jahrb. **13**: 157. 1890; Howard, Jour. Arnold Arb. **30**: 420. 1949, **37**: 317–339. 1956.

Coccoloba swartzii var. (?) *portoricensis* Meisner, DC. Prodr. **14**: 160. 1856.
Coccoloba barbadensis Lindau, Engl. Bot. Jahrb. **13**: 148. 1890, not Jacquin.
Coccoloba diversifolia Lindau, Symb. Antill. **1**: 223. 1899, and most recent authors, not Jacquin.

Trees 24 to 60 feet tall, branches terete, the youngest puberulent, becoming glabrate, the nodes slightly tumid; ocreae 10–12 mm. long, the basal portion 3–5 mm. long, coriaceous, persistent, the upper portion membranaceous and deciduous, puberulent to glabrate; leaves of normal shoots with petioles 10–18 mm. long, puberulent or glabrate, the blades ovate to elliptic, 2.2 × 1.3, 7 × 5, 11 × 9, 15 × 7.5 cm. long and broad, coriaceous, usually turning black on drying, glabrous, having pit-like depressions on the upper surface and small glands on the lower surface, the apex acute, often rounded, the base narrowed, rounded or slightly cordate and usually oblique, the margin entire; midrib and veins inconspicuous or flat above, prominent below, the primary veins 6 or 7 pairs, arcuate, anastomosing, the secondary venation conspicuous, reticulate; leaves of adventitious shoots with petioles 1.5–2.5 cm. long, the blades generally ovate to lanceolate 23 × 8.5, 45 × 18.5, to 70 × 25 cm. long and broad, the apex acute to acuminate, the base rounded; inflorescences terminal, 10–15 cm. long, the rachis glabrous or with glandular exudate, rarely papillose; staminate flowers in clusters of 3–5 flowers at each node, tightly surrounded by membranaceous ocreolae which form a truncate cylinder after the flowers have fallen, the pistillate flowers borne singly at each node, the bracts ovate, 0.5 mm. long, the ocreolae 1–1.5 mm. long, membranaceous, the pedicels shorter than the ocreolae; hypanthium 0.5 mm. long, the perianth lobes 1–1.5 mm. long, the fertile stamens 1–1.5 mm. long, the sterile stamens rudimentary, 0.5 mm. long; fruit ovoid, 8–10 mm. long, 6 mm. diameter, the perianth lobes 1–1.5 mm. long and coronate in fruit; the achene dark brown.

DISTRIBUTION: Jamaica, Bahamas, Dominican Republic, Puerto Rico, St. Croix, St. Jan, Virgin Gorda, St. Thomas, Saba, St. Kitts, Montserrat, Antigua, Guadeloupe, Dominica, Martinique, St. Lucia and Barbados.

Dominican Republic. DISTRICTO DE SANTO DOMINGO: San Isidro, *Ekman H-11014* (A, S, US). PROV. PUERTO PLATA: Puerto Plata, *Wright, Parry and Brummel 472* (GH, US), *473* (GH, US). PROV. TRUJILLO: Villa Altagracia, *Taylor 414* (NY), *431* (NY, US), *433* (B, NY, US).

A full discussion of the variation in form of this species and the correct application of the names *Coccoloba barbadensis*, *C. diversifolia* and *C. swartzii* was published as the second paper of this series (Jour. Arnold Arb. 37: 317–339. 1956). If the var. *portoricensis* were recognized, the specimens seen from the Dominican Republic would be referred there. However, gradation from Puerto Rico to Jamaica, including this outlying population in the Dominican Republic, does not warrant the recognition of Meisner's variety.

Coccoloba uvifera L. Syst. Nat. ed. 10. 1007. 1759.

Polygonum uvifera L. Sp. Pl. 365. 1753.
Guaiabara uvifera House, Amer. Midl. Nat. 8: 64. 1922.

Tree of strand areas, 6–50 feet tall, the branches terete, stout, papillose to pilose, the nodes not tumid; ocreae rigid, coriaceous at the base, membranaceous at the apex, 3–8 mm. long, papillose to pilose; leaves of normal shoots with petioles stout, 7–10 mm. long, papillose to pilose, the blades orbicular to reniform, 6 × 8, 11 × 13, 13 × 18 cm. long and broad, thick and fleshy when fresh, coriaceous when dry, glabrous and minutely punctate on both surfaces, the apex rounded, truncate or emarginate, the base rounded to broadly cordate, one lobe often extending around the petiole, the midrib and primary veins prominent on both surfaces, frequently brightly colored when fresh, the primary veins 3–5 pairs, usually straight, bifurcate and weakly anastomosing near the margin, commonly barbate in the axils of the basal veins, the secondary venation minutely reticulate or obscure; leaves of adventitious shoots usually variable in size and shape, commonly obovate; inflorescences stout, 15–30 cm. long, the rachis puberulent; staminate flowers in clusters of 1–7, the pistillate flowers solitary at each locus, the bracts ovate, 1–1.5 mm. long, 2 mm. broad, puberulent, the ocreolae membranaceous, 1 mm. long, puberulent, the flowering pedicels 1–2 mm. long, the perianth yellow-white or greenish, the hypanthium 2–3 mm. long, the perianth lobes 4 mm. long, 3–4 mm. wide, the fertile stamens to 4 mm. long; fruiting pedicels 3–4 mm. long; fruit obpyriform, 1.2–2 cm. long, 8–10 mm. in diameter, narrowed at the base, rounded-truncate at the apex, the perianth lobes appressed against the apex of the achene, the perianth rose-purple when mature, the achene black.

LOCAL NAMES: *Raisin la mer* (H), *Uva caleta, Uva de mar, Uvero de playa, Uva de playa* (DR).

DISTRIBUTION: Along the shores of Florida, Bermuda and through the Caribbean Islands to Mexico, Central and South America. Spontaneous in Africa and the Pacific Islands.

Dominican Republic. PROV. LA ALTAGRACIA: Punta Macao, *Howard 9767* (A); east of Jovero, *Abbott 2878* (US); Llano Costero, Jaina, *Ekman 19475* (US). PROV. BARAHONA: Barahona, *Fuertes 247* (US), *1143* (F, GH, US); Beata Island, *Howard 12489* (GH); Alta Vela Island, *Howard 12453* (GH); El Caiman near Enriquillo, *Howard 12188* (GH), *12191* (GH). PROV. MONTE CRISTI: Los Siete Hermanos, Monte Grande, *Howard 12523* (GH). PROV. SAMANÁ: Samaná *Abbott 1187* (US).

Haiti. DEPT. DU NORD OUEST: Port de Paix, *E.C. & G.M. Leonard 11169* (A, GH, US); Ile de la Tortue, La Vallée, *Leonard 11701* (US). DEPT. DU NORD: Bayeux near Port Margot, *Nash 907* (NY). DEPT. DE L'OUEST: Petit Gonave Island, *Leonard 5239* (GH, US); Morne a Bateau, Port-au-Prince, *Ekman 8162* (S, US).

This common strand plant is certainly more abundant in Hispaniola than the collections cited above would indicate. It is also commonly cultivated as an ornamental shrub or tree.

Coccoloba uvifera L. × **Coccoloba pubescens** L.; Howard, Jour. Arnold Arb. **36**: 225. 1955.

Shrub or tree to 18 feet tall with habit of *Coccoloba uvifera*, i.e., some branches erect, some branches semi-prostrate; branchlets terete, sulcate when dry, pubescent or puberulent, the nodes slightly enlarged; ocreae to 1 cm. long, deeply cleft, the basal portion persistent; leaves of normal shoots with petioles to 1 cm. long, puberulent or pubescent, attached at the bases of the ocreae; blades usually orbicular, 8.5 × 9.5, 11 × 14, 12.5 × 13, 15 × 19 cm. long and broad, thick or fleshy, plane or slightly bullate, drying yellow-green in color, short pubescent on the midrib and primary veins above, the rest glabrous, persistently short pubescent on the veins below, the lower surface dark-glandular-dotted, the apex rounded, occasionally broadly and shortly mucronate, the base cordate, the lobes overlapping, the margin entire, slightly undulate, the primary veins usually 5 pairs, impressed above, arcuate and conspicuously anastomosing near the margin; adventitious shoots with ocreae 1–2 cm. long, the leaves with petioles to 1 cm. long, stout, the blades broadly orbicular or slightly rhombic, 22 × 24 to 27 × 36 cm. long and broad, otherwise as in mature shoot leaves; inflorescences 12–25 cm. long, terminal and generally paired, with one raceme shorter than the other, the rachis puberulent; staminate flowers not seen; pistillate flowers 3–10 at each locus, these seemingly scorpioid in development, the bracts triangular, to 1 mm., the ocreolae membranaceous, 1 mm. long, the pedicels to 2.5 mm. long, puberulent, the hypanthium short, to 0.5 mm. long, the perianth lobes ovate, 1.5–2 mm. long, 1–1.5 mm. wide in bud, the stamens rudimentary, the anthers abortive, the pistil 1.5–2 mm. long; fruit obovoid, 12–13 mm. long, 6–7 mm. diameter, narrowed to a short stalk-like base 2–3 mm. long, the apex rounded, the fleshy perianth lobes imbricated, red; achene obovoid to globose, light brown, smooth or slightly pitted.

Dominican Republic. PROV. BARAHONA: El Caiman between Enriquillo and El Can, *Howard 12189* (GH), *12191* (GH); Beata Island, *Howard 12499* (GH).

Haiti. DEPT. DU SUD: Miragoane, *Eyerdam 397* (GH, NY, US); Anse à Veau, *Picarda s.n.* (GH).

In 1950 Mr. George Hamor of Barahona discovered an unusual stand of *Coccoloba* along a coral shelf and rocky beach area south of Barahona. He later arranged transportation to the spot and showed me this definite hybrid. The plant described here occurs between a coastal stand of *C. uvifera* (*Howard 12188*) and an inland stand of *C. pubescens* (*Howard 12187*). Fully a dozen mature plants were found in this location. Not only is the plant intermediate in geographic location, but all of its characteristics show its hybrid origin from *C. uvifera* and *C. pubescens.* In habit the plant resembles *C. uvifera,* being a plant of low stature with some branches semi-prostrate and spreading while others are erect, giving each plant the definite clump-like appearance of *C. uvifera.* The leaf shape of the normal leaves on mature branches is that of *C. uvifera* except in texture, in which they resemble *C. pubescens,* having the conspicuous reticulate venation on the lower surface. The pubescence of the leaves combines that of the parent species. The leaves of the adventitious shoots more closely resemble those of *C. pubescens* in size, shape and aspect than comparable leaves of *C. uvifera.* In the arrangement of the flowers and the pubescence, the characters remind one of *C. pubescens,* although the presence of a smaller raceme arising laterally from the base is more common in *C. uvifera.* Only female flowers are known. The fruits are smaller than typical *Coccoloba uvifera* but resemble them in shape and are unlike those of *C. pubescens.* Fruits were abundant on the hybrid plants and appeared in the field to be fully developed. However, none of the one hundred fruits collected would germinate a month later, while eighty per cent germination was obtained from a collection of *C. uvifera* made at the same time.

A similar stand of the hybrid was found on Beata Island two weeks later and again both parents were present.

The collection *Eyerdam 397* is referred to this new hybrid. The specimen appears to have been taken from adventitious shoots and possesses larger leaves more closely resembling *Coccoloba pubescens.* As is generally true of flowering material collected from adventitious shoots, the inflorescence of this specimen is larger, approaching 35 cm. in length.

While the suggested hybrid origin of *Coccoloba antiguensis* Sandwith from Antigua has been rejected and that species referred to the synonymy of *C. pubescens,* there is no doubt in my mind as to the valid nature and the origin of the present hybrid. The hybrid nature of this collection is obvious in the field and equally so in the specimens cited.

The other hybrid plants and populations involving *Coccoloba uvifera* considered in this paper are *C. costata* × *C. uvifera*, *C. hotteana* × *C. uvifera* and *C. krugii* × *C. uvifera*.

Coccoloba venosa L. Syst. Nat. ed. 10. 1007. 1759; Fawcett and Rendle, Jour. Bot. **51**: 123. 1913.

Coccoloba punctata L. Sp. Pl. ed. 2. 523. 1762.
Uvifera arbor americana, fructu aromatico punctatus, Pluk. Alm. 394, t. 237, fig. 4. 1696, as to leaf only.
Coccoloba nivea Jacq. Hist. Stirp. Amer. 115, pl. 78. 1763; Enum. Pl. 19. 1762.
Guaiabara venosa House, Amer. Midl. Nat. 8: 64. 1922, as *Guaibara*.

Trees to 45 feet tall; branches terete, glabrous, the nodes not tumid; ocreae membranaceous, deeply cleft, acuminate on one side, or truncate, to 2 cm. long, glabrous or with flattened glands; leaves of normal shoots with petioles 5–10 mm. long, glabrous, the blades oblong-lanceolate to elliptic, 8 × 4, 10 × 4.5, 16.5 × 6.5, 21 × 9, 27 × 10.5 cm. long and broad, membranaceous, glabrous except for clusters of hairs in the axils of the veins, sparsely glandular below, the apex short-acuminate, the base narrowed and slightly cordate or cuneate or obtuse, the midrib and primary veins slightly prominent on both surfaces, the primary veins 8–13 pairs, straight or arcuate, bifurcate and anastomosing at the margins; leaves of the adventitious shoots about the same size, the internodes much elongate and the ocreae to 4 cm. long; inflorescences terminal or terminal on short lateral branches, the rachis puberulent, angular; staminate flowers in clusters of 2–5, the pistillate flowers solitary, the bracts lanceolate-ovate, to 1.5 mm. long, black, puberulent to pilose or commonly with a fringe of hairs at the apex; ocreolae to 2 mm. long, membranaceous, enlarging with the expanding bud, each flower with an ocreola, the flowering pedicels 1–2 mm. long, glabrous; hypanthium less than 0.5 mm. long, the perianth lobes broadly ovate, 1.5–2 mm. long and broad, slightly unequal, the fertile stamens to 1 mm. long; fruiting pedicels 1.5–2.5 mm. long, the perianth lobes fleshy, white or pink, enclosing the black achene, the hypanthium scarcely evident in the fruit, the fruit broadly ovoid, 3–4 mm. long and broad.

DISTRIBUTION: Cuba (introduced), Hispaniola, Puerto Rico, Jamaica (?), Virgin Islands, Lesser Antilles and Trinidad.

Dominican Republic. DISTRICT DE SANTO DOMINGO: between Ciudad Trujillo and La Caleta, *Ekman H-14231* (S). PROV. LA ALTAGRACIA: Llano Costero at La Romana, *Ekman H-12089* (B, S). PROV. SAMANÁ: Cabo Samaná near Puerto Colorado, *Ekman H-15333* (S). PROV. SEIBO: Monte Redondo, east of Jovero, *Abbott 2792* (B, US). PROV. UNKNOWN: Cupey, *Eggers 2682* (NY, US).

Haiti. DEPT. DU NORD OUEST: Ile de la Tortue, La Vallée, *Ekman H-9758* (S, US). DEPT. DU NORD: Massif du Nord, Port Margot, Bayeux, *Ekman H-2699* (S, US). Without specific location: *Sessé & Mocino 952* (F), *5431* (F).

Coccoloba wrightii Lindau, Engl. Bot. Jahrb. **13**: 151. 1890; Howard, Jour. Arnold Arb. **30**: 418. 1949.

Coccoloba scrobiculata Lindau, Engl. Bot. Jahrb. **13**: 140. 1890.
Coccoloba subtruncata Urban, Symb. Antill. **7**: 211. 1912.
Coccoloba saxicola Britton, Bull. Torrey Bot. Club **50**: 37. 1923.

Shrub or small tree to 21 feet tall; branches terete, the nodes not swollen, glabrate; ocreae membranaceous, 4–6 mm. long, puberulent to tomentose or glabrate; leaves of normal shoots with petioles 4–7 mm. long arising from the bases of the ocreae, the blades ovate, elliptic, obovate or rarely ovate-lanceolate, 5 × 2.5, 8 × 4, 10 × 7 to 11 × 10 cm. long and wide on mature shoots, coriaceous, umbonate between the veins, shining above when young but dull on both surfaces when mature, the apex acute to abruptly short acuminate or truncate, the base narrowed to obtuse, usually slightly oblique, the primary veins 4–6 pairs, arcuate, impressed above, conspicuous below, the lower surface more or less dotted with stomatal excretions; adventitious shoots with ocreae to 2 cm. long; leaves with petioles 2.5 cm. long, the blades broadly ovate to elliptic, 15 × 14 to 20 × 17 cm. long and broad, the apex of these leaves rounded to obtusely short mucronate, the bases rounded to subcordate; inflorescences terminal, 3–10 cm. long, the rachis pubescent or with resinous excretions, the bracts ovate, to 0.5 mm. long, the ocreolae membranaceous, 1 mm. long, the flowering pedicels 1 mm. long, increasing in length either in fruit or after staminate flowers have fallen to 3 mm.; staminate flowers 2–3 per locus, the pistillate flowers borne singly at each locus; hypanthium to 1 mm. long, the perianth lobes 1–1.5 mm. long and broad, the fertile stamens united at the base for 1 mm., the free portions 0.5–1 mm. long, the sterile stamens less than 1 mm. long, the functional pistil to 2 mm. long; fruit ovoid, slightly contracted at the base, rounded but only slightly coronate at the apex, 7–9 mm. long, 4–5 mm. in diameter.

DISTRIBUTION: Cuba and Hispaniola.

Dominican Republic. PROV. BAHORUCO: between El Aguacate and Pedernales, *Howard 12585* (GH). PROV. LA VEGA: Constanza, *Türckheim 3304* (B-type of *C. subtruncata*, F, GH, M, MO, NY, S, US); Arroyo Pantuflo near Constanza, *Ekman H-14089* (A, S, US); Bonao, *Ekman 16450* (S, US). Without specific location: *Schomburgk 123* (B), *Preneloup 492* (B, US), *Bertero s.n.* (B).

Coccoloba scrobiculata Lindau was described, collections by Schomburgk and Preneloup being cited, in the same publication as *C. wrightii* Lindau. Lindau attempted to distinguish between them in a key by indicating that the lesser venation was flat and inconspicuous above in *C. scrobiculata* while it was more prominent in *C. wrightii*. This is scarcely a reliable characteristic in the genus and I have no doubt that only one species is involved. No recent collections have been referred to *C. scrobiculata* and I have chosen to accept the better known and documented *C. wrightii* as the species. Although *C. scrobiculata* was described a few pages earlier, but at the same time as *C. wrightii*, I am considering it a new synonym. The venation pattern of material called *C. scrobiculata* by Lindau is easily included in the range of variation of *C. wrightii* and in all characteristics visible in the scanty flowering material, the two are identical.

Coccoloba subtruncata, described some years later by Urban, was based on a collection made near Constanza by H. von Türckheim. The species has been recollected in the same area by Ekman and additional collections are available from other areas. Urban's original diagnosis was presumably based on the one sheet of the Türckheim collection in the Berlin herbarium. I have on loan nine sheets of this number which are obviously the same but which would necessitate a new description to be accurate. Recent material (e.g., *Ekman H-16450* and *H-14089*) in fruit allows a complete diagnosis of this species which obviously is the same as *Coccoloba wrightii* of Cuba and must be referred to synonymy there. In general, the Hispaniolan specimens have less pubescence when mature than do the Cuban plants. However, the type collection of *C. subtruncata*, in spite of Urban's description, exhibits the same pubescence as *C. wrightii*, at least on the young shoots and the tips of the ocreae. *Coccoloba wrightii* has been considered to be endemic to Cuba, but its range is now extended to the Dominican Republic and specimens should be found in Haiti.

A twisted tree represented by *Howard 12585* was alongside a new road from El Aguacate to Pedernales in the Dominican Republic. In the course of road-building this tree had been pushed over at an angle and from the lower portion erect adventitious shoots had developed with large and extremely thick-coriaceous leaves. These adventitious stems were 8–10 mm. thick near the apex in contrast with the much smaller diameter of the normal growth. The largest leaves on the shoot had stout petioles 2–2.5 cm. long and broadly ovate to elliptic leaves to 19 × 15 cm. long and broad. The apex of the blade was rounded to short and obtusely mucronate and the bases were rounded to subcordate. The terminal portions of this plant produced shoots which were identical with those in the type collection of Türckheim. Similar-sized leaves of adventitious shoots of *Coccoloba wrightii* have already been reported and the previous description is amended only to include leaves which are rounded to subtruncate at the base.

The collection *Ekman H-15135* from Los Bañaderos Prietos near Laguna on the Samaná Peninsula was named by Schmidt as "*C. subtruncata* forma." Ekman's field notes state, a "small tree, alas, sterile." This material seems more appropriately referred to *Coccoloba pauciflora* Urban. It is obviously from adventitious shoots and the normal foliage is not represented. Neither *C. pauciflora* nor *C. wrightii* has been reported from the Samaná Peninsula.

A MONOGRAPHIC STUDY OF THE WEST INDIAN SPECIES OF PHYLLANTHUS *

Grady L. Webster

With four plates

Subgenus VII. **Botryanthus** Webster, Jour. Arnold Arb. 37: 345. 1956.

Trees or shrubs with non-phyllanthoid branching, the leaves on the main axes not reduced to scales, ultimate axes not regularly deciduous. Monoecious; flowers borne in thyrses or axillary clusters. Male flower: calyx-lobes 5 or 6; disk-segments 5 or 6, often massive; stamens 3, filaments connate, anthers dehiscing horizontally or obliquely; pollen grains globose, areolate. Female flower: calyx-lobes 5 or 6; disk cupuliform; ovary of 3 carpels, smooth; styles erect or spreading, usually connate (at least basally) into a column, the tips entire to bifid. Fruit capsular, sometimes very large; seeds trigonous, essentially smooth.

Subgenus *Botryanthus* is an entirely Neotropical group which includes possibly 35 species, most of these occurring in Central and South America. In addition to the dubious sect. *Diplocicca* from Brazil (based on *P. octomerus* Muell. Arg.), other South American sections may eventually be defined; but the majority of the species in the subgenus (including all the West Indian ones) clearly are referable to sect. *Elutanthos*.

From the phylogenetic point of view subg. *Botryanthus* is of especial interest because it is closely related to subg. *Xylophylla*. Its areolate pollen grains are essentially identical to those of the latter subgenus and, since its branching is non-phyllanthoid (and hence presumably unspecialized), subg. *Botryanthus* might logically be considered the ancestral group. The reduction series in inflorescence within sect. *Elutanthos* (which can be traced from the elaborate "panicle" of *P. grandifolius* to the axillary flowers of *P. nutans* ssp. *grisebachianus*) could furthermore be cited in support of such a supposition. On the other hand, it must be noted that in many ways *P. grandifolius* is a very specialized plant, for it has capsules and seeds extraordinarily large in the genus, and its male flowers with three connate stamens give no indication of primitiveness. A rather convincing argument could be put forth to read the phylogeny in precisely the opposite direction, and to assume that subg. *Botryanthus* has evolved from some group within subg. *Xylophylla* (such as sect. *Asterandra*) by a regression from phyllanthoid to non-phyllanthoid branching. Such a hypothesis would involve the assumption that a great increase in leaf and fruit size (such as occurs in *P. grandifolius*) would place a selective advantage on any reversion from deciduous to permanent reproductive axes. At present a decision for either of the alternative hypotheses can-

---

* Continued from volume XXXVIII, p. 373.

not be made, but with the accumulation of additional evidence (particularly from cytology) it should be possible to do so.

Sect. 15. **Elutanthos** Croiz. Jour. Wash. Acad. Sci. 33: 12. 1943.

Shrubs or trees with unspecialized ramification, leaves distichous on persistent axes. Monoecious; flowers in cymules in the axils of foliage leaves or of bracts (the inflorescence then thyrsoid), or sometimes solitary. Male flower: calyx-lobes 6; disk-segments 6, often massive; stamens usually 3, filaments completely united into a column; anthers dehiscing more or less horizontally (or deflexed); pollen grains globose, areolate, the areoles usually polybrochate. Female flower: calyx-lobes 6; disk patelliform; styles erect, connate at least below, entire to bifid. Capsule obscurely rugulose; seeds smooth.

TYPE SPECIES: *Phyllanthus glaucescens* H.B.K. [= *P. grandifolius* L.].

As established by Croizat, sect. *Elutanthos* included seven species of Central and South America; but there are undoubtedly a number of others which are to be referred here, including the following six species from the West Indies. The West Indian plants differ from the mainland *P. grandifolius* and its allies in their smaller capsules and less elaborate inflorescence, but the similarities are so striking that there is obviously a close affinity.

The combination of an indefinite branching pattern and usually raceme-like inflorescence distinguishes the species of sect. *Elutanthos* from all other woody West Indian species. However, the expression of inflorescence is quite variable and the typical thyrses are not developed in *P. nutans* ssp. *grisebachianus* and some forms of *P. nutans* ssp. *nutans*. Where the raceme-like thyrses occur, they often appear to be terminal, but close inspection will show that each thyrse does not represent a continuation of the branch axis but is rather inserted just below the abortive tip of the axis; often an additional thyrse is produced at one or more additional nodes below. In addition, cymules may also occur in the axils of foliage leaves; in such cases, these axillary cymules tend to be male and the ones in the "racemes" female. The homology between the more or less naked thyrses and the leafy branch-ends is as ill-defined as that between branch-orders, for the degree of distinctiveness of thyrse development is at least partially dependent on the vigor of the branches. Sometimes there may be long "leader" shoots which bear short thyrsiferous branchlets in distichous order, but in other instances the thyrsiferous branchlets may themselves be of the penultimate order and produce additional leafy axes as well as "racemes" of flowers.

Ecologically the West Indian representatives of sect. *Elutanthos* are characterized by a xerophytic tendency, most of the species appearing to grow in open scrub formations at low altitudes. The widespread *P. nutans*, however, occurs in a considerable variety of habitats, including some of the wettest rain forest in Jamaica.

KEY TO THE SPECIES

1. Calyx-lobes of male flowers less than 1.5 mm. long; capsules trigonous; plants of the southern Caribbean.
    2. Styles subentire (truncate-emarginate), completely erect and connivent (with no reflexed portions); disk of female flower extremely massive; plants completely glabrous; Curaçao. . . . . 43. *P. botryanthus*
    2. Styles with bifid sharply reflexed tips; disk of female flower tenuous; branchlets and inflorescence axes hirsutulous; Barbados. . . . . .44. *P. anderssonii*
1. Calyx-lobes of male flowers over 1.5 mm. long; capsules rounded; plants of the northern Caribbean.
    2. Staminal column with 3 apiculae alternating with the anthers; leaf-blades densely hirsutulous beneath, sparsely hirsutulous above; style-tips entire or merely emarginate; Haiti. . . . . 47. *P. urbanianus*
    2. Staminal column without apiculae; leaf-blades glabrous or sparsely hirsutulous beneath, glabrous above; styles definitely bifid.
        3. Leaf-blades rigidly coriaceous, the main veins distinctly sunken above; stipules indurate, dark and shiny, colored as the branch; Cuba. . . . . 46. *P. pachystylus*
        3. Leaf-blades chartaceous, the veins not sunken above; stipules not indurate; Jamaica and Cuba. . . . . 45. *P. nutans*

43. **Phyllanthus botryanthus** Muell. Arg. in DC. Prodr. **15**(2): 323 1866. (PLATE XXIV, *figs*. A–B).

Diasperus botryanthus (Muell. Arg.) O. Ktze. Rev. Gen. **2**: 598. 1891.
Phyllanthus euwensii Bold. Fl. Dutch W. Ind. **2**: 50–51, *pl. 4*. 1914.
Glochidion botryanthum (Muell. Arg.) Pax & Hoffm. Naturl. Pflanzenfam. ed. 2, **19c**: 58. 1931.

Glabrous shrub or small tree c. 1–4 m. high; branches slender, terete, furrowed, reddish-brown, c. 1.5–4 mm. thick; leader shoots up to 25 cm. long, lateral branchlets (of current year) c. 3–20 cm. long, with 5–15 leaves. Leaves: stipules triangular, mostly 0.8–1.1 mm. long and 0.5–0.6 mm. broad, acute, scarious, reddish- or blackish-brown, persistent (at least the basal portion), more or less entire. Petioles dark, grooved above, angled, 2.5–4 mm. long. Leaf-blades membranous or chartaceous, mostly ovate, c. (3–) 4.5–7.5 cm. long, (2–) 2.5–5 cm. broad, acute or obtuse (rarely emarginate) at the tip, obtuse or rounded at the base; above darkened in drying, the midrib and laterals very slightly raised; beneath more or less pruinose, the midrib salient, the laterals (c. 6–8 on a side) arching, slightly raised, branching to form a reticulum; margins unthickened, plane.

Monoecious; flowers mostly in bisexual cymules on leafless thyrses at distal nodes of ultimate axes; female flowers usually 1 or 2, males 3–6 per cymule, or the sexes more or less segregated onto different thyrses.

Male flower: pedicel capillary, c. 1 cm. long. Calyx-lobes 6, subequal, elliptic-oblong, c. 1–1.2 mm. long and 0.5–0.8 mm. broad, obtuse, purple-stained except for the narrow scarious entire margins, midrib unbranched or nearly so. Disk-segments 6, massive, subcubical, foveolate, c. 0.3-0.4 mm. broad. Stamens 3; column c. 0.35–0.4 mm. high; anthers sessile, discrete, triangular, acute, c. 0.25–0.35 mm. long, 0.35–0.4 mm. broad; anther-sacs divergent, the slits not confluent, dehiscing horizontally; pollen grains mostly 22–26 μ in diameter, areoles oligobrochate, c. 5 μ across.

Female flower: pedicel capillary, (10–) 13–16 (–19) mm. long. Calyx-lobes 6, triangular-oblong, c. 1.2–1.3 mm. long and 0.7–0.8 mm. broad, acute or subacute, purple-stained as the male, the narrow scarious margin more or less entire, the midrib sparingly branched. Disk convex, extremely massive, circular or angled, nearly 2 mm. across, foveolate. Styles erect, connate or coherent into a column 0.3–0.45 mm. high, slightly dilated and merely truncate-emarginate at the apex.

Capsule oblate, trigonous, c. 3 mm. high and up to 6 mm. broad, somewhat rugulose, the veins obscure or conspicuous. Columella 1.7–2 mm. high. Seeds plano-convex, plump, umbonate (heliciform), 3.3–3.6 mm. long, 2.7–2.9 mm. broad, light brown, smooth (finely striolate).

Collected in flower and fruit May to January.

TYPE: Colombia, Carthagena, *Triana 3664* (P, LECTOTYPE; K, W, ISOTYPES).

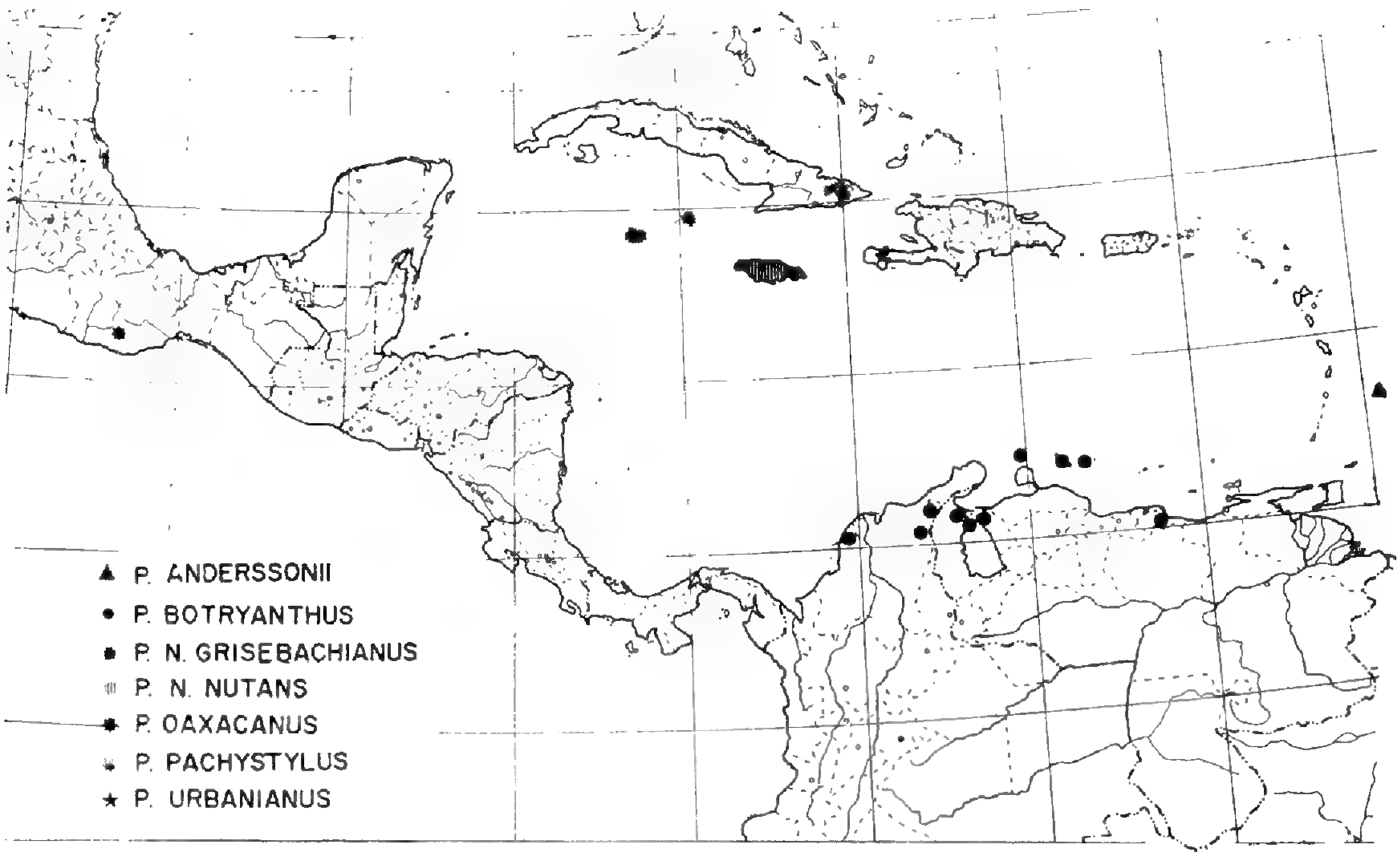
DISTRIBUTION: coastal plain, northern South America (MAP XVIII).

ARUBA: Kristalberg, 1885, *Suringar* (L). CURAÇAO: road near Antonyberg, *Boldingh 5141* (C); road near Wacao, *Boldingh 5252* (L); calcareous soil near San Pedro, *Boldingh 5279* (NY, ISOTYPE of *P. euwensii*); Tafelberg, *Curran & Hamman 164* (A); Hofje Abau, *Curran & Hamman 180* (A); rif-hospitaal, Hato, Savonet, *Suringar* (L). BONAIRE: klip Slachtbaai, *Suringar* (L). (Additional localities cited by Boldingh, loc. cit.)

The Curassavican plants represent merely a small outlying population of this species which is widespread and common in lowland areas along the northern coasts of Colombia and Venezuela. The specimens from the Dutch islands show no evident differences from the mainland plants, so that Boldingh's proposed *P. euwensii* cannot be maintained even at subspecific rank. Boldingh did not give any distinguishing characters for his intended new species, nor did he discuss its relationships; apparently he was unaware that the species also occurred on the mainland or that it had already received a name.

Because of its essentially entire styles associated in a column, *P. botryanthus* was placed by Mueller in his artificial sect. *Hemiphyllanthus*; it was therefore one of the species transferred to *Glochidion* by Pax and Hoffmann (loc. cit.), who arbitrarily assigned all species of *Phyllanthus* with entire styles to *Glochidion*. This betrayed mere bibliographic acquaintance with the plants, for *P. botryanthus* and *P. ovatus* (the other West Indian representative of Mueller's sect. *Hemiphyllanthus*) are neither closely related to one another nor to species of *Glochidion*.

The habit, floral structure, and pollen grains of *P. botryanthus* together indicate an unquestionable relationship with the other species of sect. *Elutanthos*. Within the section, the closest West Indian relation appears to be *P. anderssonii*, which has very similar vegetative parts and male flowers but utterly different female flowers with bifid reflexed styles and a tenuous disk. In contrast, the female flowers of *P. botryanthus* are distinguished by the subentire erect styles and extraordinarily massive disk, which even in the bud stage is massive and swollen and which expands precociously to cause the calyx-lobes to become reflexed. However, the Mexican *P. oaxacanus* has a similar massive disk and, despite its very different styles, is probably the most closely related species.



MAP XVIII. Distribution of some Caribbean species of sect. *Elutanthos*.

44. **Phyllanthus anderssonii** Muell. Arg. in DC. Prodr. **15**(2): 395. 1866 (as *P. anderssoni*). (PLATE XXIV, *figs.* C–D).

Phyllanthus barbadensis Urb. Symb. Ant. **3**: 287. 1902.

A shrub c. 1 m. high [ex Eggers], with slender leader shoots up to c. 30 cm. long bearing distichous branchlets which terminate in naked thyrses (or leaders serving directly as thyrse-bearing axes); ultimate axes (branchlets) reddish brown, terete, sparsely to rather densely hirsutulous, mostly 4–10 cm. long, 0.6–1 mm. thick, with c. 6–15 nodes. Leaves: stipules triangular-lanceolate, 0.75–1 mm. long, 0.3–0.5 mm. broad, acute or acuminate, more or less hirsutulous, scarious, becoming reddish brown and at least the base persistent, entire or denticulate. Petioles dark and slender, flattened and hirsutulous adaxially, convex and glabrous abaxially, 1–1.8 mm. long. Leaf-blades membranous or chartaceous, elliptic to mostly ovate, c. 2.5–4.5 cm. long, 1.2–2.5 cm. broad, obtuse or subacute at the tip, cuneate at the base; above olivaceous or drying blackish, hirsutulous proximally on the midrib but otherwise smooth and glabrous, nerves slightly raised; beneath glabrous, pale or pruinose, the midrib distinctly raised, the laterals (c. 7–10 on a side) ascending, slightly raised, connecting intramarginally, the tertiaries forming a rather inconspicuous reticulum; margins scarcely thickened, plane.

Monoecious; cymules mostly unisexual; male cymules several-flowered, borne at proximal axils of branchlet usually axillary to foliage leaves; female cymules with 1–4 flowers, borne on the thyrsiform terminal portions of branchlets (the leaves becoming more or less abruptly reduced to scales); one or two cymules at the transitional region often bisexual.

Male flower: pedicel capillary, up to c. 8 mm. long. Calyx-lobes 6, chartaceous, subequal, elliptic to oblong or obovate, c. 1–1.3 (–1.5) mm. long, 0.75–1 mm. broad, obtuse or subacute, entire or obscurely crenulate, the midrib unbranched. Disk-segments 6, very massive (about as large as the anthers), deeply furrowed and pitted, c. 0.3–0.4 mm. broad. Stamens 3; column c. 0.5–0.7 mm. high, c. 0.25 mm. thick; anthers sessile atop the column, discrete, the common connective convex, c. 0.2–0.3 mm. long and 0.35–0.4 mm. broad; anther-sacs divergent, dehiscing horizontally, the slits not confluent; pollen grains c. 21–25 μ in diameter, areoles polybrochate, c. 5–7 μ across.

Female flower: pedicel slender, 7–13 mm. long. Calyx-lobes 6, subequal, ovate-oblong or obovate, 1–1.4 mm. long, 0.7–0.9 mm. broad, rounded or subtruncate at the tip, entire or obscurely crenulate, the midrib sparsely branching. Disk cupuliform, enclosing up to ⅓ of the ovary, the tenuous rim crenulate, pitted. Styles connate or loosely coherent into a column c. 0.4–0.7 mm. high, the free ends sharply reflexed, bifid up to ⅔ their length, the tips subulate, obtuse and entire or again emarginate or bifid.

Capsule oblate, trigonous, 6-sulcate, dark purplish brown, obscurely venose, c. 5.5–6 mm. broad, the valves c. 4.5 mm. long. Columella 1.8–2 mm. high. Seeds plano-convex, plump, umbonate, 2.7–3.3 mm. long, 1.7–2.3 mm. radially, 1.8–2.4 mm. tangentially, pale brown with very irregular longitudinal bands of slightly raised transversely elongated reddish-brown cells; hilum submedian.

Collected in flower Jan., Feb., June, Nov.; in fruit Feb., Nov.

TYPE: "Caracas," collector unspecified (Prodromus Herbarium, G, HOLOTYPE). The typification of this species is unfortunately fraught with difficulties which at this time cannot be wholly resolved. In Mueller's original description the origin of the type collection was indicated as follows: "Prope Caracas (hb. holm. sub n. 288! a cl. Dr. Andersson miss.)." Presumably the specimen was not collected by Andersson, since during his trip on the "Eugenie" he did not visit anywhere within the Caribbean area, his closest approach being the Pacific coast of Panama (cf. end-map in Skogman, Fregatten Eugenies Resa Omkring Jorden. 1854–55). If the plant was really collected near Caracas it seems unlikely that it could have escaped notice subsequently, although this cannot be entirely ruled out. It appears more likely that the specimen was actually obtained on Barbados but was subsequently mislabelled. A search through the literature indicates that there is at least one possible source of the collection, for Robert Schomburgk spent several months on Barbados in 1846–47 and his citation (Hist. Barbados 593. 1848) of *P. nutans* can hardly refer to any species other than the present one. The figure "222" for the citation in Schomburgk's list does not agree with the "288" cited by Mueller, but the latter might be a field number. Of course, none of these circumstances constitutes proof that Andersson's specimen is a duplicate of a Schomburgk collection, so that it is impossible to decide conclusively whether the type collection of *P. anderssonii* is from Venezuela or from Barbados. Although it differs in a few minor particulars, the type specimen of *P. anderssonii* corresponds so well (e.g., in its hirtellous axes, massive male disk-segments, and sharply reflexed styles) with the specimens of *P. barbadensis* that it must be conspecific; and Mueller's name must thus take precedence over the much later one of Urban.

DISTRIBUTION: endemic to Barbados (MAP XVIII).

BARBADOS: Lion Hill Gully, St. James, *Dash 334* (NY); Forster Hall Wood, *Eggers 7130* (A, GOET, US; LECTOTYPE COLLECTION of *P. barbadensis*); Cole's Cave, St. Thomas, *Freeman & Bovell* (NY); Highland Gully, St. Thomas, *McIntosh* (K); Jack-in-the-box Gully and under Hackleton's Cliff, *Waby 15* (K); Bathsheba, *Warming 27* (C).

Beard (Nat. Veg. Leeward & Windward Isl. 166. 1949) has pointed out that practically all of the natural vegetation on Barbados has disappeared and that many plants endemic to Barbados have become extinct. However, since *P. anderssonii* has been collected at a number of different localities up to 1935, it seems possible that it may still survive, even though Beard failed to encounter it in his own reconnaissance of the island.

Urban compared *P. anderssonii* (as *P. barbadensis*) with *P. nutans*, to which indeed it shows some similarities; but its closest relationship is undoubtedly with *P. botryanthus*. In the face of their present distributions, the affinity between *P. anderssonii* and *P. botryanthus* has some anomalous aspects. It seems curious, for instance, that the female flowers (which are the best distinguishing character) of *P. botryanthus* are much more highly modified than those of *P. anderssonii*, for one might expect that it would be the latter, which presumably has been derived by colonization from South America, that would show the greater specialization. It also seems surprising that no related forms occur in a gap of about 500 miles between the state of Miranda, Venezuela (the easternmost known station for *P. botryanthus*) and Barbados. One possible explanation is that *P. anderssonii* may represent a relict of an extensive population which occupied the ancient land-mass of "Paria"; according to Schuchert (Hist. Geol. Ant.-Car. Reg. 19. 1935) this region extended from Maracaibo to Barbados at some time during the Cenozoic, but later foundered and is now represented only by some of the off-shore islands of northern South America.

45. **Phyllanthus nutans** Sw. Prodr. 27. 1788; Fl. Ind. Occ. 1103. 1800; Muell. Arg. in DC. Prodr. **15**(2): 375. 1866; Fawc. & Rend. Fl. Jam. **4**: 253–254. 1920.

Diasperus nutans (Sw.) O. Ktze. Rev. Gen. 2: 600. 1891.

A diffuse extremely variable shrub or slender tree 1–7 m. high, irregularly branching, the new axes borne distichously on older branches, often ending in nodding racemiform inflorescences, reddish brown, terete or angled, smooth or scabridulous or hirsutulous, 2–25 cm. long, 1–2.5 mm. broad, internodes 4–40 mm. long. Leaves: stipules scarious-chartaceous, deciduous or persistent, ovate to narrowly lanceolate, (2–) 3–5 (–9) mm. long, (1–) 1.5–4 (–6) mm. broad, obtuse to acute at the tip, truncate to cordate at the base, entire, yellowish, stramineous, or brownish. Petioles smooth or scabridulous to copiously hirsutulous, usually somewhat angled or margined, 1.5–4.5 mm. long. Leaf-blades chartaceous, quite variable in size and shape but most often ovate or elliptic, c. 3.5–8 (–11) cm. long, 2–5 (–8) cm. broad, obtuse or more rarely acute at the tip, cuneate to rounded at the base; above olivaceous, dull, the veins scarcely raised; beneath paler, sometimes glaucous or purplish-tinged, the midrib and lateral veins (5–8 on a side) raised, brownish or stramineous, the reticulum of veinlets usually conspicuous; margins unthickened, plane or revolute.

Monoecious; inflorescence variable; male cymules several-flowered, borne axillary or on pseudoterminal thyrses; female cymules 1–3-flowered, usually confined to the pseudoterminal thyrses (at least in ssp. *nutans*).

Male flower: pedicel capillary, 8–15 (–30) mm. long. Calyx-lobes 6, chartaceous, or somewhat fleshy, subequal, oblong to obovate, 2.3–3.2 mm. long, 1.3–2.2 mm. broad, rounded and obscurely crenulate or denticulate at the tip, often reddish at least below with thin creamy-yellow scarious margins but sometimes greenish throughout, the midrib with a few often conspicuous lateral branches. Disk-segments 6, thickened and fleshy, orbicular or reniform, obscurely to conspicuously foveolate-pitted, c. 0.35–0.7 mm. broad. Stamens 3; column c. 0.7–1.1 mm. high, tapering slightly to the apex; anthers sessile atop the column, discrete, usually deflexed but sometimes horizontal, broadly triangular to elliptic in outline, c. 0.4–0.6 mm. long and broad; anther-sacs slightly to markedly divergent, dehiscing horizontally or obliquely downwards, the slits confluent across the apex; pollen grains c. 21–26 μ in diameter, the areoles polybrochate, c. 6–8 μ across.

Female flower: pedicel terete, slender, smooth and glabrous or sometimes sparsely hirsutulous, reddish or olivaceous (sometimes pruinose), (6–) 10–27 mm. long. Calyx-lobes 6, erect at anthesis, biseriate, the outer elliptic-oblong and obtuse at the tip, the inner obovate and broader and more rounded at the tip; lobes 2–3.2 mm. long, 1–2.5 mm. broad, colored as the male, the scarcely raised midrib simple to conspicuously branched. Disk patelliform, fleshy, 6-angled or slightly lobed, foveolate. Styles erect, the undivided portions connate into a column 0.5–2.3 mm. high, the free ends ordinarily sharply reflexed, bifid or parted nearly to the stylar column, the tips narrow or dilated, flattened, acute, 0.4–1.2 mm. long.

Capsule oblate-spheroidal, obscurely 6-ribbed, rounded in outline, c. 6 mm. high and 10 mm. broad, rugulose, the veins completely obscure. Columella c. 3–4 mm. high. Seeds trigonous (only slightly asymmetrical if at all), 4.2–7 mm. long, 2.8–4 mm. radially and tangentially, smooth, mottled light brown; hilum submedian.

Flowering probably throughout the year.

The populations of this extremely variable species of Cuba, the Cayman Islands, and Jamaica may be assigned to one or the other of the two following subspecies.

45a. **Phyllanthus nutans** ssp. **nutans** (PLATE XXIV, *figs.* E–F).

Phyllanthus nutans Sw. Prodr. 27. 1788.
Phyllanthus nutans β purdiaeana Baill. Adansonia 2: 15–16. 1862.
Phyllanthus nutans var. *trojanus* Webster, Contr. Gray Herb. **176**: 47. 1955.

Stipules thin, usually precociously deciduous although conspicuous on young growth, ovate to lanceolate, (2–) 3–5 (–9) mm. long, (1–) 1.5–4 (–6) mm. broad, truncate or cordate at the base, glabrous, stramineous or greenish. Leaf-blades mostly ovate but often elliptic, glabrous beneath (except sometimes at the very base), usually obtuse or subacute at the tip and obtuse to rounded at the base; margins usually plane. Male cymules axillary or often at the proximal nodes of thyrses; female cymules 1–3-flowered, usually borne on more or less nodding pseudoterminal naked thyrses (i.e., ultimate axes with reduced leaves), sometimes the lowermost cymules in the axils of partially or wholly unreduced leaves. Calyx-lobes of male and female flowers subentire or obscurely denticulate, thickened at the base, the midrib simple or sparingly branched. Stylar column 0.5–2.3 mm. high; style-ends usually sharply reflexed, the lanceolate acute tips 0.4–1.2 mm. long.

TYPE: southern Jamaica, *Swartz*.

DISTRIBUTION: Jamaica and Cayman Islands (MAPS XVIII–XXI).

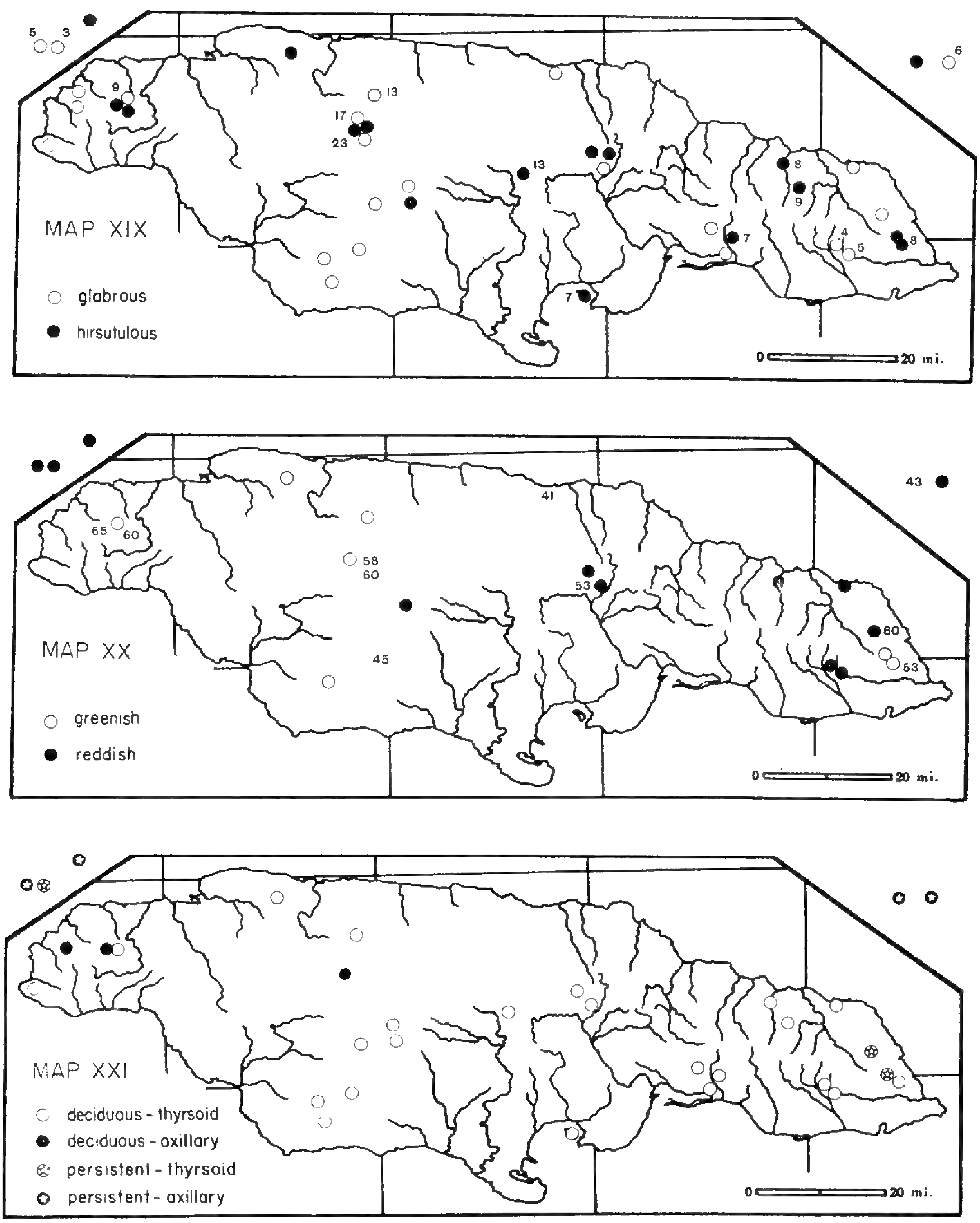
CAYMAN ISLANDS. GRAND CAYMAN: Grape Tree Point, dry rocky woodland, *Proctor 11977* (GH); between Old Isaacs and Wintersland, *Proctor 15245* (GH).

JAMAICA. Without locality: *Alexander* (A, GOET), *Hooker* (W), *Jacquin* (W), *Swartz* (S, HOLOTYPE; A, C, G, P, S, ISOTYPES), *Wilson 232* (NY), *Wullschlaegel s.n.* (GH), *900, 1053, 1114* (GOET), *1318* (W). HANOVER: Fish River Mountains, *Britton & Hollick 2167, 2170* (F, NY), *Harris 10260* (F, NY, US); Dolphin Head, *Britton 2314* (F, NY), *Harris 10309* (F, US), *Webster & Wilson 5075* (A, JAM). WESTMORELAND: Negril, rocky wooded hills, *Britton & Hollick 2082* (NY). ST. JAMES: Chatham, alt. 300 m., *Guilbride & Barkley 22J174* (MICH). ST. ELIZABETH: Potsdam woodland, *Harris 9778* (F, US); New Buildings, south of Gutters, *Howard & Proctor 14992* (A); Santa Cruz Mountains, near Hampton School, alt. 2400 ft., *Webster & Proctor 5293* (A, JAM). TRELAWNY: Ramgoat Cave, *Howard 14129* (A); Tyre, alt.

1750 ft., *Proctor 9936* (GH); road to Troy, *Harris 8687* (F, NY, US); Troy and vicinity, *Britton 929* (NY), *Perkins 1331* (GH, HOLOTYPE of var. *trojanus*). MANCHESTER: Brown's Town to Porus, hillside, *Britton 3272* (F, NY); vicinity of Mandeville, *S. Brown 248* (A, NY); 1.5 miles north of Shooters Hill, *Howard 14107* (A). ST. ANN: interior of St. Anns, *Purdie* (P, type collection of var. *purdiaena*); Guys Hill, Moneague, *Alexander* (G); Union Hill, near Moneague, *Britton & Hollick 2747* (F); Discovery Bay, *Hunnewell 18844* (GH). CLARENDON: Croft's Mountain, alt. 2500 ft., *Harris 11212* (F, NY). ST. CATHERINE: Old Harbour Bay, Little Goat Island, rocky woods, *Britton & Hollick 1855* (F, NY); Great Goat Island, southeastern side, *Harris 9301* (A, C, JAM, NY), *9337* (A, C, NY); Devil's Race Course, *Proctor 7213* (MICH). ST. ANDREW: valley of Yallahs River, *Alexander* (NY); Rock Fort, *Campbell 6412* (NY); near Hope, *Harris 8601* (JAM, NY), *8950* (JAM, NY, US); Hope River gorge, August Town, *Powell 297* (A). PORTLAND: Swift River gorge at Eden, *Proctor 11868* (GH); Uncommon Hill, *Proctor 8555* (GH); Port Antonio, Cave Hill near railway station, *Wight 199* (F, NY); John Crow Mountains, above Ecclesdown, rain-forest, *Howard, Proctor & Stearn 14769* (A). ST. THOMAS: Mansfield, *Britton 3557* (NY); Golden Valley, *Harris 5423* (F, NY); Plantain Garden River gorge, northwest of Whitehall, *Proctor 7419* (GH); Whitehall to Big Hill, *Proctor 7671* (JAM); Big Level, southeast end of John Crow Mountains, *Proctor 11820* (GH), *Webster & Proctor 5516* (A, BM, JAM, MICH, US).

Not only is *P. nutans* one of the most variable of the West Indian species, but its Jamaican representative (ssp. *nutans*) is certainly one of the most widespread woody plants on that island; it occurs from sea-level (at Rock Fort) to 2,500 ft. in the hills of the interior, and from such arid localities as Great Goat Island to dripping rain forest in the John Crow Mountains where the precipitation certainly exceeds 200 inches per year. The only sizeable area on the island where it appears to be absent is the upper slopes of the Blue Mountains (above 3,000 ft.); although it has most often been collected on limestone, it has also been found growing on serpentine (e.g., *Proctor 7419*).

In view of its ubiquitous distribution on Jamaica, it is not surprising that ssp. *nutans* should exhibit so much variability; but any attempt to categorize these variations can only encounter great difficulty. Even the distinction between the two subspecies is not very well-marked and may prove to be untenable when more collections are available from the Cayman Islands and Cuba. Since it has not proved very useful to express the intraspecific variation in terms of conventional taxa, a series of maps plotted for individual characters has been prepared. Many characters, of course, show a purely random distribution, as Map XIX shows for the presence or absence of pubescence. It is curious, however, that in the related species of this section, *P. barbadensis* and *P. botryanthus*, there is no variation in this respect, all individuals being hirsutulous and glabrous respectively. The distribution of reddish color in the calyx, plotted on Map XX, is a somewhat more doubtful case, for it might appear that there is a bicentric distribution of green calyces; however, the number of samples is small (due to the difficulty in ascertaining the color if there



Maps XIX–XXI. Distribution of certain morphological characters in populations of *Phyllanthus nutans* Sw. The symbols separated by heavy lines in the upper left-hand and right-hand corners refer to the disjunct populations in the Cayman Islands and eastern Cuba, respectively. The numbers associated with the dots in Map XIX indicate the mean stylar length (in tenths of a millimeter) of the individual samples, while the numbers in Map XX refer to the mean seed length in tenths of a millimeter. All herbarium specimens from definite localities are plotted in Map XIX, but some of these do not appear in Maps XX and XXI because of incomplete data.

are no label data) and it seems likely that further collections may break down the apparent distinction.

There are, however, a number of characters which show undoubted geographically correlated variation and it might be thought that these could serve as the basis for the recognition of subspecies or varieties. For instance, it is quite evident that in seed size, length of stylar column, and inflorescence-type the plants from the western part of the island show differences from the eastern populations. But a closer inspection will show that although there is a *general* east-west separation (and this holds, on a larger scale, between Jamaica and Cuba), the characters vary independently of one another to such an extent that no satisfactory minor taxa can be defined within the Jamaican plants as a whole. Thus var. *trojanus*, which was previously defined on the basis of plants with a long stylar column, must be relegated to synonymy, for the plants from Dolphin Head which otherwise agree with the plants from Troy in their inflorescence and leaves have much shorter stylar columns. The var. *purdiaeanus* recognized by Baillon and Mueller is an even less significant variation (of conspicuously bracteate inflorescences) which has a purely random distribution.

The two most striking character differences within *P. nutans* certainly deal with the stipule and inflorescence types, and it is indeed upon this fact that the two subspecies are recognized. It must be admitted, however, that even here the correlation is far from perfect. The Cuban ssp. *grisebachianus* clearly differs from most forms of ssp. *nutans* in its solitary axillary flowers and persistent stipules; but some plants in western Jamaica have essentially axillary flowers, while in the Cayman Islands and in the John Crow Mountains at the eastern end of Jamaica occur some anomalous forms with persistent stipules but which in other respects are more or less typical for ssp. *nutans*. It is clear, in the case of the John Crow plants, that the persistent stipules have been derived independently of those in ssp. *grisebachianus*; and a collection from the central part of the John Crow range (*Howard & Proctor 14769*) is furthermore so divergent that it was at first thought to represent a distinct species. In this collection the leaves are conspicuously corrugated, quite unlike any other specimens of *P. nutans*, even though the difference becomes obscured in drying. However, the inflorescence is typical for ssp. *nutans*, and the persistent stipules are shared by a collection from the Big Level area of the John Crow Range (*Webster & Proctor 5516*) which seems otherwise to represent ssp. *nutans*. Thus, despite the importance of the morphological divergence in the John Crow Mountains population, it does not seem practicable to designate it as a species or even subspecies.

The plants from the Cayman Islands, although not showing any divergence as extreme as the bullate-leaved form from the John Crows, are of great interest in that they bridge rather nicely the gap between the two subspecies. The two collections from Grand Cayman seem assignable to ssp. *nutans* by virtue of their ovate leaves, but they are to some extent transitional, because *Proctor 15245* has the axillary flowers of ssp. *grisebachianus* combined with the deciduous stipules of ssp. *nutans*, while

Proctor 11977 has the thyrsoid flowers of ssp. *nutans* combined with apparently persistent stipules as in ssp. *grisebachianus*. The collection from Little Cayman (*Kings LC42*), on the other hand, is clearly referable to ssp. *grisebachianus*, since it has elliptic, revolute leaves, persistent brownish stipules, and flowers axillary (or mostly so). While it is perhaps arbitrary to assign the Grand Cayman plants to ssp. *nutans*, there is in any event no doubt that the Cayman Islands population forms a connecting link between the two subspecies. Possibly the key to understanding the present distribution of *P. nutans* lies in the geological history of the Cayman Islands.

45b. **Phyllanthus nutans** ssp. **grisebachianus** (Muell. Arg.) stat. nov. (PLATE XXIV, *figs*. G–H).

Phyllanthus grisebachianus Muell. Arg. Linnaea **32**: 26. 1863; DC. Prodr. **15**(2): 380. 1866.

Diasperus grisebachianus (Muell. Arg.) O. Ktze. Rev. Gen. Pl. **2**: 599. 1891.

Stipules scarious, chartaceous, persistent (at least the basal portion), lanceolate, 2–3.5 mm. long, 0.7–1.5 mm. broad, truncate at the base, glabrous or hirsutulous, dark brown. Leaf-blades elliptic, glabrous or hirsutulous beneath, acute at tip and base, margins narrowly revolute. Flowers entirely axillary, solitary or the male and female paired at each axil. Calyx-lobes of male and female flowers denticulate, thin, the midrib conspicuously branched. Stylar column c. 0.5–0.7 mm. high; style-ends reflexed, dilated, bifid or notched, the tips recurved. Seeds c. 4.5 mm. long.

TYPE: eastern Cuba, *Wright 582*.

DISTRIBUTION: eastern Cuba (Sagua-Baracoa range) and Cayman Islands (MAPS XVIII–XXI).

CAYMAN ISLANDS: Little Cayman, South Town, *Kings LC42* (BR, NY). CUBA. ORIENTE: "Cuba Orientali," *Wright 582* (G, HOLOTYPE; A, BR, G, GH, GOET, ISOTYPES); Monte Verde, 10 May 1859, *Wright 1436* ex. p. (BR, G, GH, S; mixed in some collections with *Margaritaria scandens*).

As here circumscribed, ssp. *grisebachianus* is readily distinguishable from ssp. *nutans* except in the Cayman Islands. The association of the Kings collection from Little Cayman with ssp. *grisebachianus* rather than with the Grand Cayman plants (which are assigned to ssp. *nutans*) is based on its pointed revolute leaves hirsutulous beneath (on the midrib) and its dark persistent stipules. However, it must be granted that the Little Cayman specimen shows several discrepancies as compared with the Cuban plants, for it has female pedicels 15–30 mm. long and female flowers which are neither all solitary nor all axillary to unreduced leaves, whereas the Cuban collections show pedicels 6–14 mm. long and have completely solitary, axillary flowers. The population on Little Cayman may, therefore, be classified as transitional between the two subspecies but with the stronger leaning to ssp. *grisebachianus*, whereas the Grand

Cayman plants fall closer to ssp. *nutans*. Additional collections, particularly from Cayman Brac and from Cuba, might provide a decisive test of the practicability of the present classification. It may prove to be unfeasible to maintain two subspecies if additional break-down in the characters is shown to exist; but, for the present, the Cuban and Jamaican populations appear to be sufficiently distinct from one another to warrant separation.

46. **Phyllanthus pachystylus** Urb. Symb. Ant. 3: 286. 1902. (PLATE I, *fig.* 2; PLATE XXIV, *figs.* I–L).

A slender sparsely branching shrub (usually with a single main stem) becoming 1–1.5 m. high; main stem 3–5 mm. thick, terete, bark burnished and reddish brown becoming greyish and fissured; branches mostly steeply ascending, reddish brown angled, furrowed, glabrous or rarely hirsutulous, becoming mostly 8–25 cm. long, c. 1.2–2.5 mm. thick, with c. 5–15 nodes. Leaves: stipules lanceolate to linear-lanceolate, (1.2–) 1.5–2 (–3) mm. long, 0.4–1 mm. broad, acute, glabrous, becoming darkened and indurate, persistent, entire. Petioles stout, glabrous or rarely hirsutulous, 2.5–5 mm. long. Leaf-blades becoming rigidly coriaceous, mostly elliptic-oblong (varying to narrowly elliptic, ovate, or lanceolate), mostly 3.5–7 (–9) cm. long, (1–) 1.5–3.5 (–4.5) cm. broad, obtuse, rounded, or retuse at the tip, acute to obtuse at the base; above dark purplish (drying blackish) when young, becoming more or less olivaceous-plumbeous, essentially smooth (often somewhat wrinkled), the midrib and lateral veins noticeably sunken; beneath much paler, alveolar-pruinose, the midrib prominently raised, the spreading to ascending laterals (5–7 on a side) somewhat raised, the reticulum of veinlets often visible; margins thickened, conspicuously revolute.

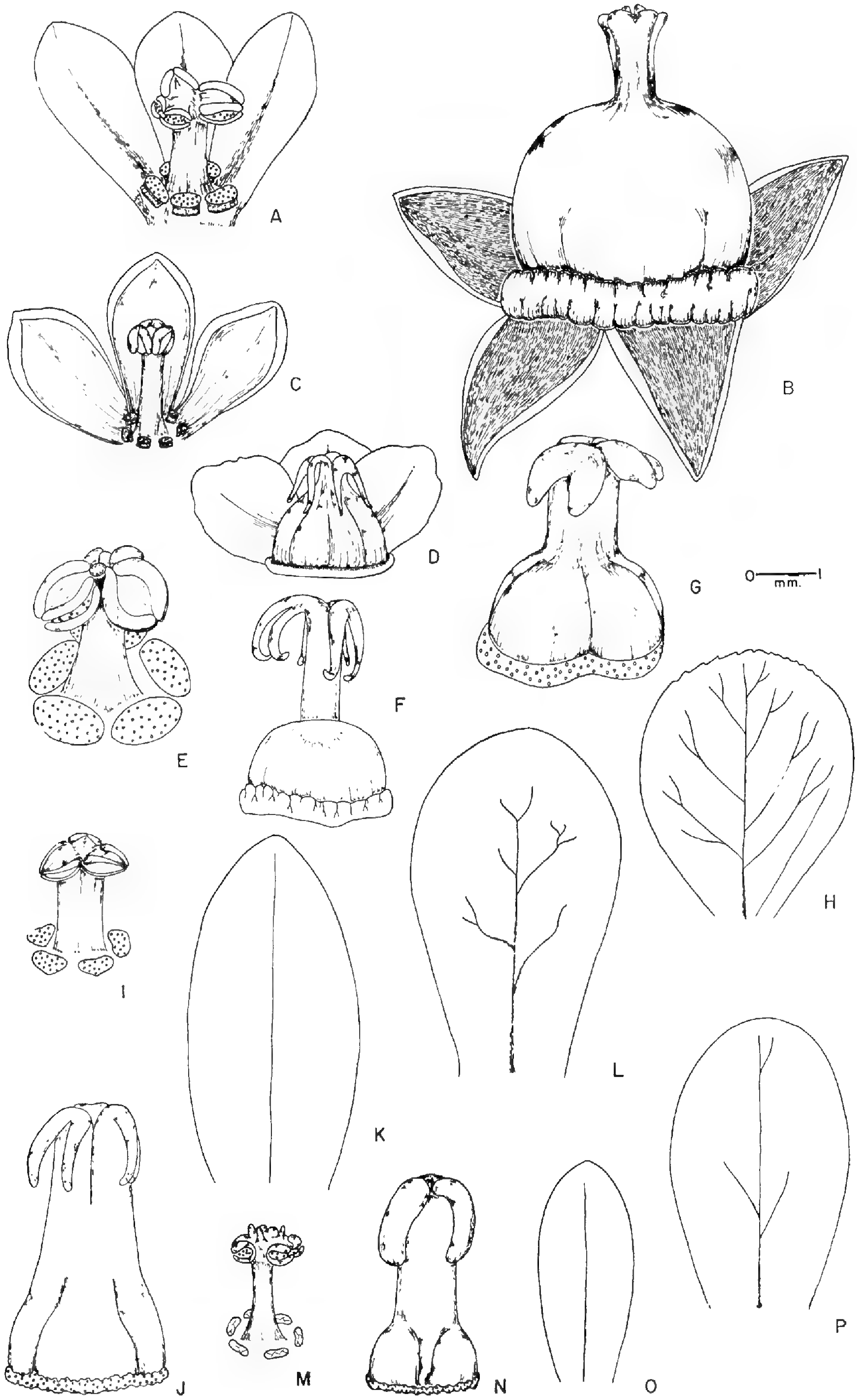
Monoecious; cymules mostly bisexual, each with 1–3 female and 2–10 male flowers, in the axils of bracts on naked pseudo-terminal thyrses (the thyrses produced from one or several axils immediately below the tip of the branchlet); cymules sometimes unisexual.

Male flower: pedicel capillary, smooth or rarely hirsutulous, 7–12 mm. long. Calyx-lobes 6, rather fleshy, biseriate (but sometimes obscurely so),

---

PLATE XXIV. FLOWERS OF SECT. *Elutanthos*.

FIGS. A–B. Male and female flowers of *Phyllanthus botryanthus* Muell. Arg. (*Haught 6556* [GH]). FIGS. C–D. Male and female flowers of *Phyllanthus anderssonii* Muell. Arg. (*Warming 27* [C]). FIGS. E–F. Androecium and gynoecium of *Phyllanthus nutans* Sw. ssp. *nutans* (*Proctor 15245* [GH], *Webster & Wilson 5075* [A]). FIGS. G–H. Gynoecium and female calyx-lobe of *Phyllanthus nutans* ssp. *grisebachianus* (Muell. Arg.) Webster (*Wright 1436* [S]). FIGS. I–L. Androecium, gynoecium, inner and outer female calyx lobes of *Phyllanthus pachystylus* Urb. (androecium, *Howard 6199* [GH]; others, *Ekman 15037* [S]). FIGS. M–P. Androecium, gynoecium, and inner female calyx-lobes of *Phyllanthus urbanianus* Mansf. (*Ekman H10435* [S]).



Webster, West Indian Phyllanthus

(2–) 2.3–3 mm. long, outer lobes usually oblong and obtuse, c. 1.3–1.6 mm. broad, with midrib simple or nearly so, inner lobes usually obovate, c. 1.5–2 mm. broad, with midrib usually sparsely branched (occasionally simple); lobes entire or sparsely denticulate. Disk-segments 6, usually rather massive, reniform to elliptic, foveolate, c. 0.3–0.6 mm. across. Stamens 3; column rather stout, (0.6–) 0.75–0.9 (–1) mm. high, mostly 0.4–0.6 mm. thick; anthers sessile atop the column, basally connate, the common connective plane or umbonate, triangular, c. 0.3–0.55 mm. long and 0.4–0.6 mm. broad; anther-sacs divergent, dehiscing horizontally, the slits not confluent; pollen grains c. 21–24 μ in diameter, areoles polybrochate, c. 4–6 μ across.

Female flower: pedicel slender, terete, more or less reddish, glabrous or rarely hirsutulous, 2.5–6 (–8) mm. long, 0.3–0.5 mm. thick. Calyx-lobes 6, distinctly biseriate, (2–) 2.5–3.5 (–4) mm. long, entire or obscurely denticulate; outer lobes narrowly oblong with midrib almost or quite unbranched (rarely copiously pinnately branched), c. 1–1.5 (–1.9) mm. broad; inner lobes obovate or spathulate with midrib always pinnately branched, c. 1.4–2.2 mm. broad; lobes entire or obscurely denticulate. Disk shallowly cupuliform, angled, finely crenulate. Styles connate or coherent into a massive column (0.5–) 0.7–1 (–1.5) mm. high which is not sharply demarcated from the ovary; free ends of styles recurved, 0.4–0.6 (–0.9) mm. long, more or less dilated, parted ½ to ¾ their length, the tips broadly triangular to lanceolate, obtuse to acute.

Capsule rounded in outline, c. 5 mm. high and 8 mm. broad, rarely remaining entire, the valves rugulose. Columella rather massive, (3–) 4 (–4.5) mm. high. Seeds trigonous, nearly symmetric, (4–) 4.5–5.4 mm. long, 2.7–3.1 mm. radially, 2.9–3.5 mm. tangentially, light brown, smooth (very finely striolate); hilum submedian; micropylar end sometimes developing a conspicuous whitish caruncle.

Collected in flower and fruit April through September.

TYPE: Cuba, Oriente, *Wright 1947.*

DISTRIBUTION: endemic to the Sagua-Baracoa massif, eastern Cuba (MAP XVIII).

CUBA. ORIENTE: Sierra de Nipe, near Río Piloto, *Ekman 2274, 6028, 15037* (S); Charrascal de la Cueva, Mayarí, *León et al. 19888* (MICH); wooded hillside, San José, *Howard 6199* (GH, NY); near Woodfred, deciduous woods and thickets, *Shafer 3617* (NY); edge of savannas near Sagua de Tánamo, 3 April 1861, *Wright 1947* (GH, LECTOTYPE; G, GOET, ISOTYPES); pinares near Moa, *Acuña 12503* (US), *Bucher 102, 107* (NY), *Clemente 3555* (MT), *Marie-Victorin et al. 21565* (A, MT), *21705* (MT); Franklyn Mine, *Clemente & Alain 3890* (MICH); Playa La Vaca, *Clemente 4918* (MICH); Cerro de Miraflores, *Marie-Victorin et al. 21557* (A, MT); dense pine woods 15 kms. southwest of Moa mill, *Howard 5955* (GH); pinelands on serpentine between Río Moa and Río Yagrumaje, *Webster 3757, 3771* (MICH); Cayo Chiquita, 8 km. south of Moa, *Webster 3848* (GH, MICH); pine scrub 10 km. south of Moa, *Webster 3895* (GH, MICH); scrublands 16 and 18 km. south of Moa, *Webster 3906, 3907* (GH, MICH).

This species has a very characteristic appearance in the field due to its shiny, coriaceous, purplish leaves and nodding inflorescences which may even be twining in dense undergrowth. Unlike the other West Indian species of sect. *Elutanthos*, which are predominantly calciphiles, *P. pachystylus* appears to be confined to serpentine; and like many species in other genera growing on the limonite soils of the Moa region, it shows a greater degree of apparent morphological adaptation to dry conditions than do its related congeners. Ekman noted on his labels that in the Sierra de Nipe the species is rare and becoming extinct; but in the Moa area it is certainly still thriving and in fact is one of the commonest undershrubs in the open pinelands there.

The closest relationship to *P. pachystylus* appears to be shown by *P. nutans* ssp. *grisebachianus*, which occupies a clearly allopatric range in the Monte Verde area, although the gap in range may be no more than about 20 or 25 miles. The thinner stipules and leaf-blades, solitary axillary flowers, longer female pedicels, and less massive styles of that plant present so many distinctions that there can be no doubt as to the specific distinctness of *P. pachystylus*.

47. **Phyllanthus urbanianus** Mansf. Repert. Sp. Nov. 32: 86. 1933. (PLATE XXIV, *figs.* M–P).

A small shrub (probably with the aspect of *P. pachystylus*); main stem subsimple, c. 2.5 mm. thick, terete, bark dark reddish brown, reddish hirsutulous; ultimate branches reddish brown, terete, somewhat furrowed, reddish hirsutulous, c. 20–35 cm. long, 0.9–1 mm. thick, with c. 20–45 nodes. Leaves: stipules narrowly lanceolate, 1.2–1.8 mm. long, 0.25–0.5 mm. broad, acute, thin and scarious, olivaceous becoming dark brown and persistent. Petioles rather slender, reddish- or hyaline-hirsutulous, c. 3–4 mm. long. Leaf-blades chartaceous, elliptic, c. 4–6.5 cm. long and 1.2–2.7 cm. broad on main stem, decreasing to 1.5–3 cm. long and 0.4–1.2 cm. broad at tips of branches, acute at the tip, acute to obtuse at the base; above dark olivaceous, reddish hirsutulous along the scarcely raised midrib and laterals; beneath pale, copiously hirsutulous throughout, the midrib and laterals (4 or 5 on a side) raised, light brownish; margins unthickened, narrowly revolute.

Monoecious; cymules mostly bisexual, each with a single central female flower and several lateral males, in the axils of semi-reduced (still leaf-like) bracts on distal branches (which are homologous with the "naked" thyrses of *P. nutans*); individual cymules occasionally replaced by depauperate inflorescence axes.

Male flower: pedical capillary, smooth to copiously hirsutulous, c. 8–10 mm. long. Calyx-lobes 6, c. 2.2–2.5 mm. long, more or less biseriate: outer lobes narrowly oblong, c. 0.75 mm. broad, inner lobes elliptic-oblong, slightly over 1 mm. broad; lobes all rounded at the tip, reddish with rather ill-defined yellowish margins, the midrib simple or sparingly branched. Disk-segments 6, flattened, roundish, foveolate, c. 0.2–0.3 mm. across.

Stamens 3; column c. 0.8 mm. high, slightly constricted above; anthers sessile, c. 0.25 mm. long and 0.4 mm. broad, alternating with three erect apiculae c. 0.2 mm. long; anther-sacs rather broadly divaricate, dehiscing horizontally; pollen grains 18–21 μ in diameter, areoles transitional between oligobrochate and polybrochate, c. 4–6 μ across.

Female flower: pedicel slender, terete or nearly so, sparsely to copiously hirsutulous, 12–15 mm. long. Calyx-lobes 6, biseriate: at anthesis, outer lobes linear-oblong, obtuse, with simple midrib, 2–2.3 mm. long and 0.8–0.9 mm. broad, inner lobes obovate, rounded at the tip, with sparingly branched midrib, 2.7–3 mm. long and 1.3–1.5 mm. broad; lobes chartaceous, reddish, essentially entire, becoming reflexed in fruit. Disk shallowly cupuliform, 6-angled, rather fleshy, crenulate. Styles connate into a massive column c. 1 mm. high and 0.5 mm. broad; free ends of styles recurved, dilated, oblong, obtuse or emarginate, c. 0.4–0.6 mm. long.

Capsule c. 4 mm. high and 7 mm. broad, somewhat rugulose. Columella c. 2.5 mm. high. Seeds trigonous, slightly asymmetric (somewhat umbonate at one corner), c. 4.2 mm. long, 2.7 mm. radially, 2.9–3 mm. tangentially, smooth, mottled light brown; hilum submedian.

TYPE: Haiti, Dept. Sud, Massif de la Hotte, western group, Les Roseaux, Hab. Gros-Roche, rocky forest, hard limestone, alt. 400 m., rare, 27 June 1928, *Ekman H-10435* (S, HOLOTYPE; A, US, ISOTYPES).

DISTRIBUTION: known only from the type collection (MAP XVIII).

This rare endemic species is of particular phytogeographic interest, because it is the only representative of the section on Hispaniola. It resembles both *P. pachystylus* and *P. nutans* (especially ssp. *grisebachianus*), but differs in its more hirsutulous parts and very distinctive staminal column and styles, so that there would appear to be no reason to question its specific distinctness. The Cuban and Jamaican affinities of *P. urbanianus* provide another good demonstration (in addition to species relationships in sects. *Cyclanthera* and *Hemiphyllanthus*) of the profound floristic division between the Sellean peninsula of Haiti and the remainder of Hispaniola.

Subgenus VIII. **Xylophylla** (L.) Pers. Syn. Pl. 591. 1807; emend.

Xylophylla L. Mant. 2: 147–148. 1771.

Trees or shrubs with phyllanthoid branching, the branchlets pinnatiform or bipinnatiform; monoecious or very rarely dioecious. Male flower; calyx-lobes 4–6; disk of as many segments, these free or united; stamens 2–15, free or more commonly united; anthers dehiscing vertically to horizontally; pollen grains globose, areolate. Female flower: calyx-lobes 5 or 6 (rarely 4); disk cupuliform or patelliform; ovary of 3 carpels; styles bifid or multifid, sometimes dilated at the tips. Fruit capsular; seeds 2 in each locule.

Included in this large, entirely American subgenus of about a dozen sections and 60 species are the majority of the neotropical woody species of *Phyllanthus*. The West Indies are definitely the center of distribution and apparently also of the evolution of the group, but a few additional sections (e.g., *Oxalistylis* and *Ciccastrum*) are confined to South America. In Mueller's treatment in the "Prodromus" the sections and species here brought together were much scattered, the following of his sections belonging (at least in part) to subg. *Xylophylla*: 12, 16–19, 34 (in small part), 35–36, and 44. Persoon's original conception of subg. *Xylophylla* as including only the phylloclade-bearing species was of course much narrower than that here adopted, and in fact corresponds to sect. *Xylophylla* alone.

Because of the dominant position of representatives of subg. *Xylophylla* in the West Indies, its relationships are of particular interest. However, although certain lines of affinity are very apparent within the group, there are several unresolved problems which make impossible an accurate tracing of phylogeny. It is certain that there is a close relationship between subg. *Xylophylla* and subg. *Botryanthus*, and the approach is nearest between sects. *Asterandra* and *Elutanthos*, respectively. Some of the Central American species of sect. *Elutanthos* (e.g., *P. grandifolius*) resemble sect. *Asterandra* so clearly that there can be little doubt of a significant kinship. However, there are some obstacles, to be discussed more fully farther on, which make it at least uncertain that subg. *Xylophylla* can be directly derived from subg. *Botryanthus* via sect. *Asterandra*. The small number of stamens in the flowers of *Botryanthus* and the large capsule of such species as *P. grandifolius* are features which appear to be derivative; so that it is possible to read the evolutionary series the other way around and to postulate that subg. *Botryanthus* has been derived from sect. *Asterandra* by reduction in the androecium accompanied by loss of phyllanthoid branching and increase in fruit size.

Within subg. *Xylophylla* two main phyla can be discerned: a series beginning with sect. *Williamia* and running through sects. *Thamnocharis* and *Orbicularia*; and a series proceeding from sect. *Asterandra* to sects. *Epistylium*, *Hemiphyllanthus*, and *Xylophylla*. Standing alone is sect. *Omphacodes*, which is aberrant in many respects and which in fact resembles sect. *Ciccopsis* of subg. *Cicca* more than it does any single section of subg. *Xylophylla*. It is classified here because of its areolate pollen grains, but without strong conviction, and its relationships need to be further investigated.

The initial dichotomy between sect. *Williamia* and sect. *Asterandra* has some puzzling aspects which cannot yet be resolved. That the higher stamen number in *Williamia* may be a primitive character is attested by the clearly documented reduction-series to a lower number in the derived sections; furthermore, the seeds of *Williamia* are less highly modified than those of *Asterandra*. However, the South American sect. *Oxalistylis*, which is closely related to *Asterandra*, has more unspecialized seeds, and perhaps can be thought of as a group more or less coördinate with *Williamia*, if indeed the two are not descended from some immediate common ancestor.

The anatomical evidence from leaves, as shown earlier in this study

(Jour. Arnold Arb. 37: 220. 1956), demonstrates for many taxa of this subgenus an interesting correlation between floral modification and increasing sclerification of foliar tissue. The rationale for this would appear to be that the evolutionary history of many of the groups of subg. *Xylophylla* has been one of increasing adaptation to xeric conditions. However, the adaptive radiation has been rather complex, so that no over-all generalizations on the ecology of the species can be made. In both the *Williamia* and *Asterandra* lines, however, the end-products of evolution (viz., sects. *Orbicularia* and *Xylophylla*) comprise species so altered in appearance that their ancestry could scarcely be guessed if it were not possible to trace it back through intervening species.

KEY TO THE SECTIONS

1. Branchlets pinnatiform.
    2. Styles each terminating in a dilated more or less crenate to lacerate stigma.
        3. Disk-segments of male flower free or at least not completely united; seeds thin-walled, neither fissured nor mottled; petioles without undulate marginal ridges.
            4. Leaves obtuse or emarginate at the tip; styles not calyptriform or if so then branchlet leaves opposite; stamens 3–15. . . 16. **Williamia**
            4. Leaves acuminate; styles calyptriform or united into a massive column; stamens 2 or 3 (rarely 4); at least some inflorescences cauliflorous (except in *P. axillaris*). . . . . 21. **Epistylium**
        3. Disk-segments of male flower connate into a massive ring.
            4. Leaves acuminate, neither revolute nor golden beneath, the petiole with conspicuous undulate-ruffled margins; seeds thick-walled, mottled (as in *Ricinus*); stamens 3–5. . . . . 20. **Asterandra**
            4. Leaves blunt at the tip, revolute, golden beneath, the petiole without ruffled margins; seeds thin-walled, blackened and fissured; stamens 2. . . . . 22. **Glyptothamnus** [19]
    2. Styles bifid, the branches usually slender, never lacerate (rarely adaxially auriculate).
        3. Capsule somewhat fleshy, tardily dehiscent; leaf-blades chartaceous, the blade decurrent on the petiole; stamens 3. . . . . . . 19. **Omphacodes**
        3. Capsule dry, promptly dehiscent; leaf-blades chartaceous to coriaceous, the blade not decurrent on the petiole; stamens 2–6.
            4. Leaf-blades small (less than 2 cm. long), with conspicuous mesophyllar sclereids, often concave beneath and with revolute margins; seeds less than 3 mm. long; stipules more or less persistent; flowers mostly appearing after the leaves. . . . . 18. **Orbicularia**

---

[19] Sect. **Glyptothamnus**, sect. nov. Frutices monoicae, foliis coriaceis revolutis subtus aureis; cymulis unisexualibus; flore masculo laciniis calycis 4, disco integro summopere dilatato, staminibus 2 filamentis connatis, antheris horizontaliter dehiscentibus, granis pollinis globosis areolatis; flore femineo laciniis calycis 5, disco magno integro, stylis dilatatis laceratis; seminibus fuscis sulcatis. — Species typica *Phyllanthus chryseus* Howard (sectional epithet from Gr. *glyptos*, carved, and *thamnos*, shrub, in allusion to the appearance of the massive flowers and leaves).

4. Leaf-blades larger, the sclereids aggregated within the plane, thickened marginal rim (rather than in the mesophyll); seeds over 3 mm. long; stipules caducous; flowers appearing with the leaves. . . . . 17. **Thamnocharis**

1. Branchlets bipinnatiform, or modified into phylloclades.
   2. Branchlets not greatly dilated, bearing typical leaves, the penultimate axis incrustate or scurfy. . . . . 23. **Hemiphyllanthus**
   2. Branchlets dilated and transformed into phylloclades, the leaves normally absent except on seedlings; axes never incrustate or scurfy. 24. **Xylophylla**

Sect. 16. **Williamia** (Baill.) Muell. Arg. Linnaea 32: 4. 1863; DC. Prodr. 15(2): 328. 1866.

Williamia Baill. Etud. Gen. Euphorb. 559, *pl. 27, figs. 9–10.* 1858.

Shrubs with phyllanthoid branching; leaves chartaceous to coriaceous, stipules deciduous or persistent. Monoecious, cymules bisexual, the flowers maturing after the leaves. Male flower: calyx-lobes 5 or 6; stamens 3–15 (very rarely 2), filaments united into a column, anthers in 1–3 whorls; pollen grains areolate. Female flower: calyx-lobes 5 or 6; disk plane, angular, often massive; ovary sessile or definitely stipitate; styles erect or spreading, free or connate, the distal ends dilated and lacerate or dentate. Capsule oblate, dry, not veiny; seeds colliculose or verruculose, less than 3 mm. long.

TYPE SPECIES: *Williamia pruinosa* Baill. (= *Phyllanthus discolor* Poepp. ex Spr.).

As here defined, the circumscription of sect. *Williamia* is enlarged from that previously held (Contr. Gray Herb. **176**: 57. 1955; Jour. Arnold Arb. **37**: 220. 1956) by the inclusion within it of sect. *Williamiandra*. The emended section thus comprises seven Cuban species which are indubitably related, although they are morphologically so far divergent from one another that the group might at first sight appear to be an unnatural one. A well-marked evolutionary series of increasing specialization may be traced between *P. discolor*, with its thin, unsclerified leaves and androecium of up to 15 stamens, and *P. incrustatus*, which has highly sclerified leaves and only 2–4 stamens. However, despite the prominence of these phylogenetic trends, the relationships of the species of the three subsections cannot be visualized as a simple and clear-cut "family tree."

The affinity of sect. *Williamia* with sects. *Orbicularia* and *Thamnocharis* is particularly clear in view of the fact that the latter appear to be its direct offspring. In fact, the ancestry of both sections may with reasonable confidence be traced back to subsect. *Discolores*, since *Orbicularia* and *Thamnocharis* would appear to have been derived from progenitors similar to *P. microdictyus* and *P. discolor*, respectively. In both instances differentiation of the derived taxa has involved increased foliar sclerification, but this has occurred in a strikingly different manner, for the sclereids are scattered through the mesophyll in sect. *Orbicularia*, whereas they are aggregated within the marginal rim of the lamina in sect. *Thamnocharis*.

Because of its ancestral relationship to sects. *Orbicularia* and *Thamnocharis*, as well as the relatively unspecialized morphological features of its subsection *Discolores*, sect. *Williamia* has been placed first in the linear arrangement of sections under subg. *Xylophylla*. However, this is not intended necessarily to imply that *Williamia* is the most primitive of all the taxa within the subgenus. The differences in stamen number on which Mueller laid such stress appear far less significant in the light of present knowledge, for the stamen number of *P. discolor* is mostly 10-13 instead of the 15 reported in the literature; and in any event, even the former number is by no means a certain indication of primitiveness. The sister species of *P. discolor*, *P. microdictyus*, is more similar in floral characters to the South American sect. *Oxalistylis*. It appears that *P. discolor* and *P. microdictyus* may best be regarded as vicarious descendants from a common ancestor, specialization having progressed further in the flowers of the former and the leaves of the latter.

The flowers of *P. salviaefolius*, the type (and only?) species of sect. *Oxalistylis*, are so similar to those of *P. microdictyus*, particularly with regard to the gynoecium, that the possibility of uniting sects. *Oxalistylis* and *Williamia* might possibly be considered. However, the South American species differs by having several female flowers per cymule, differently ornamented seeds, and very different leaves much more like those of sect. *Asterandra*; so, for the time being, it seems justifiable to maintain the two sections as distinct.

KEY TO THE SUBSECTIONS AND SPECIES

1. Leaves of branchlets alternate; stigmas (style-tips) not calyptriform.
    2. Stems smooth, lenticels (if present) sparse and inconspicuous; stamens 6–15. . . . . Subsect. 16a. **Discolores**
        3. Leaves chartaceous, not highly sclerified.
            4. Calyx-lobes of female flower 2–3 mm. long; styles less than 2 mm. long; stamens mostly 9–13; leaf-blades irregularly reticulate above. . . . . 48. *P. discolor*
            4. Calyx-lobes of female flower 7–8.5 mm. long; styles 3.5–5 mm. long; stamens 6–10; leaf-blades finely and evenly reticulate above, the areoles straight-sided. . . . . 49. *P. microdictyus*
        3. Leaves coriaceous, with abundant mesophyllar sclereids. . . . . 50. *P. cristalensis*
    2. Stems incrustate, the bark breaking up into small platelets separated by spongy tissue; stamens (2–) 3–6. . . . . Subsect. 16b. **Incrustati**
        3. Stipules of branchlets acicular-conduplicate, mostly caducous; staminal column prolonged into a terminal apiculum; disk of female flower with a crenate upturned rim; leaves mostly 1.5–2.5 cm. long. . . . . 51. *P. williamioides*
        3. Stipules of branchlets nearly plane, indurate and persistent; staminal column not apiculate; disk of female flower plane, entire.
            4. Leaf-blades 2.5–4.5 cm. long, prominently reticulate beneath;

pedicel of female flower 10–15 mm. long; stamens 5 or 6. . . . . 52. *P. excisus*

4. Leaf-blades 0.7–1.5 cm. long, obscurely reticulate beneath; pedicel of female flower 1–3 mm. long; stamens 3 or 4 (rarely 2). . . . . 53. *P. incrustatus*

1. Leaves of branchlets opposite; stigmas (dilated style-tips) forming a cap covering most of the ovary; axes with conspicuous lenticels. . . . . Subsect. 16c. **Mirifici**

Only species . . . . 54. *P. mirificus*

Subsect. 16a. **Discolores**, subsect. nov.

Williamia Baill. Etud. Gen. Euphorb. 559, *pl. 27, figs. 9–10.* 1858.

Phyllanthus sect. *Williamia* (Baill.) Muell. Arg. in DC. Prodr. **15**(2): 328. 1866 (ex p.).

Stems smooth, lenticels obsolete or sparse; leaves of branchlets alternate, chartaceous or (in *P. cristalensis*) coriaceous and sclerified; stamens 6–15 (number unknown in *P. cristalensis*); styles erect, the tips moderately dilated.

TYPE SPECIES: *Phyllanthus discolor* Poepp. ex Spr.

There can be no doubt that subsect. *Discolores* occupies a significant position in the evolutionary sense, for sects. *Thamnocharis* and *Orbicularia* may with a high degree of probability be spoken of as derived from *P. discolor* and *P. microdictyus*, respectively. If, as suggested above, the high stamen number of *P. discolor* is secondarily derived from a 5- or 6-merous condition, there has at any rate been a reduction in number in the species of the derived taxa (subsect. *Incrustati*, sects. *Thamnocharis* and *Orbicularia*).

The inclusion of *P. cristalensis* within this subsection can only be provisional, for its floral characters are still insufficiently known. On the basis of its vegetative characters, it would appear to be related to *P. microdictyus* and *P. excisus*, since it has the smooth axes of the former and the highly sclerified leaves of the latter. Should its present position appear justified after the examination of adequate fertile material, *P. cristalensis* would represent a nearly schematic connecting link between subsects. *Discolores* and *Incrustati*.

48. **Phyllanthus discolor** Poepp. ex Spr. Syst. **3**: 21. 1826.

(PLATE XXV, *figs.* A–C).

Phyllanthus pruinosus Poepp. ex Rich. in Sagra, Hist. Nat. Cuba **11**: 216. 1850; non sensu Muell. Arg. in DC. Prodr. **15**(2): 387. 1866.

Williamia pruinosa (Poepp.) Baill. Etud. Gen. Euphorb. 560, *pl. 27, figs. 9–10.* 1858.

Diasperus discolor ("Spr.") O. Ktze. Rev. Gen. **2**: 599. 1891.

Diasperus pruinosus ("Rich.") O. Ktze. op. cit. 600.

Phyllanthus decander Sessé & Moc. Fl. Mex. ed. 2, 212–213. 1894.

A shrub becoming c. 1–2 m. high, sparsely branching, the main stem(s) slender (mostly 2–3 mm. thick), light brown, smooth, terete, with brown pith. Cataphylls not indurate, early deciduous: stipules triangular to lanceolate, acute or acuminate, 4–8 mm. long and 1–2 mm. broad (smaller on weak shoots), truncate at the base, thin and scarious, dark reddish brown with narrow paler denticulate or entire margins; blade linear-lanceolate, acuminate, 4–6 mm. long and 0.7–1 mm. broad. Deciduous branchlets 8–15 (–25) cm. long, 0.7–1.3 mm. thick, light brown or stramineous, terete to distinctly flattened, with (5–) 7–14 (–16) leaves; first internode 1.5–3 cm. long, median internodes mostly 1–2 cm. long. Leaves: stipules thin and scarious, early deciduous (except at tips of branchlets), linear-lanceolate, acuminate, (2.5–) 3.5–6.5 (–7) mm. long, (0.4–) 0.7–1.2 mm. broad, brownish, with entire margins. Petioles 2–4 mm. long, subterete, dark brownish, smooth. Leaf-blades chartaceous, mostly ovate or elliptic, (2–) 2.5–4 (–5.5) cm. long, (1–) 1.3–3 (–3.5) cm. broad, narrowed to an obtuse (less commonly rounded or emarginate) inconspicuously apiculate tip, acute to truncate or rarely subcordate at the base; above olivaceous or bright green, the midrib and the arching, crooked laterals slightly raised; beneath whitish- or creamy-pruinose (due to a waxy coating), the midrib salient, the laterals (c. 5–7 on a side) raised, minor veinlets forming a fine reticulum; margins unthickened, plane or casually revolute.

Monoecious; branchlets usually but not always floriferous; cymules bisexual, each most often with 1 or 2 (3) central female and c. 4–6 lateral male flowers; bracteoles of cymules triangular, dark brown, scarious, persistent.

Male flower: pedicel (1.5–) 2–6 mm. long. Calyx-lobes 5, chartaceous, subequal or usually unequal, rounded at the tip, entire or minutely denticulate near the apex; outer lobes ovate or oblong, 1.2–2.5 mm. long and 0.9–1.3 mm. broad; inner lobes obovate or spathulate, 1.7–3.5 mm. long and 1.3–1.9 mm. broad, 3- to 5-nerved from the base. Disk-segments 5, roundish, smooth and entire, c. 0.3–0.5 mm. broad. Stamens (7–) 9–13 (–15); filaments connate into a column c. 1–2 mm. high, the free portions 0.2–0.75 mm. long, erect or arching and spreading; stamens spirally arranged or in two superposed whorls with a whorl of 3 (–5) terminating the column; anthers c. 0.2–0.4 mm. long, 0.25–0.5 mm. broad, the upper erect or ascending, the lower often spreading or deflexed; anther-sacs slightly divergent, dehiscing longitudinally, the slits contiguous but usually not confluent; pollen grains 18–27 μ in diameter.

Female flower: pedicel slender, becoming (3–) 5–13 (–17) mm. long. Calyx-lobes 5, distinctly unequal, rounded at the tip, entire, with several veins from the base (at least in the larger); outer lobes ovate or oblong, 1.2–1.8 mm. long, 0.6–1.3 mm. broad; inner lobes (2–) 2.5–3 mm. long, 1.5–2.8 mm. broad. Disk rather massive, obtusely 5-angled, foveolate, the margins plane and entire. Ovary oblate or foveolate, with 3 low but distinct ribs, usually sessile; styles erect, somewhat unequal, free or connate at the base, c. 0.3–0.7 mm. long, the dilated ends (stigmas) roundish or crescent-shaped, crenulate or lacerate (but often appearing entire due to recurved tips of lobes), sometimes adaxially auriculate, 0.5–0.8 mm. broad.

Capsule oblate, smooth or somewhat rugulose, rounded in outline, reddish brown, c. 2.1–2.3 mm. in diameter. Columella slender, 1.2–1.5 mm. long. Seeds acutely trigonous, symmetric, 1.7–1.8 mm. long, 1.1–1.3 mm. radially, 1.2–1.25 mm. tangentially, brown with somewhat irregular longitudinal lines of transversely elongate dark reddish brown dots; hilum triangular, c. 0.4 mm. long.

Collected in flower and fruit January through August.

TYPE: "Ad rivulos Cubae in Sumidero," *Poeppig* (W, LECTOTYPE; BR, F, ISOTYPES). Poeppig's material appears to include more than one collection. The lectotype collection is the one associated with the printed label reading "Phyllanthus discolor En pl. Cub. MSS. . ."; but several additional collections made in Cuba in 1823 by Poeppig (all apparently in Matanzas province) are preserved in the Vienna herbarium. A specimen in the Paris Museum bearing the label "Phyllanthus pruinosus Poepp. (ad Spreng. ad Phyll. polygonoid. Nutt. ductus) Cuba. Sylvae lucidae" and a specimen collected for Sagra (also in the Paris Museum) represent the type material of *P. pruinosus* Poepp. ex Rich.

Although applied by Mueller and others to the plant known in this work as *P. caroliniensis* ssp. *saxicola*, the name *P. pruinosus* Poepp. ex Rich. is actually a synonym of *P. discolor*. Its publication was apparently inadvertent, for Poeppig's specific name, when it appears on the labels in script specially printed for his collection, is usually associated with specimens of *P. caroliniensis* ssp. *saxicola*. Evidently there was a mixture of labels in the case of the Poeppig specimens which went to Paris, so that Richard was misled into describing the present plant under a different name than that intended by Poeppig. Mueller (Linnaea 32: 30. 1863) independently published *P. pruinosus* for the other plant, as designated by Poeppig, but this name must of course be rejected as a later homonym.

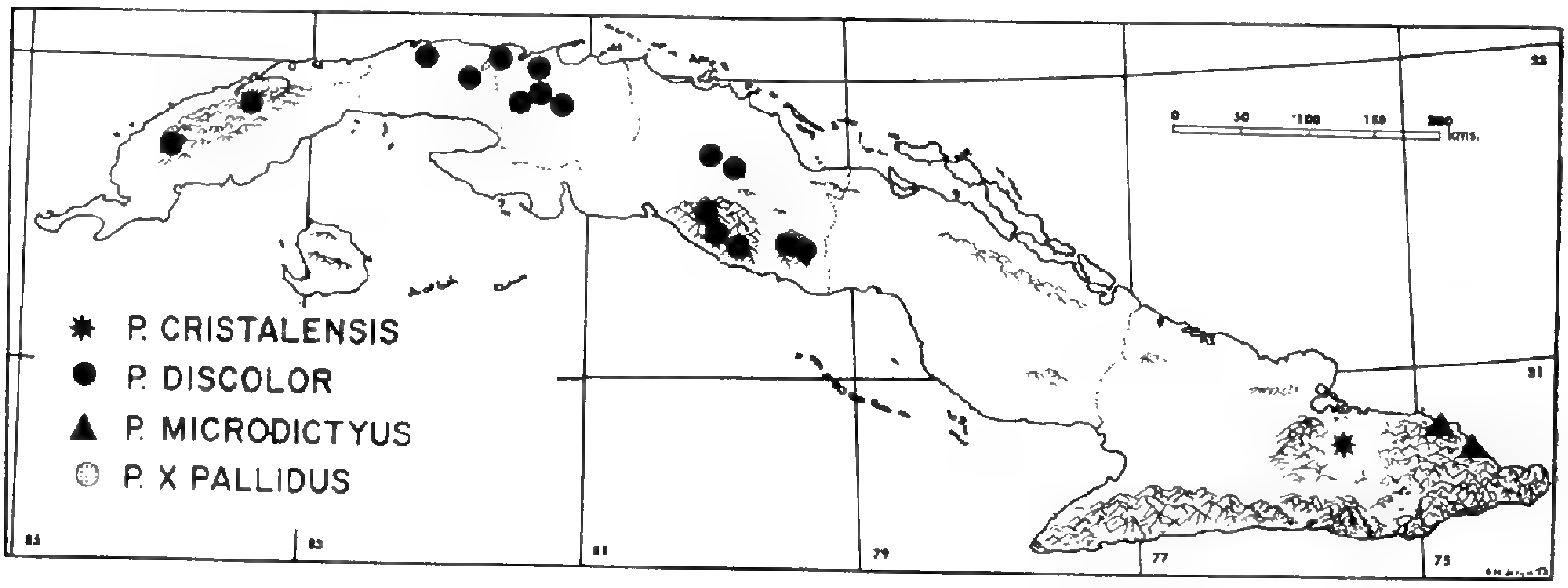
DISTRIBUTION: serpentine barrens and hillsides, central and western Cuba (MAP XXII).

CUBA: without locality, *Sagra* (A,P,W: SYNTYPES of *P. pruinosus*). PINAR DEL RIO: Sumidero, between Hoyo Colorado and Francisco, at a brook, *Ekman 18205* (S); Los Organos, Sabanilla, *Wright 1941* ex p. (F, GH, GOET, MO, NY, P, S, US; data ex GH); pinelands, Loma Cajálbana, La Palma, *Alain 2362* (GH); Sagua, Bahia Honda, *Wright 1949* (G, GH, GOET; data ex GH); Rangel, Zambumbia Hill, *León 12775* (MICH, NY). HABANA: La havane, 1821, *Leman* (P); Guanabacoa [ex Flor. Mex. ed. 2], *Sessé & Mociño 4566* (F, TYPE COLLECTION of *P. decander*); eruptive rock soil, Madruga, *Britton, Britton, & Shafer 631, 690* (NY), *León 3330* (MT, NY). MATANZAS: cuabales northwest of Pan de Matanzas, southeast of Canasí, *Ekman 16469* (S); savanna, Sabanilla de la Palma, *León, Roca, & Edmund 9652* (NY); Tetas de Camarioca, serpentine barren; *Britton, Britton, & Wilson 14063* (NY); Sumidero, *Poeppig* (W, LECTOTYPE; BR, F, MO, ISOTYPES)[20]; San Miguel de los Baños, *Killip 13867* (US),

---

[20] This collection is also a syntype collection of *P. pruinosus*.

León & Roca 8907 (NY). LAS VILLAS: Palm barren, Santa Clara, *Britton & Cowell 10202* (NY); arroyo Ciento Viejo, 12.5 km. east of Santa Clara, *Howard 5081* (GH, MT), *Webster et al. 250* (GH); Trinidad Mountains, El Cumbre, thickets at a brook, *Ekman 13949* (S); near Pico Potrerillo, road to Aguada del Santo, open hillsides, quite common, *Ekman 13977* (S); Sierra de San Juan, Mina Carlota (southeast of Cumanayagua), alt. 300–400 m., *Howard 5663* (GH, MT, NY); Buenos Aires, *Roig & Acuña 6152* (NY); Loma de Tibisial, Sancti-Spiritus Mountains, *León & Clement 6662* (NY); Lomas de Banao, *Luna 754* (NY); Lomas del Banao, Loma del Obispo, *Ekman 16282* (S), *León 1300* (NY).



MAP XXII. Distribution of sect. *Williamia* subsect. *Discolores* in Cuba.

Among the woody species of *Phyllanthus* in western Cuba, *P. discolor* is second only to *P. orbicularis* in abundance and frequency. As a consequence of the restriction of *P. discolor* to areas of serpentine outcrops, it occurs as a number of more or less isolated populations which exhibit a noticeable variation in leaf shape and stamen number. However, the variation within individuals is so high and the sampling of populations so inadequate (despite the rather considerable number of specimens examined) that the extent of geographical variation is difficult to assess. This inexact knowledge of the normal range of variation within the species presents a distinct hindrance in the analysis of some highly anomalous specimens from northern Pinar del Río.

These discordant collections, which all come from the Cajálbana region between La Palma and Bahia Honda, represent the plant to which the name *P. pallidus* has been applied. Grisebach (Goett. Nachr. **1865**: 168.) differentiated *P. pallidus* from *P. discolor* on the basis of its glaucous, thicker leaves and greater crowding of anthers on the staminal column, while Mueller (DC. Prodr. **15** [2]: 328. 1866) proposed to distinguish it by its fewer flowers, the female with equal calyx-lobes and shorter pedicels, and by the pale leaves with indistinct venation. However, even a superficial survey of the specimens at hand is sufficient to show that none of these characters is stable or diagnostic. Consequently, the Cajálbana population was recently (Contr. Gray Herb. **176**: 57. 1955) reduced to varietal rank under *P. discolor*; but even this disposition scarcely appeared satisfactory in view of the extreme fluctuation of characters and the lack of geographical separation between the two entities.

An intensive study of a population sample taken between La Mulata and San Juan de Sagua, together with a reexamination of available herbarium specimens of *P. pallidus*, has led to the following interpretation of the situation.

Phyllanthus × pallidus Wr. ex Griseb. Goett. Nachr. **1865:** 168. 1865, pro sp. (= *P. discolor* × *P. comptus.*)

Phyllanthus sagraeanus Urb. Symb. Ant. **9:** 182. 1924.
Phyllanthus discolor var. *pallidus* (Wr. ex Griseb.) Webster, Contr. Gray Herb. **176:** 57. 1955.

CUBA. PINAR DEL RÍO: Cajálbana, Bahia Honda, *Wright 1950* (GOET, HOLOTYPE of *P. pallidus*; G, GH, ISOTYPES); Loma de Cajálbana, cuabales, *Ekman 10471* (NY, S; TYPE COLLECTION of *P. sagraeanus*); dense cuabales, eastern slope of Loma Cajálbana, *Ekman 17347* (S); orillas del arroyo, cerca de la cumbre de la Cajálbana, *León & Charles 4956* ex p. (NY); San José de Sagua to San Marcos, on serpentine rock, *Shafer 11971* (F, MO, NY, US); between La Mulata and San José de Sagua, *Webster 4652, 4653, 4654, 4657* (undistributed); Bahia Honda, dry rocky hillside, *Wilson 9417* (NY); locality questionable, *Wright 1941* ex p. (NY, P, S, US).

Some of the specimens cited have been annotated by formula rather than by the hybrid name, since they resemble *P. discolor* rather strongly and show only a subordinate influence of *P. comptus*. The type collection of *P. sagraeanus* is the most nearly intermediate, and *Wright 1950* (the type of *P. pallidus*) approaches this condition. The most striking vegetative difference between the two hybridizing species, the type of cataphyll (much more massive in *P. comptus*), is obscured in most specimens by the prevalence of *discolor* characteristics. Several collections, notably *León & Charles 4956* and *Wright 1941*, contain a mixture of *P. pallidus* and a form indistinguishable from typical *P. discolor*; in other collections there are intermediates of varying degrees.

The decision to regard the plants assigned to *P. pallidus* as hybrids between *P. discolor* and *P. comptus* has been taken after an extended analysis involving comparisons of leaf anatomy, pollen and seed fertility, and gross morphology. Anatomical studies of cleared leaves indicate that in *P. pallidus* the veinlets are c. 20–40 μ in diameter and are quite intermediate between the tenuous veinlets of *P. discolor* (mostly 10–20 μ thick) and the knobby ones of *P. comptus* (mostly 30–60 μ thick). Of even greater interest, although not entirely conclusive, are the results of a study of pollen grains taken from herbarium specimens and stained in lacto-phenol with cotton blue, which show that there is pollen sterility (though to a highly variable degree) in specimens which are transitional between *P. discolor* and *P. pallidus*, and essentially complete sterility in specimens which are morphologically good *P. pallidus*.

Since the assignment of specimens to *P. pallidus* or to the "transitional" column is somewhat arbitrary, Table II does not make sufficiently explicit

TABLE II †

Pollen and Seed Fertility

P. discolor

Alain 2362	94
Ekman 13977	99 (+)
Ekman 16469	10, 46
Howard 5081	72 (+)
Howard 5563	96 (+)
Webster 250	99 (+)

P. pallidus

Ekman 10471	— (*)
Webster 4653–1	— (–, *)
4654	64, 93 (–, *)
4657	28, 40 (–)

Transitional between
P. discolor and **P. pallidus**

Ekman 17347	99
Shafer 11971	99
Webster 4652–1	83 (–)
4652–2	99 (–)
4652–3	91
4652–4	92
4652–5	20
4652–6	14
4652–7	70
4652–8	97
4652–9	100
4652–10	67
4652–11	98
4652–12	61 (–)
4653–2	86
4653–3	* (*)

† The figures following each collection number refer to the percentage of good pollen grains as determined by examination of 200 grains from each collection; in a few cases a second determination has been made from a different flower on the same plant. Only deeply stained grains of normal appearance have been counted as good; in doubtful instances they have been scored as defective. The plus and minus signs in parentheses refer to the production of seeds, any collection with fewer than 50% viable seed having been scored minus; lack of either symbol indicates that the degree of fertility could not be ascertained from the specimen. The asterisk denotes the production of monstrous flowers.

the important fact that the most nearly "typical" specimens of *P. pallidus* (i.e., ones such as *Ekman 10471* which are exactly intermediate between *P. discolor* and *P. comptus*) are completely sterile, only the monstrous rudiments of female flowers being produced. Other collections, exemplified by *Webster 4654* and *4657*, definitely lean toward *P. pallidus* but have more or less normal flowers which are partially fertile. In the transitional plants trending toward *P. discolor* the fertility is as variable as the morphological features. *Webster 4653–3* epitomizes the situation; it has vegetative features approaching typical *P. discolor*, but its completely monstrous flowers betray its reproductive instability.

The absence of collections intermediate between *P. pallidus* and the other presumed parent species *P. comptus* may appear strange, but is perhaps explained (at least in part) by the apparent rarity of the latter, which has been collected only three times. However, if this explanation is correct it raises the even knottier problem of why the hybrid form should be so much commoner than one of its parents, particularly since it appears to become fertile only when back-crossed to *P. discolor*. Possibly some ecological factor plays an important role in determining the peculiar character of the population.

The prevalence of "pallidus" characters in the Cajálbana population of *P. discolor* might be adduced as an instance of "introgressive hybridization," although it is not evident that any characters of *P. comptus* have been diffused into any populations of *P. discolor* outside of the Cajálbana area. Much more striking than any leakage of characters is the exaggerated variability of the local population as a whole; a considerable number of specimens show anomalous characteristics. An outstanding example of this is *Ekman 10433*, which vegetatively can scarcely be distinguished from typical *P. discolor* and which has highly fertile pollen; but its flowers are exceptional in the long staminal column and styles and the stipitate ovary. These peculiarities, especially the stipitate ovary, suggest a resemblance to the related species *P. microdictyus*, which is known only from Oriente province. However, it appears probable that these unusual features have some connection with the local hybridity and do not really signify any relationship to the species of Oriente.

The enhanced degree of variability is particularly marked in the stamen number, as shown in Table III. Since *P. comptus* usually has only 5 or 6 stamens, one would expect that its hybrids with *P. discolor* might have a number approaching the usual 9–13 of the latter. Insofar as the lower numbers (under 10) are concerned, this is reasonably well borne out. But the occurrence in *P. pallidus* of numbers much higher than those in *P. discolor* is entirely unexpected. Although the number of androecia counted (50 each of *P. discolor* and *P. pallidus*) is unfortunately small, there can be little doubt that mere chance cannot account for 11 of the *pallidus* flowers having a higher number than any of the *discolor* ones.

It seems quite likely that this wholly anomalous increase in stamen number in *P. pallidus* is the result of the same cause which determined the formation of a stipitate ovary in *Ekman 10433*, i.e., the morphogenetic disturbance in the hybrid plant which is presumably due to imbalance between the chromosome complements of the parents. It is conceivable that the situation in *P. pallidus* presents us with an insight into one mechanism of phylogenetic change, for if aberrant plants of *P. pallidus* with androecia of 16–18 anthers should happen to be selected out as a separate fertile population, a new species characterized by higher stamen number might result. Possibly the prevalent numbers (9–13) in *P. discolor* arose in this same way, for the primitive number in the genus is certainly 5 or 6 as in subg. *Kirganelia*; and since *P. discolor* has no other particularly primitive characters, it is probable that its increased stamen number, too, is derived.

The relationships of *P. discolor* are reasonably well-defined, for on purely morphological grounds its affinity to the following species, *P. microdictyus*, is apparent; and the general resemblance (though much less close) to *P. comptus* supports the evidence (from the existence of *P. pallidus*) that *P. discolor* can cross with that species. Furthermore, *P. comptus* in its morphological details is transitional between *P. discolor* and the other species of sect. *Thamnocharis*, so that it presumably has evolved from *P. discolor* or some common ancestor. The hybridization occurring today

TABLE III *

VARIATION IN STAMEN NUMBER IN *P. discolor* AND *P. pallidus*

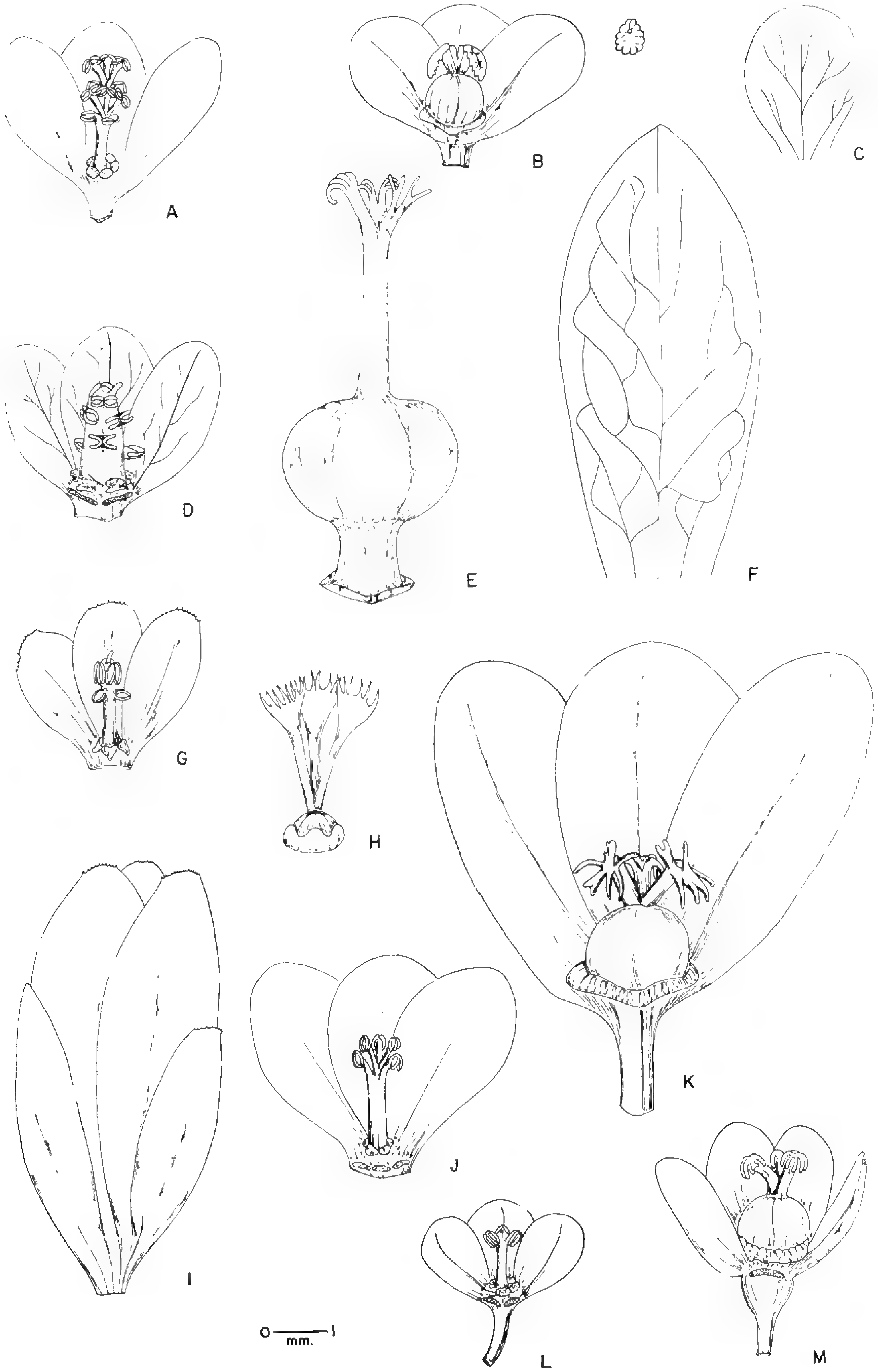
Stamen number	*P. discolor*	*P. pallidus*
18	0	1
17	0	2
16	0	2
15	0	6
14	1	4
13	12	6
12	17	7
11	6	9
10	8	5
9	4	1
8	1	4
7	1	1
6	0	1

* The figures in the two right-hand columns refer to the number of flowers having the specific stamen number. The mean number of flowers scored per collection was about 3, but there was some variation due to differences in the number of available male flowers on the specimens; this inequality in sampling may be partially counteracted by the considerable spread of variation on each plant (e.g., from 9–14 in one individual of *P. discolor*). It should be noted that the *P. pallidus* column includes collections of various transitional forms, or in other words all specimens from the Cajálbana area which are not obviously "good" *P. discolor*.

must be due to comparatively recent changes in the distribution of one or both species and, most probably, to a spread of *P. discolor* into the restricted range of *P. comptus*. It is interesting that there is no evidence of crossing between *P. discolor* and *P. orbicularis* of sect. *Orbicularia*, although the latter is also present near almost every station of *P. discolor* and shows an affinity (via *P. microdictyus*) evident enough so that crossing would *a priori* not appear impossible. Presumably there is a much stronger genetic barrier between *P. discolor* and *P. orbicularis* than between the former and *P. comptus*; this offers an interesting subject for further analysis on cytological lines.

PLATE XXV. FLOWERS OF SECT. *Williamia*, SUBSECTS. *Discolores* AND *Incrustati*.

FIGS. A–C. Male flower, female flower, and female calyx-lobe of *Phyllanthus discolor* Poepp. ex Spr. (*Webster et al. 250* [GH]). FIGS. D–F. Male flower, gynoecium, and female calyx-lobe of *Phyllanthus microdictyus* Urb. (*Marie-Victorin & Clement 21525* [A]). FIGS. G–I. Male flower, gynoecium, and female calyx of *Phyllanthus williamioides* Griseb. (*Webster 4014* [GH]). FIGS. J–K. Male and female flowers of *Phyllanthus excisus* Urb. (*Ekman 4055* [S]). FIGS. L–M. Male and female flowers of *Phyllanthus incrustatus* Urb. (*Ekman 3848* [S]).



Webster, West Indian Phyllanthus

49. **Phyllanthus microdictyus** Urb. Symb. Ant. 9: 183. 1924.
(PLATE XXV, *figs.* D–F; PLATE XXVII, *fig.* A).

A shrub c. 1 m. high with the habit of a miniature tree, the stem simple or sparsely branching near the top; bark smooth, dark brownish, becoming finely fissured on old stems but not breaking up into plates. Cataphylls deciduous: stipules triangular-lanceolate, mostly 3–4 mm. long and (1.1–) 1.5–1.7 mm. broad (smaller on weak shoots), acute, truncate at the thickened base, lightly keeled, dark brown and scarious-indurate; blade narrowly lanceolate, acuminate, c. 2.5–3 mm. long. Branchlets (6–) 9–17 (–19) cm. long, 0.9–1.5 mm. thick, brownish, smooth and pruinose, usually flattened, with (6–) 8–12 (–14) leaves; first internode (15–) 20–40 (–45) mm. long, median internodes c. 10–20 mm. long. Leaves: stipules linear-lanceolate, acuminate, (1.5–) 2.5–3 mm. long, 0.4–1 mm. broad, scarious, deciduous. Petiole 2.5–4.5 mm. long, subterete, brownish. Leaf-blades flexibly chartaceous, ovate or elliptic, (1.5–) 2.5–5 (–6.5) cm. long, (1.3–) 2–3.5 (–4) cm. broad, emarginate (or less commonly obtuse or rounded) and minutely and inconspicuously apiculate at the tip, mostly rounded to cordate at the base; above dull green (bright red when first expanded), minutely foveolate, the midrib incised, the main laterals raised, repeatedly branching and anastomosing to form a fine raised reticulum with straight-sided meshes; beneath greyish-pruinose, the midrib raised, the laterals (c. 4 or 5 on a side) and ultimate veinlets very slightly raised, pale, forming a fine and inconspicuous reticulum; margins plane, not thickened.

Monoecious; usually the proximal 2 or 3 nodes of a branchlet with male cymules of 1–3 flowers, the succeeding nodes with bisexual cymules of 1 central female and 1 or 2 lateral male flowers.

Male flower: pedicel capillary, (5–) 7–15 mm. long. Calyx greenish white, sometimes pinkish tinged: calyx-lobes 6 (rarely 5), chartaceous, subequal, oblong to obovate, 2.5–3.5 mm. long, 1.3–2.3 mm. broad, entire and rounded at the tip, faintly triplinerved or the midrib pinnately branched. Disk-segments 6 (rarely 5), round or trigonous, smooth and entire, c. 0.25–0.45 mm. broad. Stamens 6–10 (–11), the filaments 1–1.7 mm. long, connate into a rather stout column; anthers subsessile (the free portion of the filament no longer than the anther) or the terminal ones short-stalked, inserted on the column spirally or in 2 or 3 whorls, ascending or spreading, c. 0.25–0.3 mm. long, 0.4–0.5 mm. broad; anther-sacs more or less divergent, globose before anthesis, dehiscing horizontally or obliquely, the slits apically contiguous but not confluent; pollen grains 20–24 μ in diameter, with c. 7 or 8 areoles per amb.

Female flower: pedicel capillary, (5–) 7–12 (–14) mm. long. Calyx colored as in the male; calyx-lobes 6 (rarely 7), strongly convex, subequal or unequal (the outer one or two lobes often manifestly shorter than the innermost), oblong to obovate, the larger lobes 7–8.5 mm. long, 3.5–5 mm. broad, entire and obtuse or rounded at the apex, 3–5-nerved from the base, the laterals ascending and anastomosing in a rather conspicuous net. Disk 5-angled, fairly massive in the bud but becoming fused with and incorporated into the massive gynophore. Ovary oblate-spheroidal, about as high as (or somewhat higher than) the gynophore, pruinose; styles erect, (3.5–) 4–5 mm. high, connate ½ to ¾ their length, gradually dilated at their ends into conspicuously lacerate 3- or 4-parted tips.

Capsule oblate, emarginate at the apex, c. 5 mm. in diameter, smooth, reddish brown, held within the erect appressed calyx-lobes. Columella conical, somewhat constricted at the tip, 2.2–2.4 mm. long. Seeds [those examined not quite mature] plano-convex, 2.5–2.7 mm. long, 1.5–1.6 mm. radially and tangentially, dark shiny reddish brown, nearly smooth (minutely colliculose); hilum submedian, triangular, light brown.

Flowering and fruiting April through July and possibly later, but apparently sterile during the winter.

Type: Cuba, *Ekman 3705.*

Distribution: lowlands near the coast, northeastern Oriente Province, Cuba (Map XXII).

CUBA. Criente: Moa region, Cayoguan, *Acuña 12478* (SV [Herb. Roig n. 8593], US); Mina Cromita, Cayoguan, south of Punta Gorda, *Clemente & Alain 4074* (MICH); Rio Cayoguan, près du pont sur le chemin de la mine Delta, *Marie-Victorin & Clement 21525* (A, MT), *21749* (MT); same locality, cut-over forest of *Clusia, Bactris, Arthrostylidium, et al., Webster 3809* (GH, MICH); ad Taco Bay prope Baracoa in pinetis, 2 December 1914, *Ekman 3705* (S, holotype; NY, isotype fragment and photograph; sterile).

A very distinctive and well-marked species, *P. microdictyus* appears to be quite restricted in range; the first four collections cited are all essentially from the same locality, so that there are, in effect, only two known stations. Although Ekman's type specimen is sterile, the characteristic venation of the leaves — identical with that of the fertile collections from Moa — leaves no doubt as to the identity or typification of the species. Ekman's designation of the Taco Bay collection as being from pinelands suggests a somewhat different habitat from the flood-plain woods along the Río Cayoguan, but the species would in any case appear to be a relatively mesophytic one.

Because of their evolutionary significance, the several affinities of *P. microdictyus* deserve special mention. Its large female flowers with long styles and stipitate ovary are so similar to those of the South American *P. salviaefolius* that there can be little doubt of a fairly close relationship, although the latter species differs vegetatively by having hirsutulous axes and acuminate, more coarsely veined leaves. However, *P. microdictyus* is also an obviously near relation of *P. discolor,* which it greatly resembles vegetatively. Furthermore, the incipient production of mesophyllar sclereids in *P. microdictyus* presages their full development in *P. cristalensis*; and since it would appear that it is through the latter (or a similar species) that the highly specialized representatives of subsect. *Incrustati* and sect. *Orbicularia* have originated, it would not be incorrect to regard *P. microdictyus* as the progenitor of this entire phylogenetic line.

50. **Phyllanthus cristalensis** Urb. Repert. Sp. Nov. **28**: 212–213. 1930.

Glabrous shrub up to 1.5 m. high; branches shiny reddish brown, becoming grey with age, c. 1.5–3 mm. thick. Cataphylls black, indurate, soon deciduous: stipules lanceolate, c. 1.5–2 mm. long, acuminate, entire; blade narrower. Branchlets mostly 4–11 cm. long, 0.5–0.8 mm. thick, smooth, reddish brown, subterete (slightly compressed proximally), with 8–15 leaves; first internode c. 5–15 mm. long, median internodes 4–7 mm. long. Leaves: stipules reflexed, subpersistent, triangular-lanceolate, 1.7–2 mm. long, 0.7–1.1 mm. broad, rather blunt at the tip, entire, dark brown, somewhat indurate. Petiole 1.5–2.5 mm. long, slightly flattened, dark brown, nearly smooth. Leaf-blades coriaceous, broadly elliptic to suborbicular, c. 1–2.2 cm. long, 0.8–1.9 cm. broad, emarginate and with a deciduous apiculum at the tip, rounded to emarginate at the base; above dull brownish olivaceous, mottled (the cell outlines of the irregularly anastomosing veins visible under a lens), the subprominent midrib plane or sunken, the laterals rather obscure; beneath greyish or brownish, the midrib and laterals (c. 4 or 5 on a side) plane, not very prominent, the reticulum obscure; margins plane, scarcely thickened.

Monoecious (presumably); flowers [and fruit not seen, description ex Urban] few, solitary or paired, pedicels 3–5 mm. long.

Male flower: calyx-lobes 5, narrowly ovate, 2 mm. long, barely 1 mm. broad; stamen number not determined; filaments connate, anthers discrete. Female flower: pedicel narrowly obconic-thickened above; calyx-lobes 5, narrowly ovate, 2 mm. long; styles not seen.

Capsule oblate, rounded-trigonous, c. 4 mm. in diameter; seeds brownish, minutely puncticulate, c. 2 mm. long, 1.7 mm. broad.

TYPE: Cuba, *Ekman 15993.*

DISTRIBUTION: endemic to the Sierra Cristal, eastern Cuba (MAP XXII).

CUBA. ORIENTE, Sierra Cristal: at the tributary of the Río Lebisa in charrascales, alt. 600–1100 m., 15 Dec. 1922, *Ekman 15967* (S); in low *Arthrostylidium* thickets which cover the top, alt. 1100–1325 m., 15 Dec. 1928, *Ekman 15993* (NY, ISOTYPE); ridge west of Pico Cristal, mossy elfin forest, 4 Mar. 1954, *Jervis 3206* (GH).

Although still poorly known, *P. cristalensis* is evidently a very distinct species on the basis of its vegetative characters. Vegetatively it is intermediate between subsects. *Discolores* and *Incrustati*, having the smooth axes of the former combined with the highly sclerified leaves of the latter. However, until adequate flowering material can be collected its relationships cannot be satisfactorily determined.

Subsect. 16b. **Incrustati**, subsect. nov.

Phyllanthus sect. *Williamiandra* Griseb. Goett. Nachr. **1865**: 171. 1865.
Ramsdenia Britton, Mem. Torr. Bot. Club **16**(2): 72. 1920.

Stems and branchlets incrustate with dark bran-like flakes of bark;

leaves of branchlets alternate, coriaceous (heavily sclerified within); stamens (2–) 3–6; styles erect, conspicuously lacerate.

TYPE SPECIES: *Phyllanthus williamioides* Griseb.

Grisebach proposed to distinguish sect. *Williamiandra* on the basis of its androecium and styles, but his description of the androecium is erroneous and his discussion misleading. The type species, *P. williamioides*, has only 5 or 6 stamens (not 10 as reported by Grisebach), and the conical apex of the staminal column cannot serve as a sectional character since it does not occur in the two related species. Grisebach's stated distinction between the styles of *Williamiandra* (correctly likened to those of sect. *Oxalistylis*) and those of sect. *Williamia* is wholly incorrect, for he erroneously describes the styles of the latter as bifid. Except for the difference in stamen number, there are no floral characters available for separating *Williamia* from *Williamiandra*; but since the species of the two groups can be distinguished vegetatively, it seems appropriate to place them into two subsections of the inclusive sect. *Williamia.*

Britton's proposed genus *Ramsdenia,* which included *P. excisus* and *P. incrustatus,* corresponds almost exactly to the present subsection; he did not discuss its relationships or clearly define its characters, and he was apparently unaware of the existence of *P. williamioides.*

51. **Phyllanthus williamioides** Griseb. Goett. Nachr. **1865**: 169–170. 1865; Muell. Arg. in DC. Prodr. **15**(2): 328–329. 1866.
(PLATE XXV, *figs.* G–I).

Diasperus williamioides (Griseb.) O. Ktze. Rev. Gen. 2: 601. 1891.

A small shrub 0.5–1.5 (–2) m. high, with two or more stems clustered on a gnarled caudex (stem unbranched in young plants); bark of stem-base and root broken up into conspicuous patterns of squares. Stems and branchlets incrustate but the bark-platelets smooth and glabrous, dark brown, the exposed spongy tissue reddish brown. Cataphylls blackish, indurate but mostly soon deciduous: stipules lanceolate, (1.5–) 1.8–2.7 mm. long, 0.7–1.2 mm. broad; blade c. 1.8–2.5 mm. long, 0.5 mm. broad. Branchlets erect or spreading, (5–) 8–15 (–19) cm. long, 1–1.2 mm. thick, reddish-brown- or blackish-incrustate, terete or angled, with mostly 10–25 (–35) leaves; first internode (5–) 7–12 (–16) mm. long, median internodes 2–6 (–10) mm. long. Leaves: stipules acicular-lanceolate (convexly conduplicate), soon deciduous, 2.5–3.5 (–5) mm. long and 0.5–1 mm. broad, rather blunt at the tip, chartaceous, dark brown. Petiole 1.5–2.5 mm. long, brownish, smooth, flattened. Leaf-blades coriaceous, mostly orbicular or nearly so (sometimes slightly obovate or broader than long), (1–) 1.5–2.5 cm. long, (1–) 1.3–2.2 cm. broad, retuse or emarginate at the tip, cordate at the base; above olivaceous and sublucid or dully plumbeous, minutely foveolate-reticulate, the midrib slightly incised, the lateral veins and veinlets forming a fine slightly raised reticulum; beneath brownish- or olivaceous-plumbeous (minutely white-dotted with wax-covered stomata), the midrib plane, the slightly raised laterals (c. 5 or 6 on a side) anastomosing with the conspicuous tertiary veinlets to form a close reticulum; margins plane, not thickened.

Monoecious, flowers in axillary bisexual cymules; central flower female, lateral ones male (the male mostly developing after fruiting calyx has fallen, so that the arrangement on the branchlet appears to be of proximal racemes of male flowers and distal solitary female flowers); bracteoles blackish and indurate.

Male flower: pedicel c. 1.8–2 mm. long. Calyx greenish white, whitish, or reddish tinged; calyx-lobes 5, thin but coriaceous, subequal, oblong to spathulate, (1.3–) 1.5–2.3 mm. long, 0.7–1.5 mm. broad, denticulate near the apex, more or less triplinerved but nerves rather obscure. Disk-segments 5, flattened or concave, roundish or triangular, smooth and entire, 0.25–0.35 mm. broad. Stamens 5 or 6, the filaments connate into a relatively slender column 1–1.1 mm. high and 0.25–0.4 mm. thick; anthers in two series, the upper of 3, the lower of 2 or 3, the apex of the column terminated by an apiculum; anthers slightly apiculate, sessile on the column or very nearly so, the upper erect, the lower ascending or spreading, c. 0.3–0.4 mm. long and broad; anther-sacs sub-parallel, dehiscing longitudinally, the slits not confluent; pollen grains 24–27 μ in diameter, the areoles polybrochate, c. 5–6 μ across, c. 10 per amb.

Female flower: pedicel short and stout, only (0.7–) 1.2–1.8 (–2.4) mm. long. Calyx colored as in the male; calyx-lobes 5–7, quite unequal, denticulate at the apex, incrassate at the base, nerves several but obscure; outer lobes oblong, obtuse, 2.5–3.5 mm. long, 1.5–2 mm. broad; inner lobes obovate, rounded at the tip, 5–5.5 mm. long, 2.2–2.8 mm. broad. Disk a thick brownish crenate-rimmed cup, enclosing the base of the ovary. Ovary sessile, smooth, carinate between the septae; styles erect, free, 1.8–2.7 mm. high, the dilated tips more or less 3-fid, the three branches with a total of c. 8–10 slender lacerae.

Capsule subglobose, c. 4 mm. in diameter, the valves olivaceous, smooth, not veiny, 3.5 mm. long, often retained within the appressed calyx-lobes. Columella 2.2 mm. long. Seeds trigonous, somewhat asymmetric (excentrically carinate on the back), 2.2–2.3 mm. long, 1.2–1.5 mm., radially and tangentially, blackish brown, colliculose on back and sides; hilum subterminal, elliptic or ovate, c. 0.5 mm. long.

TYPE: Cuba, *Wright 1944.*

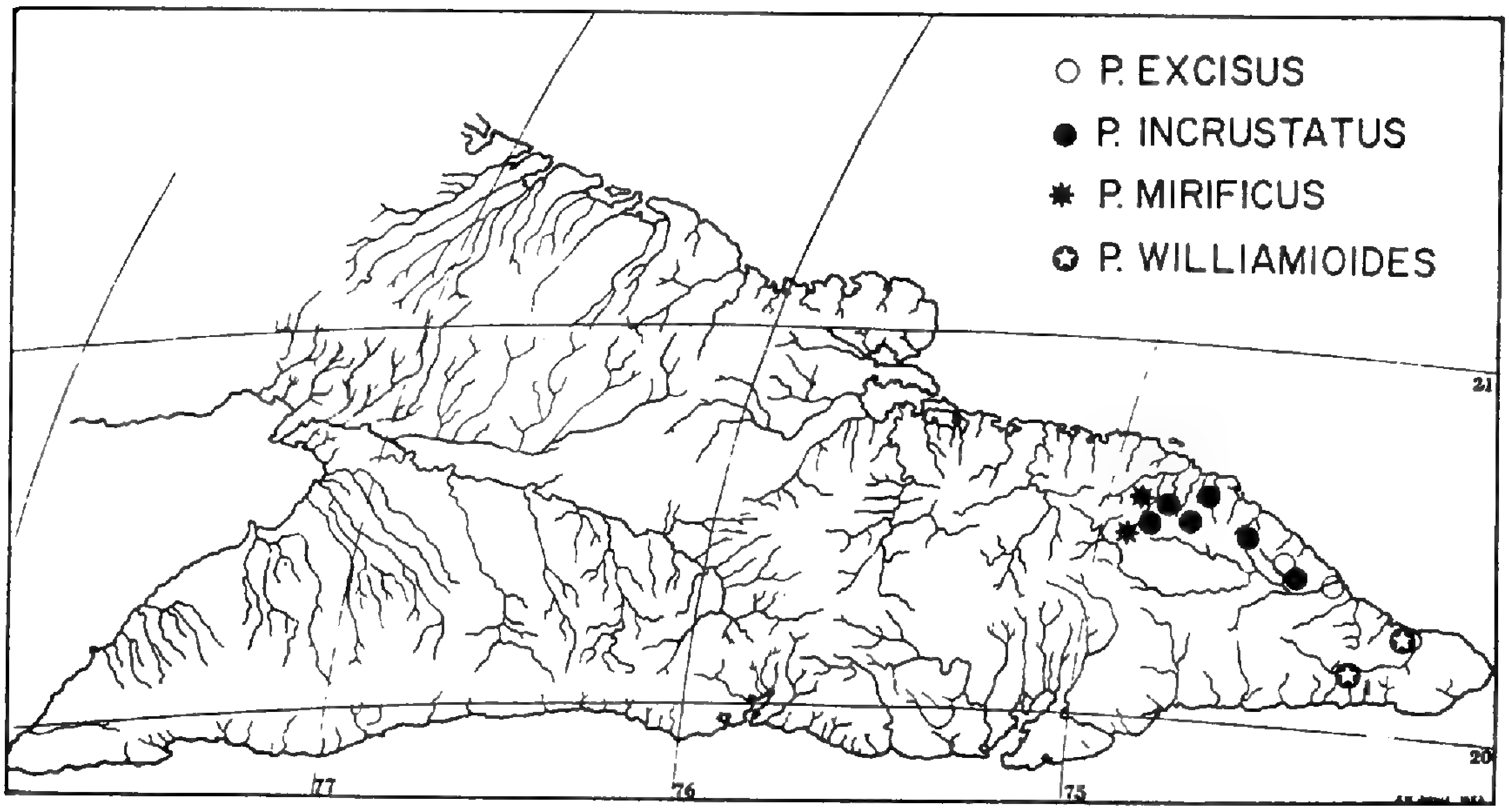
DISTRIBUTION: endemic to the Baracoa region, Oriente province, Cuba (MAP XXIII).

CUBA. ORIENTE: Cuchillas de Baracoa, *Wright 1944* (GOET, HOLOTYPE; GH, ISOTYPE; locality ex isotype); Altos de Farola, c. 20 miles south of Baracoa, pineland at 1750 ft., 3 Aug. 1951, *Webster 4014* (GH, MICH, NY); among pines and tree ferns, moist arroyo c. 12 miles east of Baracoa, 18 Mar. 1954, *Jervis 3332* (GH).

Wright's type collection differs from the other specimens in its distinctly obovate leaves. However, in the field, leaves of this shape were found on shoots from the base of plants which higher up bore orbicular leaves; it thus appears that Wright made his collection from a stump sprout or very depauperate plant.

The present species is very closely related to *P. incrustatus*, but is usually distinguishable at first sight by virtue of its smooth bark platelets (these usually scabridulous in *P. incrustatus*) and larger more elongated leaves. Actually, the concave deciduous stipules and androecium of 5–6 stamens are the best diagnostic features of *P. williamioides*, and will always permit its ready separation from *P. incrustatus*.

As in many species of subg. *Xylophylla*, the leaves of *P. williamioides* are distinctly reddish-tinged when young, though less strikingly so than in *P. pachystylus*. The undersurface is pale yellow at first and only later becomes green; this behavior, again, is characteristic of many other species.



MAP XXIII. Distribution of sect. *Williamia* subsects. *Incrustati* and *Mirifici* in eastern Cuba.

52. **Phyllanthus excisus** Urb. Repert. Sp. Nov. 13: 449–450. 1914. (PLATE XXV, *figs*. J–K).

Ramsdenia excisa (Urb.) Britton, Mem. Torr. Bot. Club 16(2): 72. 1920.

Shrub c. 2–3 m. high; pith brownish; stems and branchlets incrustate with smooth dark reddish brown platelets, the interspaces of spongy tissue light reddish brown. Cataphylls blackened, indurate, more or less persistent: stipules triangular-lanceolate, 2–2.5 mm. long, 1.5–1.6 mm. broad, acuminate; blade narrower. Branchlets stout, 9–27 cm. long, 1.7–3 mm. thick, reddish brown and incrustate, subterete (more or less angled distally), with (10–) 15–35 nodes; first internode (5–) 10–15 (–20) mm. long, median internodes 5–18 mm. long. Leaves: stipules lanceolate, 2.5–3 mm. long, 1.1–1.5 mm. broad, acuminate, quite oblique at the base, blackish, indurate, appressed or spreading, persistent. Petioles 1.5–3 mm. long, brownish, transversely furrowed, with a deep median adaxial groove.

Leaf blades coriaceous, mostly ovate or elliptic, (2.5–) 3–4.5 cm. long, 2.5–3.5 cm. broad, emarginate at the tip, obtuse to subcordate at the base; above olivaceous-plumbeous, minutely foveolate-reticulate, the midrib plane or slightly impressed, the lateral veins obscure; beneath brownish grey when dried (not white-dotted), the midrib saliently raised, the laterals (c. 6–8 on a side) and tertiary veinlets slightly raised, anastomosing to form a rather prominent reticulum; margins unthickened, plane.

Monoecious; flowers in axillary bisexual cymules, each of a solitary central female flower and a few (c. 3 or 4) male flowers on bracteolate lateral axes; bracteoles indurate, persistent in old axils.

Male flower: pedicel capillary, c. 4–5.5 mm. long. Calyx whitish (ex Shafer); calyx-lobes 5, subequal, oblong to obovate, (3–) 3.3–4 mm. long, 1.5–2 mm. broad, entire, the venation obscure. Disk-segments 5, roundish, entire, c. 0.4–0.5 mm. across. Stamens 5–6, filaments united into a rather stout non-apiculate column 1.5–1.8 mm. high and 0.5–0.6 mm. broad; anthers biseriate (upper series of 3, lower of 2 or 3) but both whorls crowded at the top, not evidently apiculate; anther-sacs subparallel, dehiscing longitudinally, the slits not confluent; pollen grains 19–22 μ in diameter, the areoles polybrochate, c. 7–11 μ long, 4–5 per amb.

Female flower: pedicel nearly straight, slender, (10–) 12–15 mm. long. Calyx greenish-white (ex Shafer); calyx-lobes 5, coriaceous, thickened at the base, subequal (the outer slightly narrower), oblong to obovate, the larger lobes 5–7 mm. long [up to 8 mm., ex Urb.], 2.5–4.5 mm. broad, entire and rounded at the tip, the venation obscure. Disk massive, obtusely 5-angled, entire (or minutely crenulate), obscurely foveolate, the margin plane, somewhat thinner. Ovary sessile, carinate dorsally; styles erect, free or shortly connate at the base, 1.8–2 mm. high, the dilated ends deeply parted into 6–7 (–10) narrow divaricate lacerae; outline of stylar apex roughly triangular, two arms extending adaxially, the third abaxial and with more lobes.

Capsule subglobose, emarginate, c. 5 mm. in diameter, smooth or slightly rugulose, brownish, not veiny. Columella c. 3 mm. long. Seeds [seen only in immature condition] c. 3 mm. long, brownish, probably with the ornamentation of *P. williamioides* when mature.

TYPE: Cuba, *Shafer 4447*.

DISTRIBUTION: endemic to the Baracoa region, Oriente province, Cuba (MAP XXIII).

CUBA. ORIENTE: Navas to Camp Buena Vista, alt. 650 m., 23 March 1910, *Shafer 4447* (NY, LECTOTYPE; F, MO, US, ISOTYPES); prope Baracoa, ad Maraví in pinetis, 26 Dec. 1914, *Ekman 4055* (S).

Apparently a rare species of restricted range, *P. excisus* is well distinguished from the two related species of subsect. *Incrustati* by its larger ovate leaves, larger flowers on longer pedicels, and different styles. Its strong resemblance to *P. microdictyus* of subsect. *Discolores* can hardly be mere coincidence, and it can be rather confidently regarded as a xerophytic derivative of that plant. The flowers of both species are similar, but *P. excisus* has fewer stamens and, of course, its incrustate stems and coriaceous leaves easily separate it from *P. microdictyus*.

The apparent rarity of *P. excisus*, as compared with the other Oriente species of sect. *Williamia*, may prove to be illusory, for the region between Navas and Baracoa has been much less visited by collectors than the Moa district, which up until recently was much more accessible.

53. **Phyllanthus incrustatus** Urb. Repert. Sp. Nov. 13: 449. 1914. (PLATE XXV, *figs.* L–M).

Ramsdenia incrustata (Urb.) Britton, Mem. Torr. Bot. Club **16**(2): 73. 1920.

Shrub 0.5–2 m. high; stems and branchlets usually scabridulous-hirtellous at the tips, below incrustate with scabridulous platelets of bark (rarely the platelets smooth). Cataphylls blackish, indurate, subpersistent: stipules triangular to narrowly lanceolate, (1–) 1.5–3.7 mm. long, 0.5–1 mm. broad, acute to acuminate (sometimes with very attenuate tips), sometimes excentrically keeled, becoming reflexed or spreading; blade narrowly lanceolate, (0.7–) 1.5–3.5 (–5) mm. long, also more or less reflexed. Branchlets (5–) 7–17 (–26) cm. long, 1–1.7 mm. thick, incrustate with dark brown usually scabridulous platelets separated by lighter reddish brown furrows, with (10–) 15–40 (–60) leaves; first internode 3–10 mm. long, median internodes 2–6 mm. long. Leaves: stipules persistent, appressed or reflexed, triangular to linear-lanceolate, (0.8–) 1.2–2.5 (–3.2) mm. long, 0.3–0.9 mm. broad, acute or acuminate, dark brown, more or less indurate. Petiole 1–1.8 mm. long. Leaf blades coriaceous, mostly orbicular or suborbicular (sometimes broader than long), c. 7–12 (–15) mm. long, 6–12 (–14) mm. broad, usually retuse or emarginate and inconspicuously apiculate, truncate or more commonly cordate at the base; above dull olivaceous or plumbeous, minutely foveolate-reticulate, the midrib impressed, the laterals usually rather obscure; beneath greyish brown or purplish brown (minutely white-dotted with wax-covered stomata), the slightly raised laterals (c. 5 or 6 on a side) anastomosing with the veinlets to form an inconspicuous reticulum; margins plane, not thickened.

Monoecious; flowers in axillary bisexual cymules; first (central) flower of cymule female, rapidly maturing and deciduous, succeeded by several male flowers on one or both lateral abbreviated axes; branchlets thus appearing (as in *P. williamioides*) to have short racemes of male flowers at proximal nodes and solitary female flowers at distal nodes.

Male flower: pedicel (0.5–) 1–1.5 mm. long. Calyx whitish (in living condition [ex Shafer], reddish when dried); calyx-lobes 5, subcoriaceous but thin, subequal, oblong to obovate or spathulate, (1.3–) 1.5–2.4 mm. long, (0.7) 1–1.5 mm. broad, rounded at the tip, entire or occasionally denticulate, nervation obscure, only the midrib at all prominent. Disk-segments 5, flattened or concave, roundish or trigonous, c. 0.25–0.35 mm. across. Stamens 3 or 4 (rarely 2), filaments connate into a slender non-apiculate column 0.6–1.2 mm. high and 0.15–0.25 mm. thick; anthers sessile, aggregated into a mass at the top of the column, 0.25–0.35 mm. long; anthers-sacs parallel, dehiscing longitudinally and vertically, the slits not confluent; pollen grains 12–19 μ in diameter, the areoles polybrochate, c. 6–7.5 μ long, c. 3–5 per amb.

Female flower: pedicel slender or incrassate above the middle, 1–3 mm. long. Calyx colored more or less as in the male; calyx-lobes 5, rather unequal, rounded at the tip, entire, the outer oblong, 1.6–2.7 mm. long and 0.8–2.3 mm. broad, the inner mostly spathulate or obovate, 1.8–3.3 mm. long and 1.2–3.3 mm. broad; nervation obscure. Disk massive, 5-angled, entire, plane, foveolate. Ovary sessile; styles free or shortly connate below, spreading or ascending, flattened, 0.5–0.6 mm. long, the dilated apices 5–6-lacerate.

Capsule subglobose, emarginate, c. 3–4.5 mm. in diameter, the valves smooth, dark brown, not veiny. Columella 1.5–2 (–2.5) mm. long. Seeds trigonous, asymmetrically carinate on the back, 1.8–2.7 mm. long, 1.1–1.8 mm. radially, 1.35–1.45 mm. tangentially, reddish brown, nearly smooth.

TYPE: Cuba, *Shafer 4020* (NY, LECTOTYPE; the original specimen of this collection in Herb. Krug & Urban destroyed during World War II).

DISTRIBUTION: wooded areas, northeastern Oriente province, Cuba (MAP XXIII).

CUBA. ORIENTE: Cumbre Cayo [Cayoguan], *Acuña 12477* (US); Mina Delta, c. 500 m. alt., échine de serpentine sur le chemin de la mine Delta, *Marie-Victorin & Clément 21754* (A, MT); Camp La Gloria, south of Sierra Moa, *Shafer 8113* (F, MO, NY, US); damp thickets between Río Yamaniguey and Camp Toa, alt. 400 m., 22–26 Feb. 1910, *Shafer 4020* (NY, LECTOTYPE); moist woods, Navas to Camp Buena Vista, alt. 650 m., *Shafer 4453* (NY, US); Minas de Iberia ad Taco Bay, alt. c. 800 m., *Ekman 3833, 3848* (S).

Evidently the commonest and most widespread of the three species of the subsection, *P. incrustatus* is morphologically the most specialized, at least with respect to its smaller leaves and androecium of fewer stamens. Although occasional large-leaved forms, such as *Ekman 3848*, simulate *P. williamioides*, the ensemble of characters of *P. incrustatus* is distinctive. In addition to its smaller leaves and fewer stamens, it also differs from *P. williamioides* in its persistent stipules and somewhat larger number of leaves per branchlet.

Although its small, roundish, coriaceous leaves suggest an affinity of *P. incrustatus* with the species of sect. *Orbicularia*, it does not appear likely that *P. incrustatus* is the progenitor of that group. Rather, it seems that the species of subsect. *Incrustati* represent a more or less parallel line of development with the representatives of *Orbicularia*.

Subsect. 16c. **Mirifici**, subsect. nov.[21]

Stems and branchlets smooth but with conspicuous lenticels; leaves of branchlets opposite, coriaceous (heavily sclerified within); stamens 5; styles obsolete, the greatly dilated stigmas (style-tips) forming a cap which covers most of the ovary.

TYPE SPECIES: *Phyllanthus mirificus* Webster.

The single very distinctive species of this monotypic taxon, only recently discovered in eastern Cuba, is unique among the New World species of *Phyllanthus* in its opposite leaves (on the branchlets) and hypertrophied stigmas. Although its leaf arrangement and androecium suggest certain Old World taxa, its areolate pollen grains, leaf structure, and aspect provide an incontestable basis for placing it in sect. *Williamia.* Its affinity with sect. *Incrustati* is evident from even superficial comparison, but its many distinctive characters amply justify the erection of a special subsect. *Mirifici.*

54. **Phyllanthus mirificus** Webster, Contr. Gray Herb. 176: 58. 1955. (PLATE XXVI, *figs.* A–C).

Definitely woody, presumably a shrub; branches slender, terete, not over 3 or 4 mm. thick (toward the ends), smooth, greyish- or reddish-brown, with conspicuous elliptic to linear lenticels. Cataphylls blackish and indurate but soon deciduous: stipules triangular-lanceolate, 2.3–3 mm. long, 1–1.5 mm. broad, acuminate, entire, carinate on the back; blade linear-lanceolate, c. 2 mm. long. Deciduous branchlets 8–13.5 cm. long, 1.5–2 mm. thick (those on lateral axes only 1 mm. thick), terete, smooth, brownish, becoming lenticellate proximally or throughout, with c. 6–8 (–11) pairs of leaves; first internode 6–20 mm. long, median internodes 3–20 mm. long. Leaves of branchlets all opposite (one node very slightly higher than its neighbor): stipules blackish and indurate but mostly soon deciduous, triangular-lanceolate, 2.2–3 mm. long, 0.6–0.9 mm. broad, acuminate, entire. Petioles 1.8–3 mm. long, brownish, plane and grooved down the middle adaxially, convex and corrugate-rugulose abaxially. Leaf-blades rigidly coriaceous, elliptic or ovate to suborbicular, 1.5–2.8 cm. long, 1.3–2.1 cm. broad, emarginate at the apex (the small short-conical dark brown apiculum of the juvenile leaf represented by a scar, or apparently absent), obtuse or rounded to subcordate at the base; above olivaceous or brownish, the midrib conspicuous, pale, plane or slightly sunken, the laterals obscured by the close-meshed slightly raised reticulum of tertiary veinlets; beneath more or less greyish-pruinose, the midrib nearly plane, the laterals (c. 5 or 6 on a side) and veinlets anastomosing in a subprominent reticulum; margins sharply differentiated, thin and acute, plane or reflexed (but not revolute).

---

[21] Subsect. **Mirifici**, subsect. nov. Ramis ramulisve lenticellatis; foliis ramulorum oppositis, coriaceis; staminibus 5; stigmatibus dilatatis, calyptratis. — Species typica *Phyllanthus mirificus* Webster.

Monoecious; flowers in axillary bisexual cymules, each with a solitary female and mostly 2 or 3 male flowers; bracteoles ovate, blackish and indurate, persistent.

Male flower: pedicel slender, c. 1–1.2 mm. long. Calyx reddish when dried; calyx-lobes 5, chartaceous, obovate, c. 1.5 mm. long, 0.9–1.3 mm. broad, rounded at the tip, entire, the midrib apparently unbranched. Disk-segments 5, ellipsoid, somewhat thickened, entire, c. 0.25–0.3 mm. across. Stamens 5; filaments connate into a column c. 0.5–0.8 mm. high, unequal in length (two anthers inserted lower than the other three); anthers subsessile, ascending or vertical, blunt, 0.3–0.4 mm. long, 0.4–0.45 mm. broad; anther-sacs divergent, dehiscing vertically, the slits not confluent; pollen grains 16–18 μ in diameter, areoles polybrochate, c. 6 μ across, c. 5–7 per amb.

Female flower: pedicel (at anthesis) 1.5–2.5 mm. long, subterete, enlarged and massive above. Calyx reddish when dried; calyx-lobes 6, subequal, biseriate, the outer broadly ovate, the inner broadly obovate, c. 1.5–1.8 mm. long, 1.1–1.4 mm. broad, entire, the veins obscure. Disk rather massive, bluntly angled, plane, the margins entire. Ovary subglobose, sessile, almost completely covered by the lower margins of the three dilated stigmas (style-ends) which are reflexed and appressed to form a close-fitting calyptra; stigmas with auricles connivent into a blunt beak at the top, the lateral margins entire, the distal margins crenulate-notched, 0.9–1.1 mm. long, 0.9–1 mm. broad across the distal edge.

Fruit and seeds unknown.

TYPE: Cuba, *León et al. 22613.*

DISTRIBUTION: scrublands and pinelands, northeastern Oriente province, Cuba (MAP XXIII).

CUBA. ORIENTE: Charrascal del Coco, south of Moa, July 1945, *León, Clemente, & Alain 22613* (MICH, HOLOTYPE; LS, ISOTYPE); charrascos y pinares, Sierra de Moa, alt. c. 750 m., 25 July 1953, *Alain 3380* (GH); pineland barrens, Charrascos de Peña Prieta, Toa, alt. 600 m., 30 Dec. 1953, *Alain 3616* (GH; sterile).

This extraordinary species, which remained undetected up until recent times, now appears to be as widely distributed in the Sagua-Baracoa range as some of the other specialized members of sect. *Williamia.* Its opposite branchlet-leaves and calyptriform stigmas at once set it apart from all of its West Indian congeners, and its androecium of 5 stamens in two unequal sets appears very similar to that in certain Old World species of subg. *Kirganelia.* Nevertheless, its phyllanthoid branching and areolate pollen grains show that it belongs in subg. *Xylophylla*, and both foliar and floral characters attest its affinity with the species of sect. *Williamia.* However, no one species of the section appears particularly close to *P. mirificus,* although *P. excisus* has a similar aspect (the type collection was, in fact, determined as that species), while *P. williamioides* has similar androecia and short-pedicellate flowers. In some ways, *P. mirificus* is intermediate between subsects. *Discolores* and *Incrustati*; this is especially true of its development of copious lenticels, which presents a condition transitional between the smooth stems of subsect. *Discolores* and the scurfy axes of subsect. *Incrustati*. Because of this intermediary position and of its very divergent features, *P. mirificus* seems best assigned to a special subsection of its own.

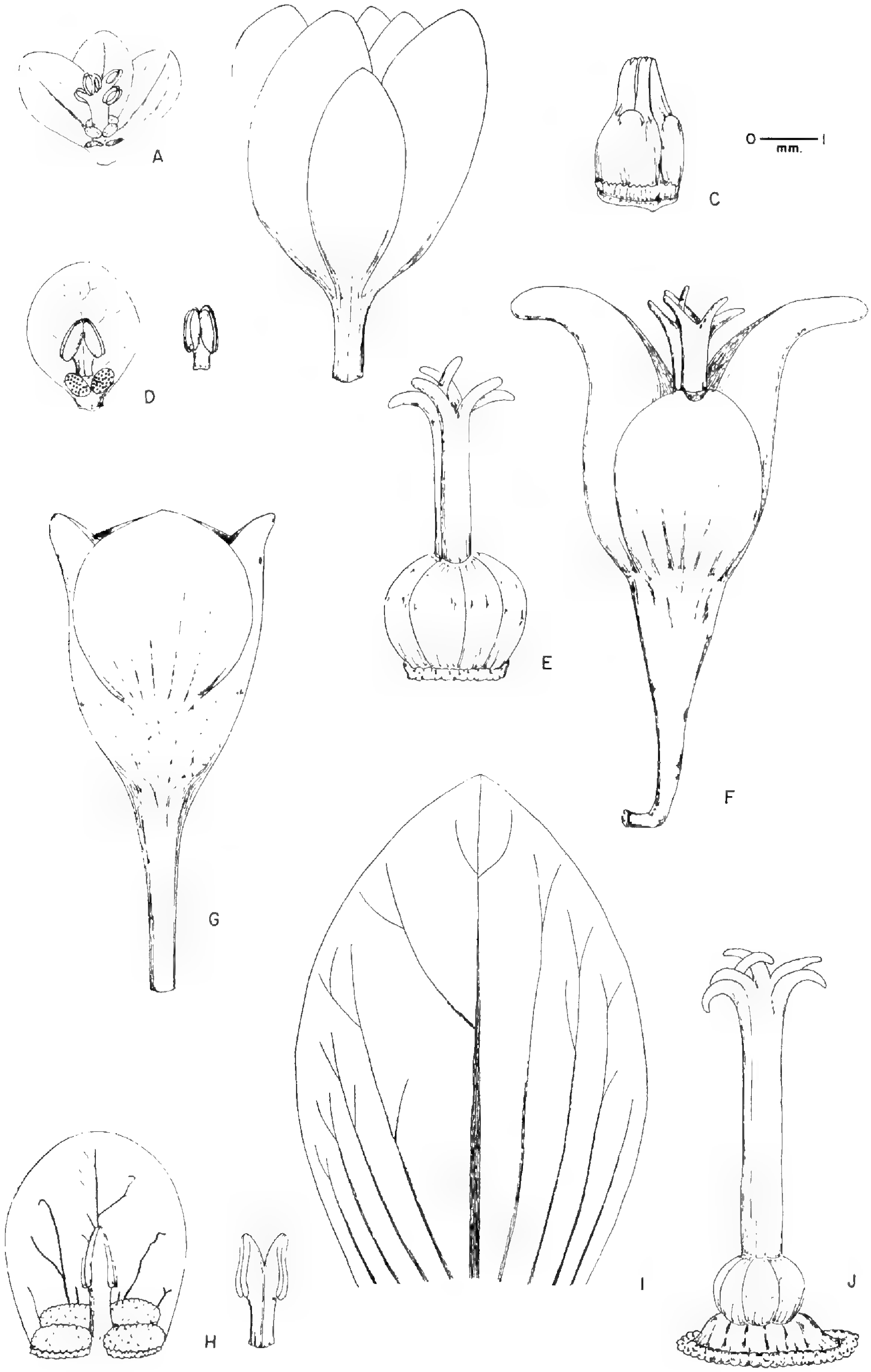
Sect. 17. **Thamnocharis** Webster, Contr. Gray Herb. **176**: 59. 1955.

Shrubs with phyllanthoid branching; cataphylls large, indurate; leaves coriaceous, stipules caducous. Monoecious; cymules bisexual, the flowers appearing with the expanding leaves. Male flower: calyx-lobes 4–6; disk-segments 4–6; stamens 2–6 (–8), filaments united (apparently free in *P. comptus*), anthers dehiscing vertically; pollen grains areolate. Female flower: calyx-lobes 4–6, coriaceous; disk entire, angled; styles free or connate, bifid, the style-branches narrowed to acute tips. Capsule subglobose, dry, not veiny; seeds smooth or rugulose.

TYPE SPECIES: *Phyllanthus cinctus* Urb.

The relationships and nomenclature of this Cuban section and its three constituent species were discussed at some length in the original place of publication (op. cit. pp. 59–62). However, subsequent investigation has shown (on the basis of the presumed hybridization between *P. discolor* and *P. comptus*) that there must be a fairly close affinity between sects. *Williamia* and *Thamnocharis*; consequently, the position of the latter in the linear arrangement of sections has been altered. Furthermore, it is now clear that sect. *Thamnocharis* need not be compared with the Asiatic sect. *Eriococcodes*, for the latter definitely belongs in subg. *Eriococcus*, and its floral similarities are simply due to parallel evolution. Despite the dissimilarity (in gross appearance and in floral details) between *P. cinctus* and *P. discolor*, a significant affinity between subsect. *Discolores* (of sect. *Williamia*) and sect. *Thamnocharis* appears highly probable.

Before male flowers of *P. comptus* and before its hybridization with *P. discolor* were known, sect. *Thamnocharis* was thought to be related to sect. *Epistylium*. The Jamaican species of that section resemble the Cuban species of sect. *Thamnocharis* in their palm-like habit, reduced androecium, and similarly veined leaves. It may yet be possible to show that sect. *Epistylium* is closely related to the Cuban plants, but since its representatives (*P. cauliflorus* and *P. cladanthus*) differ in having persistent stipules, horizontally dehiscing anthers, and dilated lacerate styles, they are placed at some distance in the present linear arrangement. Even more similar to sect. *Thamnocharis*, at least superficially, is the monotypic sect. *Glyptothamnus* which closely mimics *P. cinctus*; but that group appears to be much more closely allied to sect. *Epistylium* in its technical characters. These rather puzzling suggestions of reticulate relationships indicate that the phylogeny of the groups in question can by no means be considered finally settled.



Webster, West Indian Phyllanthus

KEY TO THE SPECIES

1. Calyx-lobes and stamens 5 or 6; styles free; pedicel of female flower 10–14 mm. long; seeds vermiculately marked, 4.5 mm. long or more; cataphyllary stipules ribless, less than 1 cm. long. . . . . 55. *P. comptus*
1. Calyx-lobes 4; stamens 2; styles united into a column; pedicel of female flower not over 6 mm. long; seeds smooth, not over 4 mm. long; cataphyllary stipules longitudinally ribbed, 1 cm. long or more.
   2. Male calyx-lobes c. 2 mm. long, with mostly 1–3 nerves from the base; anthers triangular, 0.5–0.8 mm. long; female calyx-lobes reflexed at the tips, the inner (longer) c. 3–5 (–6) mm. long; female disk tenuous, rim-like, c. 2 mm. across. . . . . 56. *P. cinctus*
   2. Male calyx-lobes c. 3–3.5 mm. long, with mostly 5–7 nerves from the base; anthers lanceolate, 0.9–1.2 mm. long; female calyx-lobes not reflexed at the tips, the inner (longer) becoming 6–8 mm. long; female disk very massive, forming a mound 3–4 mm. broad and 0.5–1 mm. high, its foveolate rim depressed. . . . . 57. *P. ekmanii*

55. **Phyllanthus comptus** Webster, Contr. Gray Herb. **176**: 61. 1955.

Glabrous shrub; branches terete, smooth, pale brown becoming greyish, c. 3–4 mm. thick. Cataphylls massive and coriaceous but deciduous: stipules triangular-lanceolate, acuminate, c. 6–7.5 mm. long, 2–3 mm. broad, obliquely truncate at the base, brownish with blackened indurate tips; blade narrower. Deciduous branchlets (5.5–) 7–14 cm. long, 1–1.5 mm. thick, stramineous or pale reddish brown, smooth, subterete (somewhat flattened proximally), with only 5–7 nodes; first internode (15–) 20–30 mm. long, median internodes c. 15–30 mm. long. Leaves: stipules caducous, ovate-lanceolate, 5–6 mm. long, 2.7–3 mm. broad, acuminate, more or less denticulate along the margin, brownish, scarious-chartaceous with more or less indurate darkish tips. Petioles plane adaxially, convex abaxially, smooth, stramineous or reddish brown, 2.5–4 mm. long. Leaf-blade coriaceous, ovate or elliptic, c. (2.5–) 3–5.5 cm. long, (1.2–) 1.5–3 cm. broad, obtuse and minutely apiculate at the tip, obtuse or rounded at the base; above sublucid, olivaceous, the midrib and chief laterals slightly raised; beneath paler, the midrib and main laterals (4 or 5 on a side) slightly raised, forming a subprominent reticulum, veinlets obscure; margins cartilaginous-thickened, light brownish, more or less reflexed.

Monoecious; flowers appearing on new branchlets with the expanding leaves, the male early deciduous; cymules usually bisexual, of 1 female and several (c. 5–8) male flowers.

PLATE XXVI. FLOWERS OF SECT. *Williamia*, SUBSECT. *Mirifici*, AND OF SECT. *Thamnocharis*.

FIGS. A–C. Male flower, female calyx, and gynoecium of *Phyllanthus mirificus* Webster (*Alain 3380* [GH]). FIGS. D–F. Male flower, female flower, and gynoecium of *Phyllanthus cinctus* Urb. (*Jervis 3355* [GH]). FIGS. G–J. Male flower, androecium, female calyx-lobe, and gynoecium of *Phyllanthus ekmanii* Webster (*Jervis 3037* [GH]).

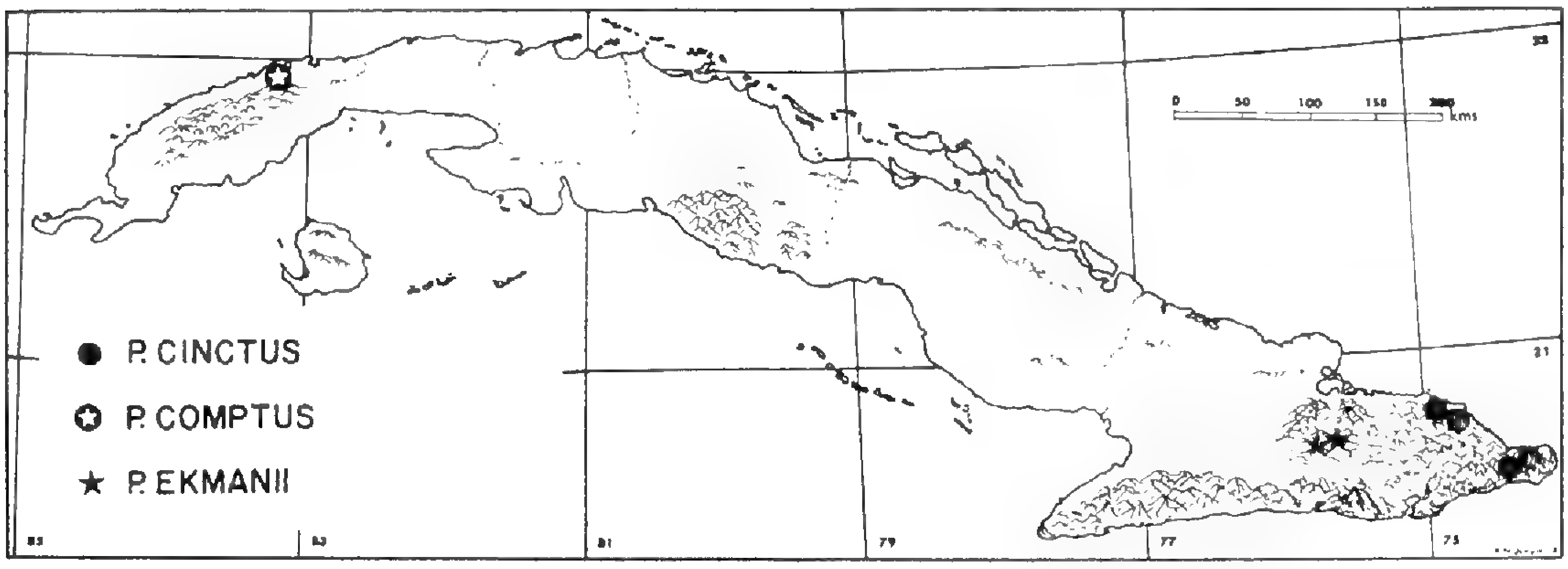
Male flower (described from immature buds): pedicel up to c. 2.5 or 3 mm. long. Calyx-lobes 6 (rarely 5), greenish, nervation obscure; disk-segments 6 (rarely 5), flattened, foveolate; stamens (4–) 5 or 6 (–8), filaments shorter than anthers and apparently not united (but staminal column perhaps not yet developed); anthers reniform, c. 0.4–0.5 mm. broad; anther-sacs divergent, dehiscing more or less vertically, the slits apically confluent.

Female flower: pedicel slender, subterete below, gradually dilated and obtusely angled above the middle, 10–14 mm. long. Calyx-lobes 6 (rarely 5), unequal, spathulate, rounded and entire at the tip, in flower 2.5–4 mm. long and 1.2–1.7 mm. broad, in fruit 3.3–4.2 mm. long, c. 1.7 mm. broad, the nerves obscure. Disk flat, 6-angled, becoming dark brown, not conspicuous. Ovary reddish brown, sulcate, emarginate at the top; styles free except at the very base, ascending, c. 1.5 mm. high, bifid; style-branches divergent, recurving, terete, narrowed to the tips.

Capsule-valves c. 7–7.5 mm. long, reddish brown, the veins obscure. Columella 3.8–4 mm. long. Seeds trigonous, asymmetric, carinate or somewhat irregular on the back, (4.5–) 4.8–5.1 mm. long, (2.5–) 3 mm. tangentially (across the back), dark brown (to the naked eye), with a vermiculate pattern of brownish-black raised lines on a light brown background; hilum submedian, c. 0.4–0.5 mm. across, the raphe conspicuous.

TYPE: Cuba, *Acuña 18222.*

DISTRIBUTION: endemic to the Cajálbana region, Pinar del Río province, Cuba (MAP XXIV).



MAP XXIV. Distribution of sect. *Thamnocharis* in Cuba.

CUBA. PINAR DEL RÍO: en arroyos, La Cajálbana, La Mulata, 28 Sept. 1952, *Acuña 18222* (SV, HOLOTYPE; fruiting); banks of a rivulet, cuabales, east of Loma Cajálbana, La Palma, Oct. 1952, *Acuña* (LS, MICH); La Cajálbana, junto a cañada, Camino de Sagua, 12 Mar. 1954, *Acuña & Schubert 19120* (GH, PARATYPE; male and female flowers).

This recently described species, which would still remain unknown were it not for the efforts of Ing. Julian Acuña, needs further study. Good material of the male flowers is sparse or lacking in most specimens of this and the other two species of sect. *Thamnocharis*, because the flowers appear with the developing leaves and the male ones are soon deciduous. The androecium of *P. comptus* is of especial interest because of the apparently free filaments and the variable number of stamens. A count of 25 flowers yielded the following distribution (the first figure being the stamen number): 4 — 3, 5 — 9, 6 — 11, 7 — 1, 8 — 1. This range of variation nicely bridges the gap between the androecium of *P. discolor*, with 9–14 stamens, and the other two species of sect. *Thamnocharis*, with only 2. The presumption that *P. comptus* represents a phylogenetically important connecting link is thus strengthened.

Although there appears to be no serious doubt regarding the kinship of *P. comptus* with *P. cinctus* and *P. ekmanii*, the differences between the Pinar del Río and Oriente plants are so profound that their separation must be ancient; they could be placed in different subsections if there were any point in subdividing so small a section as *Thamnocharis*. The recognition of the hybridization between *P. comptus* and *P. discolor* (discussed in detail under the latter) has further complicated the picture. Although these two species obviously retain some degree of genetic compatibility, the cataphylls, leaves, styles, and seeds of *P. comptus* are so different from those of *P. discolor* that each species must represent the end-product of a long-separate evolutionary line. In common with several other species endemic to the Cajálbana area, *P. comptus* bears the earmarks of a relict species the nearest relatives of which have long since disappeared.

56. **Phyllanthus cinctus** Urb. Symb. Ant. **9**: 191–192. 1924; emend. Webster, Contr. Gray Herb. **176**: 60. 1955.
(PLATE XXVI, *figs.* D–F).

Conami (?) ovalifolia Britton, Mem. Torr. Bot. Club **16**: 73–74. 1920; non *Phyllanthus ovalifolius* Forsk., 1775.
Phyllanthus brittonii Alain, Contr. Mus. La Salle **11**: 1. 1952.

Subshrub or shrub 0.15–1 m. high, with the habit of a miniature tree, the primary stem unbranched, greyish, furrowed, c. 4–8 mm. thick. Lower leaves (missing on many specimens) with petioles c. 5–7 mm. long, leaf-blades obovate or spathulate, 4–6.5 cm. long; upper leaves reduced to cataphylls: stipules triangular-lanceolate (somewhat falcate), acuminate, 10–17 mm. long, 4–5 mm. broad (on vigorous shoots; sometimes as small as 7 mm. long and 3.5 mm. broad on weak axes), obliquely truncate at the base, conspicuously longitudinally corrugate-ribbed, dull reddish brown, somewhat blackish and glandular at the base, sometimes densely hirtello-scabridulous at the base or throughout, scarious-indurate; blade acicular, 7.5–9 mm. long. Deciduous branchlets erect to spreading, (10–) 15–23 cm. long, 2.5–3 mm. broad, olivaceous, smooth or pustulate-scabridulous, distinctly flattened, with c. (4–) 8–15 leaves; first internode (15–) 20–50 (–65) mm. long, median internodes (10–) 15–25 (–40) mm. long. Leaves: stipules caducous (represented in most specimens only by small scars), broadly lanceolate, c. 3.5–4 mm. long, acuminate, entire or obscurely denticulate, brownish, scarious. Petioles subterete (somewhat flattened adaxially), rugulose or sometimes scabridulous, 2.5–5 mm. long. Leaf-blades coriaceous, oblong-elliptic, tending to be slightly obovate, (3–) 4–8 cm. long, (1.5–) 2–3.5 (–4.5) cm. broad, obtuse or rounded and with a minute blackish apiculum (sometimes obsolete) at the tip, acute to obtuse at the base; above sublucid or dully olivaceous, minutely foveolate, the midrib plane or slightly raised, the lateral and tertiary veins anastomosing in a somewhat prominent reticulum; beneath paler, the midrib prominently raised, the laterals (mostly 6–10 on a side) and veinlets forming a prominent reticulum; margins with a reflexed thickened marginal rim (which is colored as the rest of the undersurface).

Monoecious; flowers appearing on new branchlets with the expanding leaves, the male early deciduous; cymules bisexual, of 1 or 2 (rarely 3) female and c. 10–12 male flowers.

Male flower: pedicel slender, 3–5 mm. long. Calyx purplish or dark red; calyx-lobes 4, chartaceous, biseriate, the outer broadly ovate or oblong, the inner obovate or suborbicular, 1.9–2.1 mm. long, 1.4–2 mm. broad, rounded and entire at the tip, mostly 3-nerved, the irregular veins dark and conspicuous. Disk-segments 4, irregularly cubical or subglobose, foveolate-pitted, 0.4–0.6 mm. across. Stamens 2; filaments completely connate into a rather slender terete column usually 0.6–0.9 mm. high and 0.2–0.25 mm. thick; anthers erect, sessile atop the column, discrete or fused back-to-back below, triangular-ovate, (0.5–) 0.6–0.8 mm. long, 0.4–0.5 mm. broad; anther-sacs subparallel, dehiscing vertically, the slits not confluent; pollen grains c. 20–24 μ in diameter, areoles oligobrochate or transitional to polybrochate, c. 12–15 per amb, 4–6 μ across.

Female flower: pedicel terete and slender at the very base but abruptly dilated above, not angled, 4–5 mm. long. Calyx purplish or dark red; calyx-lobes 4, coriaceous, biseriate, subequal or unequal, at anthesis more or less spreading with the tips reflexed, elliptic to broadly ovate-oblong, the larger lobes c. 3–5 (–6) mm. long and 2–4 (–5) mm. broad, rounded or obtuse at the tip, triplinerved but the laterals much less conspicuous than in the male calyx, mesophyll densely crystalliferous. Disk squarish, the 4 coalesced segments forming a shallow undulate-crenulate, foveolate-pitted cup c. 2 mm. across. Ovary reddish brown, sulcate, the tips of the carpels slightly projecting above the insertion of the styles; styles erect, 2.3–3.5 mm. high, connate into a comparatively slender column 1.7–2.4 mm. high and 0.4–0.55 mm. thick; stylar branches divergent, recurving, terete and narrowed to subacute tips.

Capsule obtusely angled, c. 5.5–6 mm. in diameter, smooth, reddish-brown, not veiny. Columella 2.5–3 mm. long. Seeds trigonous, symmetric, 3.7–4 mm. long, 2.4–2.8 mm. radially and tangentially, reddish brown, smooth (minutely colliculose); hilum subterminal, elliptic, c. 0.5 mm. long.

Collected flowering Feb.–Apr., Aug.; fruiting Feb.–Mar., July.

TYPE: Cuba, *Shafer 8446*.

DISTRIBUTION: serpentine areas, usually in pinelands, eastern Oriente province, Cuba (MAP XXIV).

CUBA. ORIENTE: Cananova, sur le charrascal serpentineux du Cerro de Miraflores, 16–23 Apr. 1943, *Marie-Victorin, Clement, & Alain 21634* (MT); vicinity of Moa, Arroyo Moa, 10 Apr. 1945, *Acuña 12479* (SV, US); Moa, pinares, summer 1939, *Mrs. Bucher 61* (NY, SV); Moa, río de la scierie, 16–23 Apr. 1943, *Marie-Victorin, Clement, & Alain 21635* (MT); Moa, 29 Aug. 1917, *Roig 1545* (NY, SV); wet pinelands near Punta Gorda, 14 July 1947, *León & Clemente 23057* (MICH); rich woods, alluvial valley of Río Yamaniguey, 27 Feb. to 1 Mar. 1910, *Shafer 4228* (NY, US), *4274* (F, NY); between Yamurí Arriba and Bermejal, Feb. 1911, *Shafer 8446* (NY, LECTOTYPE); Cuchillas de Baracoa, c. 1 mi. north of Río Yumurí, pinelands, alt. c. 2000 ft., 18 Mar. 1954, *Jervis 3355* (GH).

Of the three species of sect. *Thamnocharis, P. cinctus* is the commonest and most widespread, occupying relatively mesophytic riparian habitats as well as drier pinelands or scrub. It correspondingly is the most variable of the three species, and *Jervis 3355* is particularly divergent due to its large female calyx (the longer lobes being 6 by 5 mm. instead of 3–5 by 2–4 mm.) and smaller leaves with only 5–7 lateral veins. In these respects it partially closes the morphological gap between *P. cinctus* and *P. ekmanii* and provides additional support for the possible alternative course of grouping these plants as two subspecies of a single species. Nevertheless, the gap — although narrowed — remains, and until further knowledge of the range of variation can be obtained, the present arrangement appears to be the best.

Also occurring in the Moa region within the range of *P. cinctus* is the narrowly endemic *P. chryseus* (sect. *Glyptothamnus*), which is strikingly similar in its habit, tetramerous calyx and androecium of two stamens. However, it differs in so many important respects (e.g., persistent stipules, unisexual inflorescence, annular male disk, lacerate styles) that the similarity to *P. cinctus* would seem to be ascribable to convergent development rather than to a close affinity.

57. **Phyllanthus ekmanii** Webster, Contr. Gray Herb. **176**: 60. 1955. (PLATE XXVI, *figs*. G–J; PLATE XXVII, *fig*. B).

Phyllanthus cinctus Urb. Symb. Ant. **9**: 191–192. 1924 (as to description, not as to type).

Subshrub or treelet, with the habit of *P. cinctus,* 0.3–1 m. high. Lower leaves of main axis (missing on many specimens) with petioles 5–7 mm. long, leaf-blades obovate or broadly elliptic, 3.5–6.5 cm. long and 2–4 cm. broad; upper leaves reduced to cataphylls: stipules triangular-lanceolate, acuminate, 10–17 mm. long, 4–5 mm. broad (on vigorous shoots; sometimes as small as 7 mm. long and 3.5 mm. broad), truncate at the base, conspicuously longitudinally corrugate-ribbed, dull reddish brown, scarious-indurate; blade acicular. Deciduous branchlets erect to spreading, (8–) 10–23 cm. long, 2.5–3 mm. broad, olivaceous, smooth or pustulate-scabridulous, distinctly flattened, with c. 7–15 leaves; first internode 15–45 mm. long, median internodes 10–25 mm. long. Leaves: stipules caducous (represented in most specimens only by small scars), lanceolate, c. 1.5–2 mm. long, acuminate, obscurely denticulate, brownish, scarious. Petioles somewhat flattened adaxially, rugulose, sometimes scabridulous, (2–) 2.5–4 mm. long. Leaf-blades stiffly coriaceous, elliptic to slightly ovate, (2.5–) 3–5 (–6) cm. long, 1.3–3 (–3.5) cm. broad, obtusely rounded or emarginate at the tip (the minute blackish apiculum nearly or quite obsolete), cuneate to obtuse or rounded at the base; above sublucid, minutely foveolate, the midrib plane or slightly raised, the lateral and tertiary veins anastomosing in a prominent somewhat raised reticulum; beneath paler, the midrib prominently raised, the lateral (c. 4–6 on a side) and tertiary veins forming a reticulum more prominent than that above; margins with a reflexed thickened brownish or somewhat orange marginal rim.

Monoecious; flowers appearing on new branchlets with the expanding leaves, the male early deciduous; cymules bisexual, of 1 or 2 female and c. 2–5 male flowers.

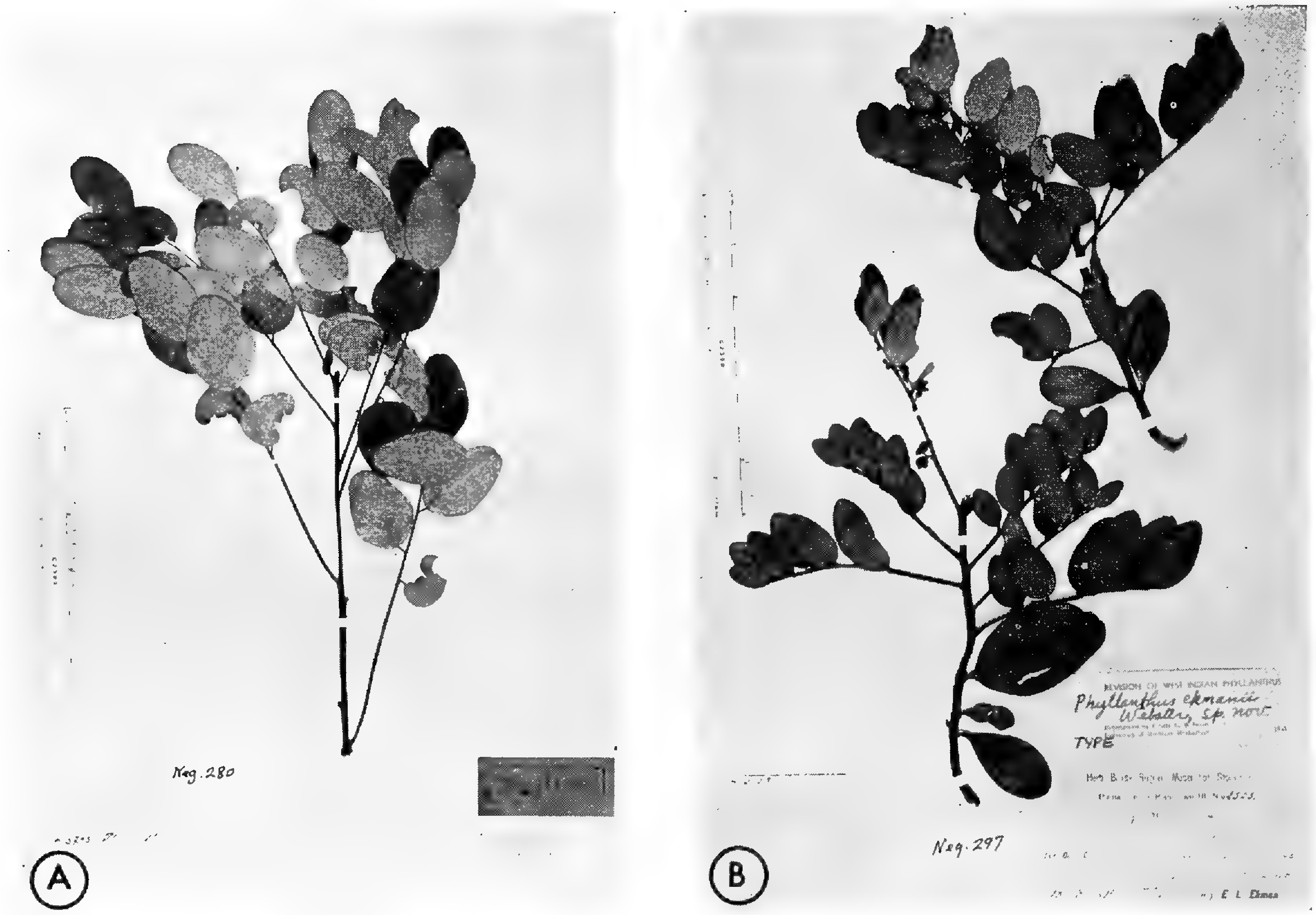
Male flower: pedicel slender, becoming 4–9 mm. long, abruptly dilated and fleshy above. Calyx dark reddish (rarely creamy-white?); calyx-lobes 4, chartaceous, biseriate, suborbicular, 3–3.7 mm. long, 2.3–2.7 (–3) mm. broad, rounded and entire at the tip, ordinarily with 5–7 nerves from the base but these not very conspicuous. Disk-segments 4, subrectangular, more or less flattened, rugulose, c. 0.7–1.1 mm. across. Stamens 2; filaments completely connate into a stout column c. 0.5–0.8 mm. high and 0.6 mm. thick; anthers erect, sessile atop the column, fused back-to-back from ⅓ to all their lengths, narrowly triangular-lanceolate, c. 1–1.2 mm. long, 0.5–0.7 mm. broad; anther-sacs slightly divergent, dehiscing vertically, the slits not confluent; pollen grains c. 24–28 μ in diameter, areoles oligobrochate, mostly 15–18 per amb, c. 4–6 μ across.

Female flower: pedicel terete and slender at the base but abruptly dilated above, not angled, 2.5–5 (–6) mm. long. Calyx dark reddish (rarely creamy-white?); calyx-lobes 4, coriaceous, biseriate, subequal, broadly ovate or elliptic (the outer strongly convex, the inner conduplicate), erect (the tips not reflexed), the larger lobes 6–8 mm. long and 3–5 mm. broad, rounded at the tip, with c. 6 or 7 subparallel conspicuously reticulate-ramifying nerves, mesophyll densely crystalliferous. Disk squarish, very massive, forming below the ovary a mound-like pedestal c. 0.5–1 mm. high and 3–4 mm. broad, the foveolate rim depressed.

Ovary reddish brown, strongly sulcate; styles erect, 3–5 mm. high, connate into a column (2.1–) 2.5–4 mm. high and c. 0.4 mm. thick (somewhat dilated upwards); stylar branches divergent, slender, recurving, terete and narrowed to subacute tips.

Capsule valves c. 5 mm. long, reddish brown, smooth, not veiny. Columella nearly 3 mm. long. Seeds trigonous, nearly symmetric, 3.3–3.4 mm. long, 2–2.2 mm. radially, 2.2–2.5 mm. tangentially, reddish brown, smooth (minutely colliculose); hilum subterminal, ovoid or elliptic, c. 0.5 mm. long.

Collected flowering Feb., Apr., Aug.; fruiting May, June, July.



GROWTH FORM IN SECTS. *Williamia* AND *Thamnocharis*. FIG. A. *Phyllanthus microdictyus* Urb. (*Ekman 3705* [S, HOLOTYPE]). FIG. B. *Phyllanthus ekmanii* Webster (*Ekman 2523* [S, HOLOTYPE]); note the unreduced leaves on the lower part of the main axis.

TYPE: Cuba, *Ekman 2523.*

DISTRIBUTION: restricted to serpentine areas of the Sierra de Nipe, Oriente province, Cuba (MAP XXIV).

CUBA. ORIENTE, SIERRA DE NIPE: Cayo del Rey, Pinar Colorado, 16 Apr. 1940, *Carabia 3587* (MICH, NY); Río Piloto, locis rupestribus, alt. 750 m., 18 Aug. 1914, 15 May 1915, *Ekman 2523* (S, HOLOTYPE; NY, ISOTYPE), *5704* (S); charrascales, Río Piloto, 10 June 1915, 27 Apr. 1919, *Ekman 6026, 19166* (S); charrascales, ad viam Bio, 27 Apr. 1919, *Ekman 9583* (S); exposed ridge, Pico Estrella, 18 Feb. 1954, *Jervis 3037, 3065* (GH).

This species endemic to the Sierra de Nipe is so closely related to *P. cinctus* that Urban's confusion (in associating specimens of the former with the name of the latter) is understandable. Although some of the distinctions between the two taxa are not quite absolute and may even further break down upon study of additional collections, there are so many points of difference that it seems preferable to rank them as closely related allopatric species rather than as two subspecies of one variable species. The larger size of the male flower, at least, always distinguishes *P. ekmanii*; and its hypertrophied female disk, which somewhat recalls the gynophore of *P. microdictyus*, is very different from the unmodified disk of *P. cinctus*. In addition, the female calyx and styles of *P. ekmanii* appear to be definitely larger than those of *P. cinctus*, but the dimensions of these organs are subject to such variation after anthesis that on the basis of specimens at hand it is difficult to make comparable measurements. There are, furthermore, additional differences in the mean values of such characters as leaf-size and vein-number which lend support to the suppositon that *P. ekmanii* and *P. cinctus* are distinct species.

In contrast to *P. cinctus*, which ranges over much of the Sagua-Baracoa massif, *P. ekmanii* has a much more restricted range; it has thus far been collected only in the southern part of the Sierra de Nipe but not in the vicinity of Loma Mensura or Bandera. The only divergent specimen noticed was *Jervis 3037* which, according to the collector, had "creamy-white" rather than reddish flowers. Unfortunately no flowers were present on the single available specimen of this collection number; but since *Jervis 3065* from the same locality has typically reddish flowers, it would appear that the whitish-flowered form is only a trivial local variant.

(*To be concluded*)

JOURNAL

OF THE

ARNOLD ARBORETUM

VOL. XXXIX APRIL 1958 NUMBER 2

NEW RECORDS OF JAMAICAN FLOWERING PLANTS, I

RICHARD A. HOWARD AND GEORGE R. PROCTOR

FOR THE PAST SEVERAL YEARS the authors have been conducting surveys of the vegetation growing on bauxitic and related soils in Jamaica, B.W.I. (Jour. Arnold Arb. **38**: 1–41, 151–169. 1957). In the course of this work it was possible to visit interesting geographical areas, sometimes *en route* between areas of mining operations, sometimes in areas off the beaten path where bauxite is only suspected to occur. In all of these forays our work was encouraged by Mr. C. Bernard Lewis, director of the Institute of Jamaica, and was financed in part by contributions from the Kaiser Bauxite Company and the Reynolds Jamaica Mines, Ltd. To Mr. Lewis and to officers and representatives of the contributing aluminum mining companies, we express our appreciation. We are also grateful to Dr. Lily M. Perry for her assistance with the Latin descriptions. The specimens cited are to be found in the herbaria of the Arnold Arboretum (A) or the Gray Herbarium (GH) and the Institute of Jamaica (IJ). A few specimens have been seen in the Hope Botanic Garden Herbarium now at the Department of Botany of the University College of the West Indies (UCWI). Duplicate specimens of our collections will be distributed to other herbaria.

Acrosynanthus jamaicensis, sp. nov. RUBIACEAE

Frutex 3 m. altus, ramis teretibus, ramulis compressis hispidulis; stipulis late triangularibus apiculatis ciliatis usque 2 mm. longis, intus petiolo coalitis; foliis 3–4.5 cm. longis, 4–8 mm. latis lineari-lanceolatis, apice acutis basi cuneatis decurrentibusque, margine integris et valde recurvis utrinque resinaceis, supra atroviridibus hispidulis, subtus sparsim hispidulis, albescentibus (vivis vel siccis); petiolo 1–2 mm. longo, hispidulo, resinaceo; inflorescentia terminali cymosa, cymis 3-floris, pedunculo 1 cm. longo, bracteis minutis, minus quam 0.5 mm. longis; pedicello 1–2 mm. longo; hypanthio obovoideo, sepalis 4–5, ovato-lanceolatis, minus quam 1 mm. longis, crassis, apice patenti-recurvatis hispidulis; corollae lobis 4, uno plerumque majore, 2.5–3 mm. longis, oblongis, apice rotundatis utrinque dense pubescentibus (pilis clavatis), tubo similiter pubescente, 2.5–3 mm. longo; staminibus 4 tubi corollae basi affixis, filamentis minus quam 0.5 mm. longis, antheris elongatis acutis vel acuminatis 1 mm. longis;

disco piloso; stylo glabro, stigmate bilobato, ovario 2-loculari, loculis 8–12-ovulatis; fructu maturo pallido-brunneo, 3 mm. diametro, seminibus pallido-brunneis tenuiter scrobiculatis.

Jamaica. PARISH OF TRELAWNY: Shrub on limestone sides of steep ravine, Ramgoat Cave district of the "cockpit" country, *Howard 14133* (A-type), *Howard & Proctor 14391* (A, IJ); *Mrs. Bernard Heineman, s.n.*, (IJ).

This is the first record of the genus *Acrosynanthus* from outside Cuba. The genus, as currently known, was established by Urban (Symb. Antill. 7: 544. 1913) and monographed by Standley (N. Amer. Fl. 32: 43. 1918). Subsequently, three additional species were described, bringing the total to eight species, all from the Oriente province of Cuba. The genus is more or less distinct within the Rondeletieae where it has been assigned; however, it is badly in need of restudy and probably of redefinition. The present species with five sepals, 4 petals, one larger than the others, having a pubescent corolla inside and out and four stamens attached at the base of a very short corolla tube does not fit readily into the limitations of the genus as recognized by Urban and Standley. *Acrosynanthus jamaicensis* is easily recognized by the resinous covering of the leaves and young stems, as is often found in species of *Phialanthus* and *Antirhea*. The white color of the under surface of the revolute leaves draws attention to this plant in the field.

Alvaradoa lewisii, sp. nov. SIMARUBACEAE

Frutex 4 m. altus, ramis virgatis strictisque; foliolis 22–25, ellipticis vel oblongis supra medium latissimis, 1.5–2.5 cm. longis, 0.7–1 cm. latis, apice rotundatis vel retusis, basi angustatis vel rotundatis, margine valde recurvis, supra atroviridibus subtus pallida flavoviridibus, glabris; petiolulo 1 mm. longo puberulo vel breviter adpresso-pubescente; inflorescentia terminali racemosa arcuatim pendula, rhachi aurea vel fulva puberula, pedicellis 9–11 mm. longis puberulis; fructu glabro, immaturo rubro, maturo flavo, lanceolato-ovoideo, 12–18 mm. longo, 6–7 mm. diametro, medio latissimo, utrinque angustato, carpellis (sterili fertilibusque) in magnitudine aequalibus.

Jamaica. PARISH OF TRELAWNY: A shrub on the steep face of a limestone ravine, Ramgoat Cave district in the "cockpit" country, *Howard 14128* (A-type).

Alvaradoa is a small genus of five species recently monographed by Cronquist (Brittonia 5: 133–137. 1944). Two of the species previously known have glabrous fruits, as does this. *Alvaradoa lewisii* differs from *A. jamaicensis*, the only species previously reported from Jamaica, in having leaflets oblong, broadest above the middle, with the margin strongly recurved, and the fruits longer than broad, but broadest at the middle and cuneate or narrowed at the base. *Alvaradoa jamaicensis* is based on a *Prior* specimen from Union Hill and most recent collections are from the central part of the island. *Alvaradoa lewisii* is from the "cockpit" country in the western third of the island of Jamaica, a region of noteworthy local endemism. The other glabrous-fruited species is *Alvaradoa arborescens*, from

Cuba, distinguishable from *A. lewisii* in having all three carpels equally developed with the styles at the same level, and in the shape of the fruit which tapers at the apex and the base.

Alvaradoa lewisii is named in honor of Mr. C. Bernard Lewis, director of the Institute of Jamaica, known for his work on the Pedro Cays, the Cayman Islands and many parts of Jamaica.

Clusia portlandiana, sp. nov. GUTTIFERAE

Frutex vel arbor epiphytica 4–7 m. alta; foliis obovatis planis, 13–18 cm. longis, 7.5–12 cm. latis, superiore ⅓ latissimis, apice rotundatis vel truncatis, versus basin angustatis, sessilibus, costa supra leviter canaliculata subtus prominente, venis numerosis parallelis; inflorescentia terminali corymbosa, 12–15 cm. longa, 12–15–flora; bracteis primariis anguste triangularibus, 9–13 mm. longis, basi 6 mm. latis, apice acutis, infrequenter foliiformibus obovatis 3 cm. longis 2 cm. latis; floribus femineis pedunculatis; pedunculo 1 cm. longo; bracteolis 4 oppositis et decussatis; sepalis 4 orbiculari-ovatis carnosis, siccis margine scariosis, 4–5 mm. longis latisque; petalis 5, ovatis carnosis 5–6 mm. longis latisque, carinatis, margine scariosis; fructu oblongo, 1–1.5 cm. longo, 1 cm. diametro, 5-loculari, apice rotundatis, stigmatibus 5, sessilibus; floribus masculinis pedunculatis; pedunculo 6–8 mm. longo; bracteis 4; sepalis 4, petalis 5 ut in flore feminea, staminibus numerosis, filamentis 4 mm. longis, antheris 1 mm. longis.

Jamaica. PARISH OF PORTLAND: In mist forest on limestone, John Crow Mountains, alt. 1500–2500 feet, 1.5–2.5 mi. southwest of Ecclesdown, *Howard & Proctor 14765* (A, IJ, fruit), *Proctor 9797* (IJ, fruit), *Proctor 993* (A-type; IJ, fruit), *Webster & Wilson 5136* (A, male); summit of John Crow Mountains, east of Millbank, *Swabey 13018* (UCWI, male).

Clusia portlandiana is similar to *C. venosa* and *C. krugiana* of the Lesser Antilles and Puerto Rico, differing from both in the larger inflorescence, longer peduncles and oblong fruit. In comparison with the other species reported from Jamaica, *C. portlandiana* is similar only to *C. clarendonensis*, differing in the larger leaves, larger inflorescence and the more numerous female flowers.

Dipholis bullata, sp. nov. SAPOTACEAE

Arbor parva usque 8 m. alta; foliis obovatis vel fere orbicularibus, plerumque 4–13 cm. longis 3.5-6.5 cm. latis, apice obtusis vel rotundatis, glabris coriaceis saepissime plus minusve bullatis propter margines revolutos, supra nitide atroviridibus subtus pallidioribus, costa subtus prominente, venis cetera subobscuris, petiolo 4–10 mm. longo; floribus in axillis 2–4, pedicello crasso minute sparsimque adpresso-strigoso, 5–10 mm., in fructu usque 15 mm. longo deinde suberoso-lenticellato; sepalis similibus *D. montana*; corolla ca. 5 mm. longa, tubo 2.5–3 mm. longo, lobis cucullatis, appendicibus lateralibus planis acuminatis sparsim erosis; filamentis ca. 1.2 mm. longis, antheris 0.6–0.8 mm. longis; staminodiis late ovatis, margine erosis, apice acutis vel subacuminatis filamentis subaequilongis vel paullo longioribus; stylo ca. 1 mm. longo, ovario glabro 5-loculari; fructu immaturo anguste ovoideo, apice truncato-apiculato, nitide olivaceo, ca. 15 mm. longo 5 mm. diametro, 1-spermo, semine immature, hilo ut videtur laterali.

Jamaica. PARISH OF PORTLAND: In elfin-woodland over limestone (elevation about 2500 feet), John Crow Mountains, 1.5–2.5 miles southwest of Ecclesdown, January 24, 1956, *Howard, Proctor & Stearn 14759* (A-type; IJ, fruit); *Howard, Proctor & Stearn 14755* (with fewer, more immature fruit); September 14, 1956, *Howard & Proctor 14842* (flowers) (A, IJ).

Though obviously related to ***Dipholis montana*** of the Blue Mountains area, the present species differs rather strikingly in its somewhat larger, shining, bullate leaves, fewer flowers per cluster, longer pedicels, slightly smaller flowers and differently-shaped fruits. It is entirely unlike *D. octosepala*, another Jamaican congener with which *D. montana* has been compared.

Myrica jamaicensis, sp. nov. MYRICACEAE

Arbor parva 3–4 m. alta, ramulis sparsim piloso-pubescentibus, pilis brevibus crispis albisque; foliis ellipticis vel obovato-ellipticis, 3.5 × 2, 4.5 × 2.5, 6 × 3 cm., apice rotundatis vel truncatis, retusis, basi cuneatis decurrentibusque, margine undulatis supra medium grosse sinuato-denticulatis, utrinque aequaliter minute foveolato-puncticulatis et glandulosis, bullatis, costa subtus sparsim, supra breviter pilosa, venis primariis 5–6-paribus subtus sparsim breviter pilosis deinde glabrescentibus; petiolo 1–2 mm. longo, crispe et breviter piloso; inflorescentia feminea 8–9 mm. longa, bracteis 0.6–0.7 mm. longis apice obtusis; fructu subgloboso 3 mm. diametro, ceraceo-papillato, dense glanduloso.

Jamaica. PARISH OF PORTLAND: John Crow Mountains at 2500 feet, 2.5 miles southwest of Ecclesdown, *Howard & Proctor 14832* (A-type; IJ).

This species differs from the two common species of Jamaica and the West Indies, *Myrica cerifera* and *M. microcarpa,* in having broader leaves, rounded and retuse at the apex, the margin undulate and sinuate and not evidently toothed, the blades bullate between the prominent primary veins. The plant is less pubescent than the other species and, while the staminate inflorescence is not known to us, the fruits of this new species are more resinous than others we have seen. The similarity of *M. jamaicensis* is with *M. microcarpa* rather than with *M. cerifera.*

Phialanthus myrtilloides Griseb. RUBIACEAE

Jamaica. PARISH OF TRELAWNY: a shrub 2.5 m. tall, with arching branches, on limestone and steep slopes of ravine, Ramgoat Cave district of "cockpit" country, *Howard 14134* (A).

Two species of *Phialanthus* have been described and reported from Jamaica, with an additional seven species known from Cuba and one from Cuba and the Bahamas. The specimen cited above does not fit either of the species known from Jamaica and is assigned to *P. myrtilloides*, a species described from Cuba but later recognized from the Bahamas, thus extending its range. *Phialanthus* is not well represented in herbaria and has not received comparative studies in the field. Certainly the taxonomic characters used by Standley in his treatment of the genus (N. Amer. Fl. 32: 281. 1934) are very weak. Further study will probably show that there are fewer species and greater variation than are currently recognized and nothing is to be gained by adding still another species at this time. The specimen cited is more heavily resinous than the other species of the genus. The leaves are lanceolate, broadest at the middle and only slightly recurved at the margin. The inflorescences are sessile and four flowers are produced. The corolla equals the calyx lobes in flower, but the calyx lobes soon expand until in fruit they exceed the tube in length. The stamens are shorter than the corolla lobes. The specimens we have seen from the Bahamas indicate a considerable variation in the size and shape of the leaves and the amount of resin produced. The Jamaican specimen can be included in this range of variation.

Schefflera stearnii, sp. nov. ARALIACEAE

Frutex 2–3 m. altus, glaber, inflorescentia excepta; ramis crassis teretibus prominenter lenticellatis; petiolo striato, 9–16 cm. longo prope basin lenticellato, ligulo simili *S. sciodaphyllum*; foliolis 5–8, majoribus minoribusque intermixtis, firme coriaceis, supra nitido-atroviridibus, subtus olivaceis, obovato-oblongis usque 18 cm. longis, 8 cm. latis, basi truncatis vel inaequalibus, apice abrupte acuminatis, margine cartilagineo integris aliquantum recurvis, costa praecipus subtus prominente, venis lateralibus utrinque prominulis, petiolulo 1–5 cm. longo; inflorescentia terminali ramosa, ramis ca. 6, 13–22 cm. longis, minute denseque ferrugineo-furfuraceo-pubescentibus, capitulis pedicellatis (pedicello 3–11 mm. longo), racemosis, 3–6-floris inter flores plus minusve setulosis; calyce coriaceo, inferiore ⅔ dense ferrugineo-puberulo, 1.5–2 mm. longo, ca. 2 mm. diametro, minute dentato; petalis puberulis, 1.5–2 mm. longis; antheris 0.5–1 mm. longis; stylis viridibus, ca. 1 mm. longis, apice valde incurvis; fructu non viso.

Jamaica. PARISH OF PORTLAND: in mossy elfin-woodland over limestone, elevation about 2500 feet, John Crow Mountains, 1.5–2.5 miles southwest of Ecclesdown, March 9, 1957, *Proctor 16255* (IJ-type); *Howard, Proctor & Stearn 14761* (A, IJ, in bud).

In his treatment of *Schefflera* in North American Flora (28B(1): 25–29. 1944), A. C. Smith ascribes two species to the Jamaican flora. One of these, *S. troyana*, is characterized by its dense white tomentum; the other, *S. sciodaphyllum*, by being nearly glabrous in contrast. Other, less striking differences can be observed by closely comparing the descriptions of the two species. Another name, *Sciadophyllum praetermissum*, is reduced to synonymy under *Schlefflera sciodaphyllum*, probably in the belief that it represents but a juvenile and more pubescent flowering stage of the latter species. This is a point which needs to be settled by further collecting.

The present new taxon entirely lacks the white tomentum of *Schefflera troyana* and, in fact, differs from that species in many details. From *S. sciodaphyllum* it differs by its shorter petioles and fewer, shorter, bicolorous leaflets of a different texture; by much shorter inflorescence branches covered with a rusty-scurfy pubescence different both quantitatively and qualitatively from the sparse, minute, whitish hairs of *S. sciodaphyllum*; by the fewer and strictly sessile (instead of pedicellate) flowers; by the slightly smaller calyx and shorter, puberulent petals; by the much shorter anthers of a different shape; and by the green (instead of carnose) styles.

Both *Schefflera stearnii* and *S. sciodaphyllum* occur in the John Crow Mountains more or less adjacent to each other. In our opinion, therefore, the differences between them cannot be attributed to contrasting environments.

Weinmannia portlandiana, sp. nov. CUNONIACEAE

Arbor 2 m. alta, ramulis ultimis compressis atro-fuscis sparsim et breviter pubescentibus; foliis oppositis trifoliolatis glabris, foliolo terminali lanceolato-elliptico, 4–4.5 cm. longo, 1.5–2 cm. lato, apice acuto, basi cuneato, margine versus apicem crenato versus basin integro, venis supra leviter impressis subtus subobscuris, foliolis lateralibus oblongis vel ellipticis apice rotundatis basi obliquis uno latere cuneatis altero rotundatis, margine saltem supra medium crenatis, 2.5 × 1.7 cm.–2.7 ×1.7 cm., petiolo 1.2–1.4 cm. longo alato, alis obovatis; inflorescentia terminali 8 cm. longa pseudoracemosa, rhaci sparsim et breviter pubescente; floribus hermaphroditis fasciculatis (2–5), bracteolis late ovatis usque 1 mm. longis, pedicello 4.5 mm. longo sparsim pubescente; calyce 4–partito, lobis ovatis usque 1 mm. longis; petalis oblongis 2–3 mm. longis; filamentis 4 mm. longis; pistillis 2, usque 5 mm. longis.

Jamaica. PARISH OF PORTLAND: John Crow Mountains at 2500 feet, about 2.5 miles southwest of Ecclesdown, *Howard & Proctor 14839* (A-type; IJ), *Proctor 11351* (IJ), *Howard, Proctor & Stearn 14770* (IJ).

The genus *Weinmannia* has been known previously in Jamaica by the variable and widespread *W. pinnata* L. and the pubescent form of the latter, *W. hirta* Sw. The present species differs from *W. pinnata* by having glabrous and strictly ternate leaves, the leaflets of which are larger than even the extreme forms of *W. pinnata*. *Weinmannia pinnata* as it occurs in the islands from Cuba to Grenada needs further taxonomic study. It is probable that a number of good subspecies or varieties will eventually be established in this complex. A comprehensive field study of various populations is required, however, to understand the morphological variations which occur and are represented in herbaria.

ARNOLD ARBORETUM
and
THE INSTITUTE OF JAMAICA

A NOTE ON THE IDENTITY OF THE GENUS BALANOSTREBLUS (MORACEAE)[1]

Frances M. Jarrett

The object of this note is to provide an identification for *Balanostreblus* Kurz, a monotypic genus of the Moraceae which has been credited to the Asiatic flora. It was assigned by Bentham and Hooker (Gen. Pl. 3: 377. 1880) to the subfamily Artocarpoideae and tribe Artocarpeae (using the modern names for these groups) and placed among the American genera of the tribe, next to *Sorocea* St.-Hil., a small genus of the tropical forest.

Balanostreblus was described by Kurz in 1873 (New Burmese Plants. Part III. Jour. Asiat. Soc. Bengal **42**: 247. *t. 19*) and his account is given in full below.

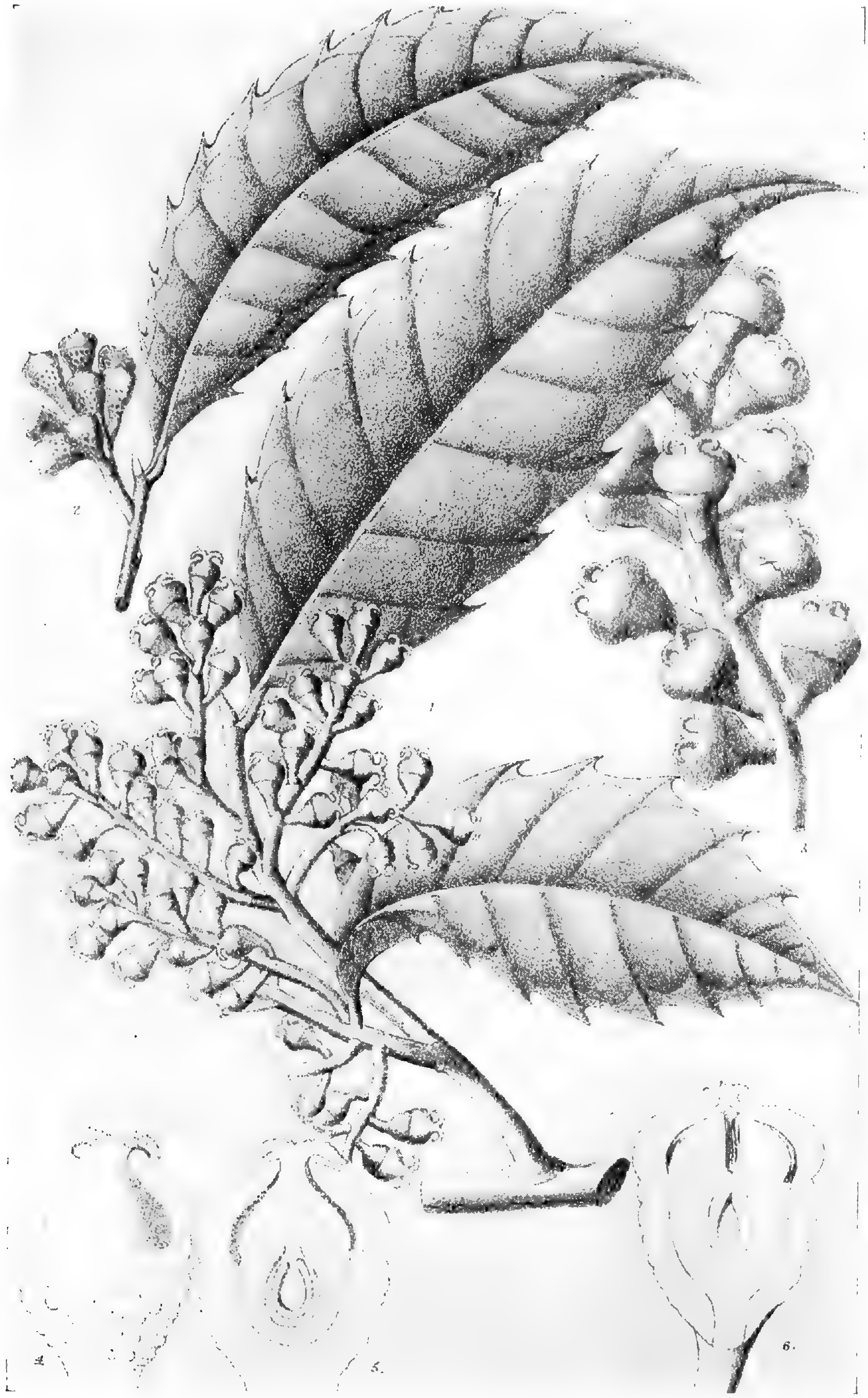
BALANOSTREBLUS, nov. gen. Flores monoici; masculi ignoti (ex inflorescentiis valde juvenilibus probabiliter amentacei?). Feminei racemosi: perianthium cum ovario connatum, sursum liberum et ovarium omnino includens, apice perforatum. Ovarium semisuperum, 1-ovulatum, ovulo pendulo; stylus perbrevis, e perianthii orificio protrudens; stigmata 2, brevia, crassa, villosula. Drupa perianthio carnoso inclusa, monosperma. Arbor lactescens, subglabra, foliis alternis grosse spinescenti-dentatis. Genus imperfecte cognitum sed distinctissimum *Antiari* affine.

BALANOSTREBLUS ILICIFOLIUS, nov. sp. Arbor ramulis scabriuscule puberulis; folia elliptica ad lato-ovalia, petiolo terete 1–2 lin. longo glabro suffulta, basi saepius subinaequali acuta v. obtusa, rigide coriacea, spinoso-acuta, grosse spinoso-dentata, 1–3 poll. longa, glabra, supra nitida costa supra immersa subtus unacum nervis lateralibus arcuato anastomosantibus valde prominente; flores parvi, viridiusculi, pedicello brevi crasso suffulti, in racemum axillarem brevem collecti; perianthium obturbinatum, rugulose-tuberculatum, c. 2 lin. longum; drupae pisi minoris magnitudine, rubrae, rugulosae, carnosae, glabrae. — *Chittagong* (Hf. et Th. sub Sapii sp. No. 4); *Ava* (J. Anderson).

The generic characters were thus based by Kurz on the female inflorescences. The plate, which is reproduced here, shows these attached to a leafy shoot and also includes dissections of the flowers. The inflorescences are raceme-like, though presumably having the cymose origin typical of the Moraceae, and their appearance is in contrast to that of the other Old World genera of the Artocarpeae, in which the inflorescences are capitate. The pedicellate flowers are likewise distinctive in structure and may be regarded as having the ovary sunken in and fused to a fleshy receptacle which is surmounted by a short, tubular, perforate perianth from which

---

[1] This paper is based on part of a thesis presented to the University of Cambridge, England, for the degree of Ph.D. Thanks are due to the Directors of the Royal Botanic Gardens, Kew, and the Muséum National d'Histoire Naturelle, Laboratoire de Phanérogamie, Paris, for their hospitality and to the latter for the loan of the collection of *Balanostreblus ilicifolius*.



Original illustration of *Balanostreblus ilicifolius* Kurz, Jour. Asiatic Soc. Bengal **42**: *t. 19.* 1873.

the bifid style projects. In this, as in the general aspect of the inflorescences, the genus resembles *Sorocea.*

Kurz did not state from which plant the drawing was made, but the identity of this was established by Hutchinson in 1918 (Kew Bull. **1918**: 147–153) when, in a paper which was primarily a revision of *Taxotrophis,* a genus belonging to the Moroideae, he also discussed the typification of *Balanostreblus ilicifolius.* He examined Kurz's material from the herbarium of the Botanic Garden, Calcutta, and found that it consisted of the specimen from Chittagong, *Hooker and Thomson 4* (also at Kew), and a specimen described as "cultivated at the Botanic Garden." Apparently no specimen from Ava was extant, since Hutchinson did not receive one, and he concluded that this might have been a living plant, though he mentioned that there was a collection under this name at Kew made by Anderson at Bhamo, about 180 miles to the north-east of Ava. Hutchinson stated that there was no doubt that the illustration had been prepared from the cultivated plant, which was female. The plant from Chittagong was male and this he identified as a collection of *Taxotrophis ilicifolia* Vidal, a variable species, which may have spiny-toothed leaves rather similar to those of the cultivated plant with which it had been matched by Kurz. Having thus shown that *Balanostreblus ilicifolius* was a *mixtum compositum*, Hutchinson redefined and redescribed the genus (l.c., 152), basing it entirely on the cultivated specimen and providing a new illustration. He still assumed that this plant was of Asiatic origin and suggested that it might be Anderson's collection from Ava. He thought that the genus should probably be removed to the Broussonetieae in the subfamily Moroideae. However, its characters are not in accord with that group.

In the course of a review of the characters of the genera of the Moraceae, *Balanostreblus* attracted my attention. The female inflorescence did not resemble that of any Old World genus and Bentham and Hooker's placing of the genus still seemed from the descriptions of Kurz and Hutchinson (in the absence of the lectotype) to be the most satisfactory, although the general classification of the Moraceae may be in need of revision. The genus thus appeared to be anomalous in the Asiatic flora.

Another possibility as to the origin of the plant was suggested by the finding under *Balanostreblus*, during a visit to the herbarium of the Muséum d'Histoire Naturelle, Paris, of a specimen which had been gathered by L. Pierre in the Botanic Garden at Calcutta in 1863, when he was assistant there. This was ten years earlier than Kurz's publication and the specimen had later been identified as *Balanostreblus ilicifolius* on the basis of Hutchinson's paper. It matched the description and plate exactly and it seems justifiable to assume that Pierre and Kurz made their collections from the same tree. The label gave the origin as "Brasilia ?? India ?" In view of this and the similarity already remarked between the female inflorescences and those of the South and Central American genus *Sorocea,* the sheet was compared with collections of that genus in the same herbarium. It was found to match almost perfectly *Guillemin 131*, Corcorado, Brasil méridional, 1838, which is the type of *Sorocea guilleminiana* Gaudichaud, Bot. Voy. Bonite, *t. 74*, 1844, except that in the latter most of the individual receptacles are enlarged and contain mature seeds. This species is characterized by the verruculose surface of the receptacles.

It is therefore concluded that *Balanostreblus* Kurz emend. Hutchinson is based on an introduced species of *Sorocea*, which is identified as *S. guilleminiana,* pending a revision of the genus. This was presumably brought in during the introduction of *Cinchona* to India, which took place at about this time and in the course of which several shipments of plants were sent from the New World under the auspices of the Royal Botanic Gardens at Kew.

A MONOGRAPHIC STUDY OF THE WEST INDIAN SPECIES OF PHYLLANTHUS *

GRADY L. WEBSTER

With five plates

Sect. 18. **Orbicularia** (Baill.) Griseb. Fl. Br. W. Ind. 34. 1859.

Orbicularia Baill. Etud. Gen. Euphorb. 616. 1858.
Roigia Britton, Mem. Torr. Bot. Club **16**: 73. 1920.
Dimorphocladium Britton, ibid. 74.
Phyllanthus sect. *Dimorphocladium* (Britton) Pax & Hoffm. Natürl. Pflanzenfam. **19c**: 63. 1931.

Shrubs with phyllanthoid branching, axes smooth and glabrous; leaves with mesophyllar sclereids, mostly coriaceous, stipules (at least proximal ones) mostly persistent. Monoecious; cymules male and bisexual, female flowers usually only one per cymule. Male flower: calyx-lobes 6 (rarely 5); disk-segments free or coalescent; stamens 3–7, filaments united entirely or below into a column; pollen grains areolate. Female flower: calyx-lobes 6 (rarely 5); disk tenuous to rather massive; ovary sessile or slightly stipitate; styles free or connate below into a column, the free ends bifid, style-branches often revolute at the tips. Capsule oblate, veins conspicuous or obscure; seeds trigonous, verruculose.

TYPE SPECIES: *Orbicularia phyllanthoides* Baill. [= *Phyllanthus orbicularis* HBK.]

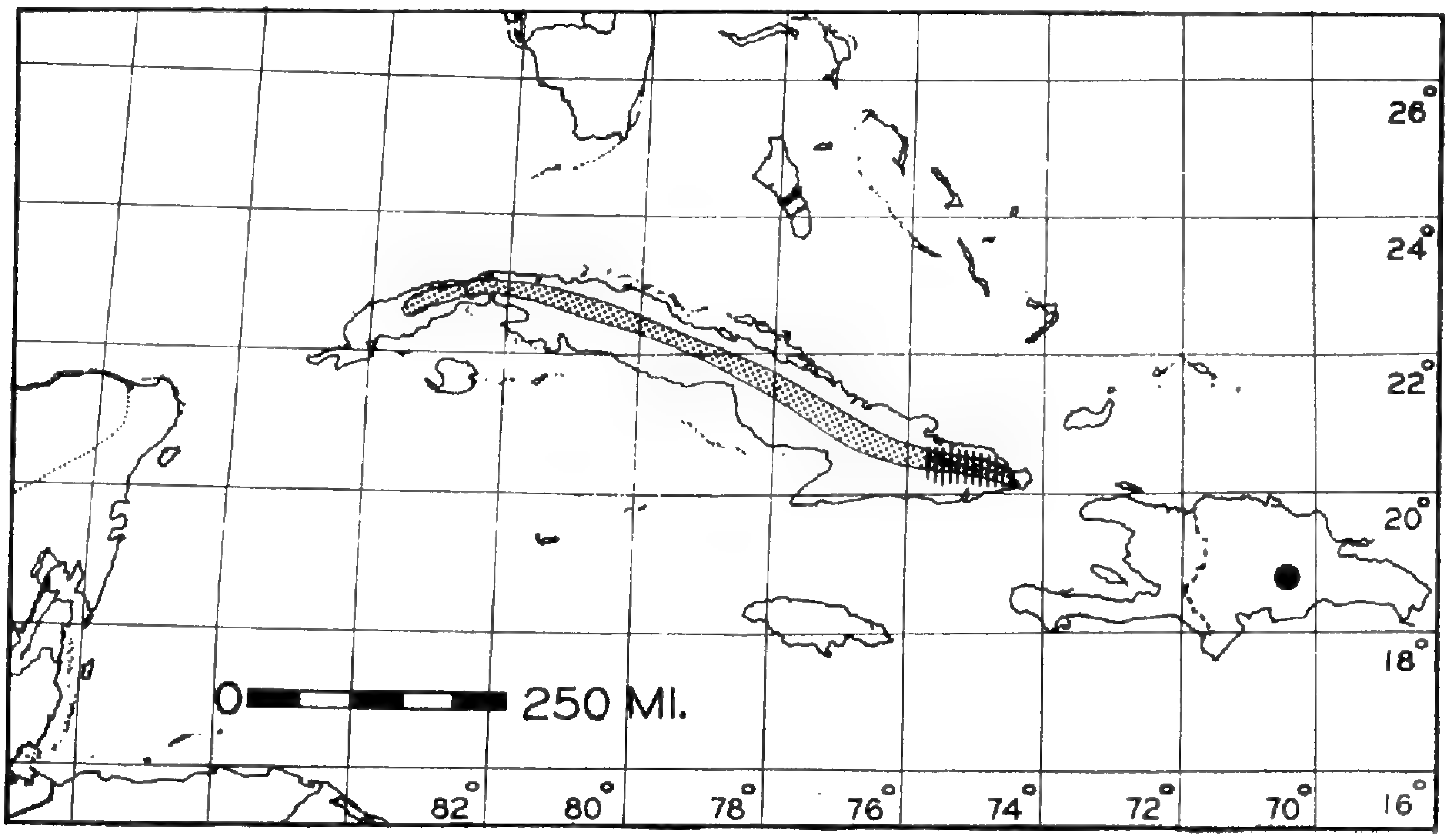
Although a well-marked and apparently monophyletic group, which here is given essentially the same circumscription as that of Carabia (Ecol. Mon. **15**: 335. 1945), sect. *Orbicularia* is rather difficult to characterize as distinct from neighboring sections in subg. *Xylophylla*. The most closely related section, from which sect. *Orbicularia* has probably been derived, is sect. *Williamia*. The species of the latter with sclerified leaves (subsect. *Incrustati*) can be distinguished from the present group only by their incrustate axes and lacerate style-tips.

After a prolonged study which has been pursued intermittently over a period of several years, the following treatment of sect. *Orbicularia* is presented with some diffidence. Despite personal field observations in Cuba in 1951 and 1953 and the analysis of a considerable number of herbarium specimens, a definitive resolution of the taxonomic problems in the group has not been achieved. Field studies have been of value in demonstrating (to the author's satisfaction, at least) that some of the confusion in the literature is traceable to the striking differences in leaf form brought about by different ontogenetic changes and/or responses to different ecological situations. Thus it appears that the very glossy and

---

* Continued from volume XXXIX, p. 100.

foveolate leaf on which *P. foveolatus* was described is only the older, more coriaceous one of *P. myrtilloides* ssp. *erythrinus*; and the convex, very glossy leaf which supposedly characterizes *P. coelophyllus* is merely the kind of leaf developed by *P. baracoensis* in drier situations. However, a much more serious difficulty to a satisfactory classification in the section is the extreme range of variability of some species, particularly *P. myrtilloides* and *P. orbicularis.* It is also possible that in certain instances hybridization has further complicated the picture by giving rise to anomalous specimens which appear to transgress the rather indistinct specific lines. It would be extremely difficult to account for the several peculiar forms from the Sierra de Nipe (described by Urban as species) except on the supposition that they represent the results of crosses between *P. chamaecristoides* and *P. phlebocarpus.* Finally, it must be remarked that Urban's usually sound taxonomic judgment failed him when treating sect. *Orbicularia,* for he described numbers of "paper species" (such as *P. breviramis, P. cardiophyllus,* and *P. melanodiscus*) which cannot be retained at any taxonomic rank.



MAP XXV. Distribution of sect. *Orbicularia*: black dot, *P. nummularioides* Muell. Arg.; stippling, *P. orbicularis* HBK.; vertical lines, remainder of species in the section.

In attempting to formulate a usable and objective classification of sect. *Orbicularia,* it has been necessary to abandon, in part, a purely morphological standard for delimitation of taxa and to rely heavily on the principle of geographical replacement as formulated by Huxley (New Systematics 36. 1940) and elucidated by Van Steenis (Fl. Mal. ser. I. 5(3): cxcv–cxcvi. 1957). The result is that, whereas Alain in the "Flora de Cuba" (1953) recognized 19 Cuban species referable to sect. *Orbicularia,* only 7 are accepted in the present treatment. It is realized that this may appear excessively radical especially since it leads to some apparent inconsistencies, but nevertheless it seems the closest approximation to the facts of nature that can be devised at this time. It is doubtful that the accumulation of additional material will bring any improvement as long as it can be analyzed only by orthodox herbarium methods; a completely satisfactory classification of the section must surely await an extensive population analysis with emphasis on cytological methods.

KEY TO THE SPECIES

1. Leaves spathulate, acute at the base, rigidly coriaceous, the margin neither reflexed nor revolute.
   2. Stipules dimorphic; leaf-blades of main stem 2–4 cm. long; branchlets 8–10 cm. long. . . . . 58. *P. formosus*
   2. Stipules subequal; leaf-blades of main stem, if unreduced, not over 1.5 cm. long; branchlets at most 5 cm. long.
      3. Pedicel of female flower mostly over 10 mm. long; anthers sessile or nearly so atop the column; calyx bright pink or purplish. . . . . 59. *P. comosus*
      3. Pedicel of female flower less than 5 mm. long; filaments united about half-way, the anthers long-stipitate; calyx whitish or faintly pinkish-tinged. . . . . 60. *P. orbicularis*
1. Leaves, if spathulate, not rigidly coriaceous nor with plane margins.
   2. Stamens mostly 5–7 (rarely 4, very rarely 3); leaves not all expanding with the flowers, not prominently reticulate on both sides with raised veins.
      3. Styles usually more than 1 mm. long, united into a column mostly 0.5 mm. high or more.
         4. Pedicel of female flower mostly more than 3 mm. long (if exactly 3 then anthers stipitate and cataphylls deciduous). . . . . 61. *P. myrtilloides*
         4. Pedicel of female flower mostly less than 3 mm. long (rarely to 3.5 mm.).
            5. Filaments of stamens mostly 1.5–2.5 mm. high, united in the lower half; branchlets mostly with less than 10 elliptic to orbicular leaves; cataphylls persistent. . . . . 60. *P. orbicularis*
            5. Filaments of stamens not over 1 mm. high, completely united or nearly so; branchlets mostly with 15–45 oblong to obovate, often falcate, leaves; cataphylls deciduous. . . . . 62. *P. chamaecristoides*
      3. Styles free or barely united at base, mostly less than 1 mm. long.
         4. Cataphylls subpersistent; branchlets 3–6 cm. long; leaves with petiole less than 1 mm. long, blade obovate or obcuneate, 3–7 mm. long, prominently apiculate; outer calyx-lobes (of both sexes) narrowly oblong, mostly less than 1 mm. broad. . . 63. *P. scopulorum*
         4. Cataphylls deciduous; branchlets mostly 6–12 cm. long; leaves with petiole 1–2.5 mm. long, blade broadly elliptic to orbicular, mostly 10–20 mm. long, at most obscurely apiculate; calyx-lobes subequal, the outer 1 mm. broad or more. . . . . 64. *P. nummularioides*
   2. Stamens mostly 3 (rarely 2 or 4); leaves and flowers expanding together,

leaf-blades with a prominent raised reticulum on both sides; styles free or nearly so, spreading, less than 1 mm. long. . . . . . 65. *P. phlebocarpus*

58. **Phyllanthus formosus** Urb. Repert. Sp. Nov. 13: 450–451. 1914. (PLATE XXVIII).

Dimorphocladium formosum (Urb.) Britton, Mem. Torr. Bot. Club **16**: 74. 1920.

Low shrub (4–6 cm. high ex Shafer), sparsely branching; main stems terete, stout (c. 5 mm. thick), more or less incrusted by the persistent stipules, foliage clustered at top. Leaves of main stems (i.e., those subtending branchlets) apparently not reduced to cataphylls: stipules blackish, indurate, acicular-lanceolate, 8–11 mm. long, attenuate-acuminate, the thin scarious lacerate margins more or less deciduous. Leaf-blades narrowed to an ill-defined petiolar base c. 4–7 mm. long, rigidly coriaceous, spathulate, 20–40 mm. long, 6–9 mm. broad, rounded and emarginate at the tip (apiculum of young leaf early deciduous), acute at the base; above olivaceous, sublucid, smooth (minutely foveolate), the impressed midrib distinct, the lateral veins (c. 10–12 on a side) less prominent; beneath paler, midrib strongly raised proximally, lateral veins obscure; margins differentiated beneath, thin and acute, plane. Deciduous branchlets spreading to erect, 8–10 cm. long, 0.8–1 mm. thick, olivaceous, densely papillate-scabridulous, terete below, somewhat compressed above, with up to 23 leaves; first internode 8–13 mm. long, median internodes 3–5 mm. long. Leaves: stipules persistent, mostly 3.5–7 mm. long, midrib portions becoming blackish and indurate, strikingly dimorphic: one of each pair oblong-lanceolate, abruptly acuminate, with broad scarious conspicuously lacerate margins, the other narrowly linear-lanceolate, attenuate-acuminate, with very narrow entire scarious margins. Petiole 1 mm. long or less. Leaf-blades as on main stems but much smaller: asymmetrically obovate or broadly oblong, 6–11 mm. long, 3.5–5 mm. broad.

Male flower [not seen, description ex Urban]: Calyx-lobes 5, ovate, reddish. Stamens 4; filaments (in bud) apparently connate; anthers free, connective broad, anther-sacs discrete, dehiscing longitudinally.

Female flowers and fruits unknown.

TYPE: Cuba, Oriente, trail from Camp La Barga to Camp San Benito, damp thickets, alt. 450–900 m., 22–26 Feb. 1910, *Shafer 4102* (NY, LECTOTYPE). The original holotype in Herb. Krug & Urban (B) presumably has been destroyed.

DISTRIBUTION: known only from the type collection (MAP XXVIII).

Although still imperfectly known, *P. formosus* is obviously a distinctive and isolated species on the basis of its vegetative characteristics, particularly the large unreduced leaves of the primary axes and the dimorphic stipules. Technically, the branching of the species could scarcely be called phyllanthoid in view of the apparent failure of the leaves on the main axes to become reduced to cataphylls. However, it is possible that such

Habit of *Phyllanthus formosus* Urb. (*Shafer 4102* [NY]).

reduction may be found to occur when additional specimens are collected. Furthermore, since the branchlets are deciduous and similar to those of *P. comosus* and since the reduction of leaves to cataphylls is often very tardy in that species, it appears that in *P. formosus* true phyllanthoid branching occurs but is masked by the reversion of cataphylls to expanded leaves.

The rigid spathulate leaves of *P. formosus* are so similar to those of *P. comosus* that the two species must be rather closely related, although when better material of *P. formosus* is available there may prove to be important distinctions in the reproductive parts. The proposal by Britton to erect a separate genus *Dimorphocladium* for *P. formosus* is quite without merit. The description of this genus was occasioned mainly by the fact that Britton failed to realize that the distinction between permanent axes and deciduous branchlets, which he noticed in *P. formosus*, also occurred in many other species of *Phyllanthus*.

59. **Phyllanthus comosus** Urb. Repert. Sp. Nov. **13:** 451. 1914. (PLATE XXIX, *figs. A–B*).

Roigia comosa (Urb.) Britton, Mem. Torr. Bot. Club **16**: 73. 1920.

Glabrous diffusely branching shrub c. 0.5–2 m. high, with short leafy branchlets often clustered at branch-tips; branches at first smooth, angular, reddish-brown, waxy, becoming terete, greyish, and with fissured bark in age, c. 1.5–3 mm. thick. Leaves of branches often unreduced on lower portions (similar to branchlet leaves), but distally becoming abruptly reduced to cataphylls. Cataphylls blackish, indurate, more or less persistent: stipules triangular to lanceolate, 0.6–1 mm. long, 0.5–0.6 mm. broad, acuminate; blade acicular, c. 0.5–0.8 mm. long. Deciduous branchlets mostly 0.5–2 (–3) cm. long, 0.3–0.5 mm. thick, stramineous, with flaky deciduous waxy coating, furrowed, terete, with (3–) 4–8 (–15) leaves; first internode 1.5–3 mm. long, median internodes 1.5–3 mm. long. Leaves: stipules persistent, triangular-lanceolate, 0.5–0.8 mm. long, 0.25–0.4 mm. broad, brownish, the scarious tips reflexed. Petiole 0.7–1.5 mm. long. Leaf-blades rigidly coriaceous, obovate to narrowly spathulate, (7–) 9–16 mm. long, 2.5–5 (–6) mm. broad, obtuse to rounded or slightly emarginate at the apex (rare individual blades with a short inconspicuous apiculum), narrowly acute at the base; young leaves more or less pinkish- or purplish-tinged; mature leaf-blade above bright green, subfoveolate (with a minute subhexagonal reticulum of raised cell walls), midrib slightly raised; beneath somewhat paler, midrib plane, lateral veins obscure; margins subdifferentiated, not especially thickened, plane.

Monoecious; flowers mostly solitary, usually only one female flower per branchlet (at the third or fourth node), other flowers male (occasionally a male and female flower at the same axil).

Male flower: pedicel capillary, 10–15 mm. long. Calyx pinkish (in life); calyx-lobes 5 or 6, membranous, crystalliferous, rather unequal, oblong to spathulate, (3.2–) 3.5–4 mm. long, 1.5–2.5 mm. broad, obtuse or rounded at the tip, entire, midrib branching, veins more or less anastomosing. Disk a fleshy more or less 3-angled ring (the 5 or 6 disk-segments completely coalesced), plane, entire, crimson-colored when fresh. Stamens 5 or 6; filaments connate into a slender sometimes apiculate column 1–1.8 mm. high, less than 0.3 mm. thick; anthers subsessile (free parts of filaments about as long as or shorter than the anthers), crowded into a single whorl atop the column (i.e., attached at more or less the same level, although 2 or 3 may be inner to the others), broadly ovate and definitely emarginate, c. 0.2–0.3 mm. long, 0.4–0.5 mm. broad; anther-sacs divaricate, well-separated on the connective, dehiscing obliquely or horizontally; pollen grains c. 22–29 μ in diameter.

Female flower: pedicel slender, curving, (10–) 12–17 (–21) mm. long, terete below, angled above, purplish. Calyx pink, becoming darker in fruit; calyx-lobes 6, chartaceous, subequal (outer ones narrower), elliptic-oblong to spathulate, 3.5–5 mm. long, 1.8–3 mm. broad, obtuse or rounded at the tip, entire, midrib pinnately branched, veins more or less anastomosing (obscure in fruiting calyx). Disk obtusely 5- or 6-angled, plane, crimson when fresh, with a thickened narrow entire rim. Ovary nearly sessile, prominently ribbed along the septa; styles erect, connate below into a column c. 0.5–0.7 mm. high (or sometimes nearly free), divergent above, c. 0.8–1.2 mm. high (not counting rolled-up portion), parted c. ⅓ to ½ their lengths; style-branches divergent, entire, circinately revolute, narrowed to the tips.

Capsule oblate, c. 4–4.5 mm. in diameter, smooth, stramineous, not veiny; valves more or less retained within the marcescent calyx. Seeds trigonous, symmetric or sometimes slightly asymmetric, 2–2.6 mm. long, 1.3–1.6 mm. radially, 1.1–1.7 mm. tangentially, when mature dark brown with rows of slightly raised reddish-brown dots; hilum subterminal, elliptic, c. 0.3 mm. long.

TYPE: Cuba, *Shafer 4242.*

DISTRIBUTION: serpentine lowlands and hills, northeastern Cuba (MAP XXVIII).

CUBA. ORIENTE: Cerro de Miraflores, Cananova, *León, Clemente, & Howard 20302* (MICH); *León 21161* (GH); *Webster 3883* (GH, MICH, NY, US); savanna southeast of Playa de Vaca, *Jervis 1650* (GH, MICH); Moa, *Mrs. Bucher 96* ex p. (SV); serpentine hills near mouth of Río Yamaniguey, *Shafer 4242* (NY, LECTOTYPE; F, US, ISOTYPES).

This species, because of the delicate purplish-pink tinging of leaf-margins and flowers, is one of the most attractive of the West Indian species of *Phyllanthus.* Unfortunately, it does not appear to lend itself to cultivation, for attempts to germinate seeds were entirely unsuccessful. In the Cerro Miraflores, the species was observed to grow in the low scrub (charrascal) on rocky serpentine soil, associated with such characteristic Moa plants as *Dracaena cubensis, Euphorbia helenae,* and *Scaevola wrightii.*

Although *P. comosus* is probably most closely related to *P. formosus,* as has been discussed under the latter, it in some respects resembles local populations of *P. orbicularis*. Both species were observed growing in the same localities at Playa de Vaca and Cerro de Miraflores, but never exactly at the same site (i.e., plants of the two species were never observed to grow side by side). In these two areas *P. orbicularis* appears to occupy somewhat lower altitudes, but their detailed ecological relationships remain to be elucidated. The presence of *comosus*-like features such as spathulate leaf-blades on the local specimens of *P. orbicularis* suggests transfer of characters between the two species. However, it is also possible that part, or all, of this similarity may be due to the fact that the eastern race of *P. orbicularis* is closely related to *P. comosus*; this is suggested by the fact that spathulate leaf-blades occur in *P. orbicularis* in areas considerably outside of the known range of *P. comosus* (e.g., the Sierra de Nipe and Maraví River near Baracoa). The verification of any hypothesis of the modification of *P. orbicularis* by "introgression" of *P. comosus* characters must therefore be tested with the alternative possibility in mind.

60. **Phyllanthus orbicularis** HBK. Nov. Gen. & Sp. **2**: 111–112. *pl. 106*. 1817; Muell. Arg. in DC. Prodr. **15**(2): 331–332. 1866. (PLATE XXIX, *figs. C–D*).

Orbicularia phyllanthoides Baill. Etude. Gen. Euphorb. 617. 1858.
Phyllanthus orbicularis α genuinus, *β ellipticus*, et *γ obovatus* Muell. Arg. loc. cit.
Diasperus orbicularis (HBK.) O. Ktze. Rev. Gen. **2**: 600. 1891.
Phyllanthus rotundifolius Sessé & Moc. Flor. Mex. ed. 2. 212. 1894.
Orbicularia orbicularis (HBK.) Moldenke, Rev. Sudamer. Bot. **6**: 178. 1940.

Glabrous shrub c. 0.5–2 m. high, usually diffusely branching, lateral branches sometimes reduced to short-shoots; branches c. 1.5–3 mm. thick, reddish brown becoming greyish, bark sometimes breaking into thin plates. Cataphylls blackish, indurate, not reflexed, more or less persistent: stipules lanceolate, (1.5–) 2–3 mm. long, acuminate, entire or denticulate; blade linear-lanceolate, c. 1.5–2 mm. long. Deciduous branchlets sometimes clustered on spur-shoots, (0.5–) 1–3 (–5) cm. long, 0.3–0.8 mm. thick, reddish brown, subterete, smooth, with (2–) 3–8 (–11) leaves; first internode (2–) 4–8 (–10) mm. long, median internodes mostly 2–6 mm. long. Leaves: stipules reflexed, persistent, lanceolate, (1–) 1.5–2 (–2.5) mm. long, acuminate, scarious to indurate, margins entire. Petioles 0.3–1 mm. long. Leaf-blades coriaceous, sometimes very thick and rigid, plane or convex, broadly elliptic or obovate to suborbicular or obcuneate (sometimes broader than long), c. 5–10 (–12) mm. long, 5–13 mm. broad, rounded or emarginate at the tip (apiculum obsolete or minute), acute to rounded or often emarginate at the base; above olivaceous, in age plumbeous or dark brown and mottled, veins obscure to conspicuously raised and reticulate, foveolate; beneath yellowish or brownish, midrib and laterals (c. 4–6 on a side) slightly raised, branching crookedly, the reticulum often prominent; margins differentiated (with narrow epidermal cells) but no thicker than blade, plane or occasionally reflexed but never revolute.

Monoecious; cymules with mostly 2–5 flowers, male or bisexual, female flowers one per cymule.

Male flower: pedicel 2–5 (–7) mm. long. Calyx whitish or pink-tinged; calyx-lobes 6 (rarely 5), membranous or chartaceous, subequal, elliptic or oblong to obovate or spathulate, (2–) 2.5–4 (–5) mm. long, 1.3–2 mm. broad, obtuse and entire at the tip, midrib sparingly to conspicuously branched. Disk-segments usually 6, flat or concave, rather fleshy, cuneate or quadrate, c. 0.3–0.5 mm. broad, closely contiguous or sometimes united in pairs, dark red (drying brownish). Stamens mostly 6 (less commonly 5 or 7, rarely 3 or 4); filaments (1–) 1.5–2.5 mm. long, unequal (3 anthers usually distinctly higher) erect, united usually about halfway into a column c. 0.8–1.3 mm. long; anthers stipitate in two whorls (free portion of filament usually much longer than anthers), ovate, dehiscing more or less vertically or obliquely (occasionally lower anthers horizontal or nearly so), c. 0.2–0.3 mm. long, 0.3–0.5 mm. broad; pollen grains (21–) 23–27 (–29) μ in diameter.

Female flower: pedicel 0.5–2.5 (–3.5) mm. long. Calyx whitish or pinkish-tinged; calyx-lobes 6, subequal, scarious or chartaceous, elliptic or oblong to spathulate, 3–4 (–6) mm. long, 1.5–2.5 (–3.5) mm. broad, obtuse at the tip, entire, midrib usually conspicuously branched but veins often obscure. Disk hexagonal, flat, rim slightly thickened, entire, red (drying brownish). Ovary sessile or slightly stipitate; styles erect and connate into a column (0.3–) 0.5–0.8 (–1.2) mm. high, free ends erect to recurved, parted usually c. ¼ their length (rarely parted to the column), tips of style-branches often revolute.

Capsule 3–3.8 mm. in diameter, reddish brown, smooth or slightly rugulose, veins obscure. Columella 1.2–1.8 mm. long. Seeds trigonous, sometimes asymmetric, (1.6–) 1.8–2.2 (–2.4) mm. long, 1.1–1.4 (–1.6) mm. radially and tangentially, reddish brown with rows of dark slightly raised points; hilum elliptic, 0.3 mm. long, micropylar end rarely obscurely carunculate.

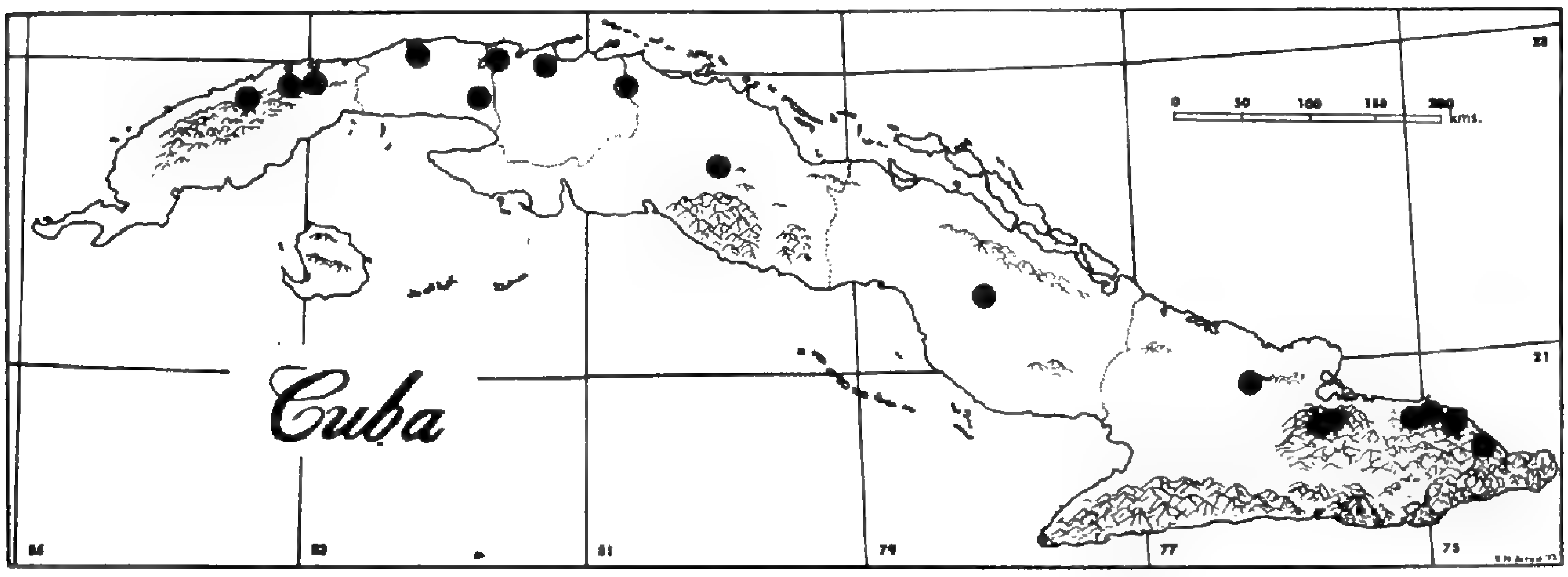
Collected flowering and fruiting throughout the year.

TYPE: "Insula Cubae prope Regla et Havana," *Humboldt* (P, TYPE COLLECTION).

DISTRIBUTION: thickets, serpentine barrens, Cuba (MAPS XXV and XXVI).

CUBA. Without specific locality, *Sessé et al. 4565* (F, probably TYPE COLLECTION of *P. rotundifolius*). PINAR DEL RÍO: San José de Sagua to San Marcos, *Shafer 11969* (F, NY, US); La Cajálbana area, *Acuña & Alain 15669* (SV), *Ekman 10474* (S), *León & Charles 4959* (NY), *Webster 4650, 4655* (GH); Bahia Honda, *León* (MT), *Wilson 9412* (F, NY, US), *Wright 1942* ex p. (GOET, S); Cuabal de Lechuza near San Claudio, *Ekman 12988* (S). HABANA: Regla and Havana, *Humboldt* (P, TYPE COLLECTION); Madruga, *Britton et al. 613* (NY), *León 3328* (NY), *Van Herman 15328* (SV); Guanabacoa, Loma de la

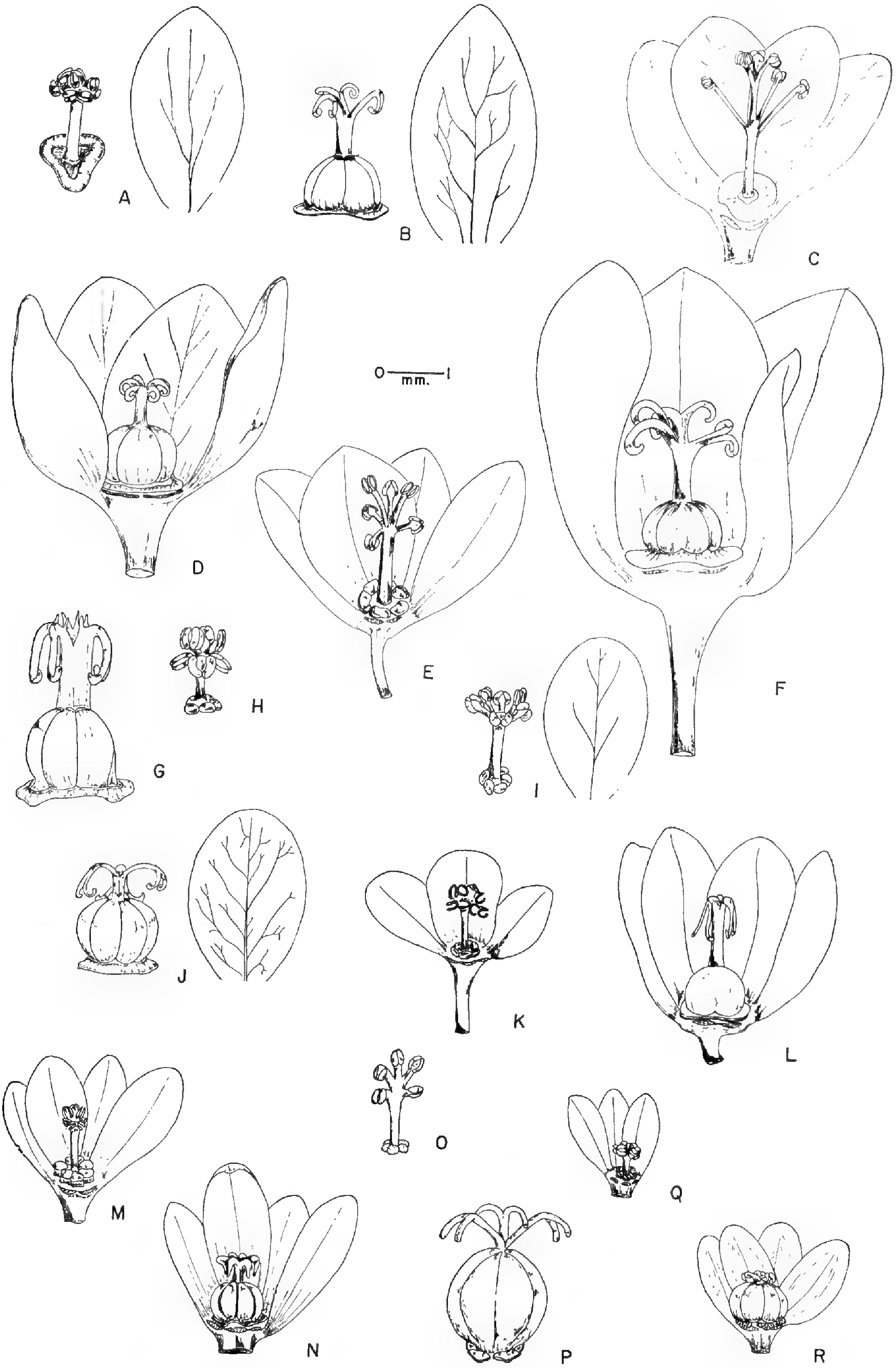
Jata, *Ekman 16535* (S), *Shafer & León 12055* (NY). MATANZAS: cuabales NW of Pan de Matanzas, *Ekman 16476* (MICH, S); Cuabal del Espinal, east of Canasí, *León & Roig 12949* (NY); Tetas de Camarioca, *Britton et al. 14078* (F, GH, NY, US). LAS VILLAS: Motembo, sabana, *León 9368* (NY); Santa Clara, *Britton et al. 6187* (NY), *Britton & Cowell 13304* (NY, US). CAMAGÜEY: La Ciega, Caobilla, *Acuña 13518* (US); hills near Camagüey, *Britton et al. 13232* (F, GH, NY, US); Camagüey to Santayana, *Britton 2416* (F, NY, US); Sabana de la Matanzas, *Roig, Luaces, & Arango* (SV). ORIENTE: Holguín, at base of Cerro de Fraile, *Ekman 3223* (S); Holguín, Aguasclaras, *Ekman 7660* (MICH, S); base of Loma Pilón, near Holguín, *Shafer 1213* (F, NY, US); Holguín, Holguín to Mayarí, *Wright 1942* ex p. (GH, GOET); Sierra de Nipe, along creek 5 km. south of Woodfred, *Howard 6132* (GH, MICH, NY, US); Mayarí, Río Miguel, *Alain et al. 5845* (GH); Cananova, Cerro de Miraflores, *Marie-Victorin et al. 21493* (A, MT), *Webster 3884* (GH, MICH, NY, US); Playa de la Vaca, *Acuña 12505, 13159* (SV), *Clement 3655* (GH, MT, US), *Marie-Victorin et al. 21475, 21747* (A, MT), *Webster 3867* (GH, MICH, NY, US); Moa, *Mrs. Bucher 95, 96* ex p. (NY, SV); plain between Moa and Yaguaneque, *León et al. 20289* (NY); hills near mouth of Río Yamaniguey, *Shafer 4246* (F, NY, US); pinelands near sea-shore, Río Maraví, near Baracoa, *Ekman 4032* (S).



MAP XXVI. Distribution of *P. orbicularis* HBK.

PLATE XXIX. FLOWERS OF SECT. *Orbicularia.*

FIGS. A–B. *Phyllanthus comosus* Urb. A, androecium and male calyx lobe; B, gynoecium and female calyx lobe (*Jervis 1650* [GH]). FIGS. C–D. Male and female flowers of *P. orbicularis* HBK. (*Webster 4650* [GH]). FIGS. E–F. Male and female flowers of *P. myrtilloides* Griseb. ssp. *myrtilloides* (*Alain 3073* [GH]). FIGS. G–H. Gynoecium and androecium of *P. myrtilloides* ssp. *alainii* Webster (*Alain 5563* [GH]). FIGS. I–J. *Phyllanthus myrtilloides* ssp. *spathulifolius* (Griseb.) Webster. I, androecium and male calyx-lobe; J, gynoecium and female calyx-lobe (*Webster 4897* [GH]). FIGS. K–L. Male and female flowers of *P. chamaecristoides* ssp. *baracoensis* (Urb.) Webster (*Ekman 4326* [S]). FIGS. M–N. Male and female flowers of *P. scopulorum* (Britton) Urb. (*Webster 3800* [GH]). FIGS. O–P. Androecium and gynoecium of *P. nummularioides* Muell. Arg. (*Allard 16066* [US]). FIGS. Q–R. Male and female flowers of *P. phlebocarpus* Urb. (*Carabia 3573* [GH]).



Webster, West Indian Phyllanthus

Phyllanthus orbicularis is the commonest and most widespread woody species of the genus in Cuba; it occurs always in relatively dry serpentine areas in scrub thickets, savannas, or palm barrens. In its original publication the species was also said to occur in "opacatis Orinoci prope Carichana," but this record remains unconfirmed and is surely an error; Humboldt must have confused the Cuban plant with a South American species of sect. *Microglochidion.* It is apparent, even on superficial inspection, that the species contains a number of strikingly divergent local populations. The most outstanding of these is represented by *Ekman 7660* from the vicinity of Holguín, which has much larger flowers than plants from all other localities. However, there is also a notable difference between plants of the eastern and western parts of the islands, so that it is possible to recognize two major subspecific races: a western race characterized by smaller male flowers, branchlets with more leaves, and thinner leaves with the nerves conspicuous above; and an eastern race with larger male flowers, shorter few-leaved branchlets, and thick rigid leaves with the nerves obscure above. The boundary between the two races would be drawn west of the Sierra de Nipe, and if the differences were really sharp two subspecies could be defined. It does not seem worth-while to recognize any formal subspecific categories, however, in view of the impossibility of defining two natural subspecies which could be separated by a key. In the case of the number of leaves per branchlet, there appears to be a cline running from Pinar del Río, where the mode is commonly 6 to 8, to the Moa region of Oriente, where it is usually 4 to 5. Unfortunately the number of samples with male flowers is too small to demonstrate whether there is a cline in this character too, but it seems not unlikely.

There appears to be a considerable amount of fluctuating or random variability within *P. orbicularis*, particularly with regard to stamen number and stylar configuration. In the original description of the species the stamen number was given as 4–10, and Mueller noted it as 6–9, rarely to 12. These reports have not been confirmed, for although a few flowers with only 4 (or very rarely 3) stamens have been observed, none have been seen with more than 7. In view of the large range of variation in the species, it is not impossible that flowers with 10, or even 12, stamens occur but it seems more likely that the observations in the literature are erroneous.

There is yet another factor which must be considered in attempting to account for the variation patterns shown by *P. orbicularis.* It is possible that the distinctive characters of the eartern race of the species may be partially the result of hybridization with *P. comosus.* The obovate leaves with acute bases and the spathulate calyx-lobes of the Moa plants of *P. orbicularis* strongly suggest the influence of *P. comosus.* In the Cerro de Miraflores both species were seen growing together in the scrubland, where there certainly does not appear to be any ecological barrier to their crossing. However, no plants with intermediate characters were observed and it could not be determined whether or not hybridization is occuring at the present time.

61. **Phyllanthus myrtilloides** Griseb. Mem. Amer. Acad. Sci. **8:** 158. 1860.

Glabrous bushy shrub or small tree c. 0.5–4 m. high; branches of current year straight, slender (c. 1–3 mm. thick), smooth, terete, sometimes furrowed or cracking open, dark brown or greyish. Cataphylls blackish, indurate, often reflexed, more or less deciduous: stipules triangular to lanceolate, mostly 1–3 mm. long, acute to acuminate, entire or denticulate; blade linear-lanceolate, c. 0.5–1.5 mm. long. Deciduous branchlets spreading or ascending, (2–) 3–8 (–11) cm. long, 0.3–0.8 mm. thick, stramineous or olivaceous, subterete, more or less smooth, with mostly 8–18 (–25) leaves; first internode mostly 2–12 mm. long, median internodes mostly 2–10 mm. long. Leaves: stipules reflexed, subpersistent or often mostly deciduous, subentire, lanceolate, acute or acuminate, the proximal ones partly or entirely blackish and indurate, c. 1–3 mm. long and 0.4–0.8 mm. broad, the distal ones brownish and scarious, c. 0.5–1 mm. long. Petioles mostly 1–2.5 mm. long. Leaf-blades chartaceous to rigidly coriaceous, spathulate to obovate or suborbicular, mostly 8–25 mm. long and 4–15 mm. broad, obtuse to rounded or sometimes emarginate at the tip, the scarious apiculum obsolete or up to c. 1 mm. long, acute to rounded or rarely subcordate at the base; above olivaceous or plumbeous, dull to sublucid (or sometimes polished in age), veins plane or slightly raised, obscure to subprominent (veinlets obscure); beneath yellowish or whitish, midrib, main lateral veins (c. 3–5 on a side) and sometimes the veinlets slightly raised, reticulum subprominent to obscure; margins plane to conspicuously revolute.

Monoecious; proximal cymules usually with 2 or 3 male flowers, some distal cymules unisexual with 1 female and 1–3 male flowers, or flowers subsolitary (rarely 2 female flowers per axil).

Male flower: pedicel mostly 7–15 (–25) mm. long. Calyx whitish or pinkish-tinged; calyx-lobes 6 (rarely 5), membranous or somewhat fleshy, subequal or sometimes quite unequal, the outer lobes oblong to obovate, the inner ovate to spathulate, c. 1.7–3 mm. long, obtuse or rounded and entire to denticulate at the tip, midrib branched or unbranched. Disk-segments usually 6, flat, thin or somewhat fleshy, roundish or squarish, free or occasionally connate, mostly 0.4–0.5 mm. across. Stamens 6 (rarely 5, very rarely 4); filaments connate into a column 0.7–2 mm. long; anthers sessile to stipitate (the free distal portions of filaments up to 0.8 mm. long), broadly ovate, mostly 0.25–0.4 mm. long and 0.3–0.5 mm. broad; anther-sacs divergent, the upper (inner) dehiscing more or less vertically, the lower (outer) dehiscing more or less horizontally, slits apically contiguous but not confluent; pollen grains c. 18–26 μ in diameter.

Female flower: pedicel slender, c. 3–15 (–20) mm. long. Calyx whitish, greenish, or sometimes pinkish-tinged; calyx-lobes 6 (rarely 5), scarious to subcoriaceous, subequal, elliptic or oblong to obovate (inner lobes often broader); larger lobes c. 3–4 (–4.5) mm. long, mostly 1.5–2.5 mm. broad, obtuse or rounded at the tip, entire or denticulate, midrib usually more or less branched but veins often obscure. Disk plane, tenuous to rather massive, more or less angled, sometimes inconspicuously pitted. Ovary sessile, smooth, 3-sulcate, ribless or inconspicuously carinate; styles united c. ½ their length into a column c. 0.5–1.5 mm. high, free ends bifid or parted to the column, style-branches tapering to slender more or less revolute tips.

Capsule oblate, c. 2–2.7 mm. high, 3–4 mm. in diameter, dark reddish brown, veins subprominent or completely obscure. Columella c. 1.5–2 mm. long. Seeds trigonous, sometimes slightly asymmetric (one face carinate), 1.5–2.2 mm. long, 1–1.5 mm. radially and tangentially, reddish brown becoming fuscous, with regular or irregular rows of dark slightly raised points; hilum subterminal, elliptic to triangular, c. 0.3–0.4 mm. long, micropylar end sometimes (in ssp. *spathulifolius*) carunculate.

In the greatly enlarged circumscription here adopted, *P. myrtilloides* is a variable polytypic species common and widespread in the serpentine lands of northern Oriente province, Cuba. It may appear excessively conservative to combine such different plants as *P. spathulifolius*, with chartaceous narrowly obovate revolute leaves and whitish or greenish flowers, and *P. erythrinus* with plane nearly orbicular coriaceous leaves and at least the floral disk dark reddish or purplish. It must be admitted that — due to insufficient sampling — clear zones of intergradation between the five taxa have not been demonstrated, and indeed in most cases intermediate specimens have not been observed. However, the five taxa in the *P. myrtilloides* complex have *in toto* neatly allopatric and adjoining ranges, and display varying combinations of essentially a single overall pattern of characteristics. Although these taxa could still be maintained as five closely related species, their degree of relationship is so close that it seems more realistic to regard them as five unusually distinctive subspecies.

KEY TO THE SUBSPECIES

1. Anthers all stipitate, dehiscing vertically or obliquely; fruiting pedicel c. 3–7 (rarely to 9) mm. long; leaves prominently apiculate (at least when young), not or scarcely revolute. .... ssp. *myrtilloides* (61b)
1. Anthers not all stipitate, at least the lower whorl sessile or subsessile and dehiscing more or less horizontally; fruiting pedicel mostly 8–20 (rarely as low as 5) mm. long; leaves various.
    2. Style-branches adaxially auriculate, recurving from the top of the stylar column; leaves plane, not revolute. .... ssp. *alainii* (61c)
    2. Style-branches not auriculate; leaves various.
        3. Young leaves and floral disk dark reddish or purplish; leaves neither strongly apiculate nor revolute; staminal column mostly 1.5–2 mm. long. .... ssp. *erythrinus* (61a)
        3. Young leaves and floral disk greenish or at least not purplish; leaves strongly revolute.
            4. Cataphylls reflexed; staminal column 0.5–1 mm. long; larger calyx-lobes of male flower c. 2 mm. long, midrib unbranched; seeds 1.9–2.2 mm. long. .... ssp. *shaferi* (61d)

4. Cataphylls not reflexed; staminal column 1–1.7 mm. long; large calyx-lobes of male flower c. 2.5 mm. long or more, midrib branched; seeds 1.6–1.8 mm. long. ...... ssp. *spathulifolius* (61e)

61a. **Phyllanthus myrtilloides** ssp. **erythrinus** (Muell. Arg.), stat. nov.

Phyllanthus purpureus Wright ex Griseb. Goett. Nachr. **1865**: 168. 1865; non *P. purpureus* Muell. Arg., 1864.
Phyllanthus erythrinus Muell. Arg. in DC. Prodr. **15**(2): 332. 1866.
Diasperus erythrinus (Muell. Arg.) O. Ktze. Rev. Gen. **2**: 599. 1891.
Orbicularia foveolata Britton, Mem. Torr. Bot. Club **16**: 73. 1920.
Phyllanthus cardiophyllus Urb. Symb. Ant. **9**: 190. 1924.
Phyllanthus melanodiscus Urb. ibid.
Phyllanthus foveolatus (Britton) Alain, Contr. Occ. Mus. La Salle **11**: 2. 1952.

Shrub 0.5–3 m. high; cataphylls not reflexed, stipules 1–2 mm. long, the tip deciduous, the blade c. 1–1.5 mm. long. Branchlets (2.5–) 4–8 (–11) cm. long, often bright yellow proximally, with (6–) 8–17 (–25) leaves; first internode (4–) 6–12 (–15) mm. long, median internodes 4–12 mm. long. Leaves: proximal stipules c. 1–1.5 mm. long, distal stipules c. 0.5–0.8 mm. long; petioles c. 1.5–2.5 (–3.5) mm. long; leaf-blades chartaceous to coriaceous, conspicuously purplish when young, mostly broadly elliptic to suborbicular, mostly 13–25 mm. long and 10–18 mm. broad, the apiculum very short (0.3 mm. long or less) or obsolete; margins plane or reflexed but never definitely revolute.

Male flower: pedicel 10–20 mm. long; calyx more or less purplish-tinged; calyx-lobes mostly 2.5–3 (–3.5) mm. long, 1.8–2 mm. broad, midrib usually conspicuously branched; stamens 6, staminal column (1–) 1.5–2 mm. long; anthers substipitate (free portions of filaments about as long as to shorter than the anthers), dehiscing vertically or obliquely. Female flower: pedicel (5–) 10–20 mm. long; calyx-lobes (3–) 3.5–4 mm. long, 1.5–2.5 mm. broad, midrib more or less branched; disk flat, colored dark reddish or purplish; styles erect, coherent or usually connate into a column c. 0.5–0.8 mm. high, free ends parted c. ½ their length. Seeds 1.6–1.8 mm. long, 1.1–1.3 mm, radially and tangentially.

Collected in flower Mar., June, July, Nov.–Dec.; in fruit, July, Dec.

TYPE: Cuba, Oriente, *Wright 1943.*

DISTRIBUTION: scrub or pineland, mountainous serpentine areas, eastern Cuba (MAP XXVII).

CUBA. ORIENTE: Sierra de Moa, alt. 800 m., *Alain 3414* (GH); Baracoa, El Yunque, north side, *Ekman 3546* (S, TYPE COLLECTION of *P. cardiophyllus*); between Taco and Nibujon, charrascales, pinales, *Ekman 3724* (S, TYPE COLLECTION of *P. melanodiscus*); pinelands, road between Baracoa and Florida, *Ekman 3989* (S); Lomas de Cuaba [Duaba], *Ekman 4265* (S); upper valley of Río Navas, thickets by river, *Shafer 4412* (GH, NY); Loma Santa Teresa, near El Yunque, *Shafer 7734* (NY), *7736* (F, GH, NY); Camp La Gloria, south of Sierra Moa, *Shafer 8271* (NY, HOLOTYPE of *Orbicularia foveolata*); pine woods, Baracoa, *Underwood & Earle 1349* (NY); Sierra de Moa, c. 20 km. south of Moa lumber mill, *Webster 3899* (GH, MICH, NY, US); pinal near Baracoa, *Wright 1943* (GOET, HOLOTYPE; G, GH, ISOTYPES). A sterile specimen from Charrascos de Peña Prieta, Toa, *Alain 3597* (GH), is probably referable to this subspecies.

Of the five subspecies of *P. myrtilloides*, the present one appears to be the most widespread and also the most xerophilous. Although it has been collected in river thickets (*Shafer 4412*), it seems to be mainly a plant of open pinelands, so that ecologically it corresponds more to *P. baracoensis* than to any of the other subspecies of *P. myrtilloides*. The purplish color of the unfolding leaves and floral disk is most conspicuous in the living plant and at once distinguishes it so well that in the field it might be taken for a distinct species. However, in almost all respects except pigmentation ssp. *erythrinus* is very similar to ssp. *myrtilloides*, although it can be distinguished by its shorter stipules, non-apiculate leaves, and usually longer fruiting pedicel.

Despite its rather formidable synonymy, ssp. *erythrinus* does not appear to be an unusually polymorphic taxon. The two species proposed by Urban, *P. cardiophyllus* and *P. melanodiscus*, are trivial variants. Alain (Flora de Cuba 3: 51. 1953) has already reduced the latter, and the supposed difference in leaf-shape of *P. cardiophyllus* is quite inconsequential. In contrast, Britton's *Orbicularia foveolata* (which Alain has transferred to *Phyllanthus*) cannot be disposed of so easily. The holotype (*Shafer 8271*) is a nearly sterile specimen with strikingly shiny coriaceous suborbicular leaves which are conspicuously foveolate due to the prominent anticlinal walls of the hexagonal epidermal cells. Shafer noted on the label that the flowers were white, which would be unusual for the usually pinkish-flowered plants of ssp. *erythrinus*; unfortunately, the floral material is too inadequate to provide the necessary additional information as to floral characters. However, the glossy leaves which are supposedly the main distinguishing feature of *P. foveolatus* can be matched closely by those on older branches of a plant encountered in the Sierra Moa (*Webster 3899*) probably not far from Shafer's original locality. It thus appears that the proposed species *P. foveolatus* was founded on a specimen which differs from typical ssp. *erythrinus* only in its ontogenetic stage (and possibly also in its development in a drier environment). Foveolate-leaved specimens may be expected throughout the range of the subspecies.

61b. **Phyllanthus myrtilloides** ssp. **myrtilloides** (PLATE XXIX, *figs. E–F*).

Phyllanthus myrtilloides Griseb. Mem. Amer. Acad. Sci. **8**: 158. 1860.
Diasperus myrtilloides (Griseb.) O. Ktze. Rev. Gen. **2**: 600. 1891.

Bush or small tree c. 2–4 m. high; cataphylls more or less reflexed, stipules mostly 1–1.5 mm. long, blade c. 1 mm. long. Branchlets (3–)

5–11 cm. long, with 10–15 (–20) leaves; first internode 2–7 mm. long, median internodes 3–7 mm. long. Leaves: proximal stipules 1.5–3 mm. long, distal stipules c. 1 mm. long or less; petioles c. 1–2.5 mm. long; leaf-blades chartaceous or subcoriaceous, elliptic to suborbicular, mostly 10–20 (–27) mm. long and 7–14 (–17) mm. broad, obtuse to rounded or sometimes emarginate and, when young, conspicuously apiculate at the tip (apiculum c. 0.5–1 mm. long, more or less deciduous in age), acute to obtuse at the base, margins plane or reflexed (or at most slightly and casually revolute).

Male flower: pedicel 5–12 mm. long; calyx whitish (drying reddish), calyx-lobes c. 2–3.2 mm. long, the outer elliptic-oblong and c. 0.8–1.5 mm. broad, the inner obovate and c. 1.2–1.8 mm. broad, midrib unbranched or nearly so; disk-segments free; stamens 6 (rarely 5), staminal column mostly 1–1.5 (–1.8) mm. long, anthers usually stipitate (free portion of filaments definitely longer than at least the inner anthers), dehiscing vertically or obliquely. Female flower: pedicel 3–7 (–9) mm. long; calyx greenish white (drying reddish), calyx-lobes mostly 3–4 (–4.5) mm. long and 1.5–2.5 mm. broad, midrib unbranched or nearly so; styles erect and connate into a column c. 0.5–1 mm. high, the free ends bifid c. ½ their length. Seeds c. 1.5–2 mm. long, 1–1.3 mm. radially and tangentially.

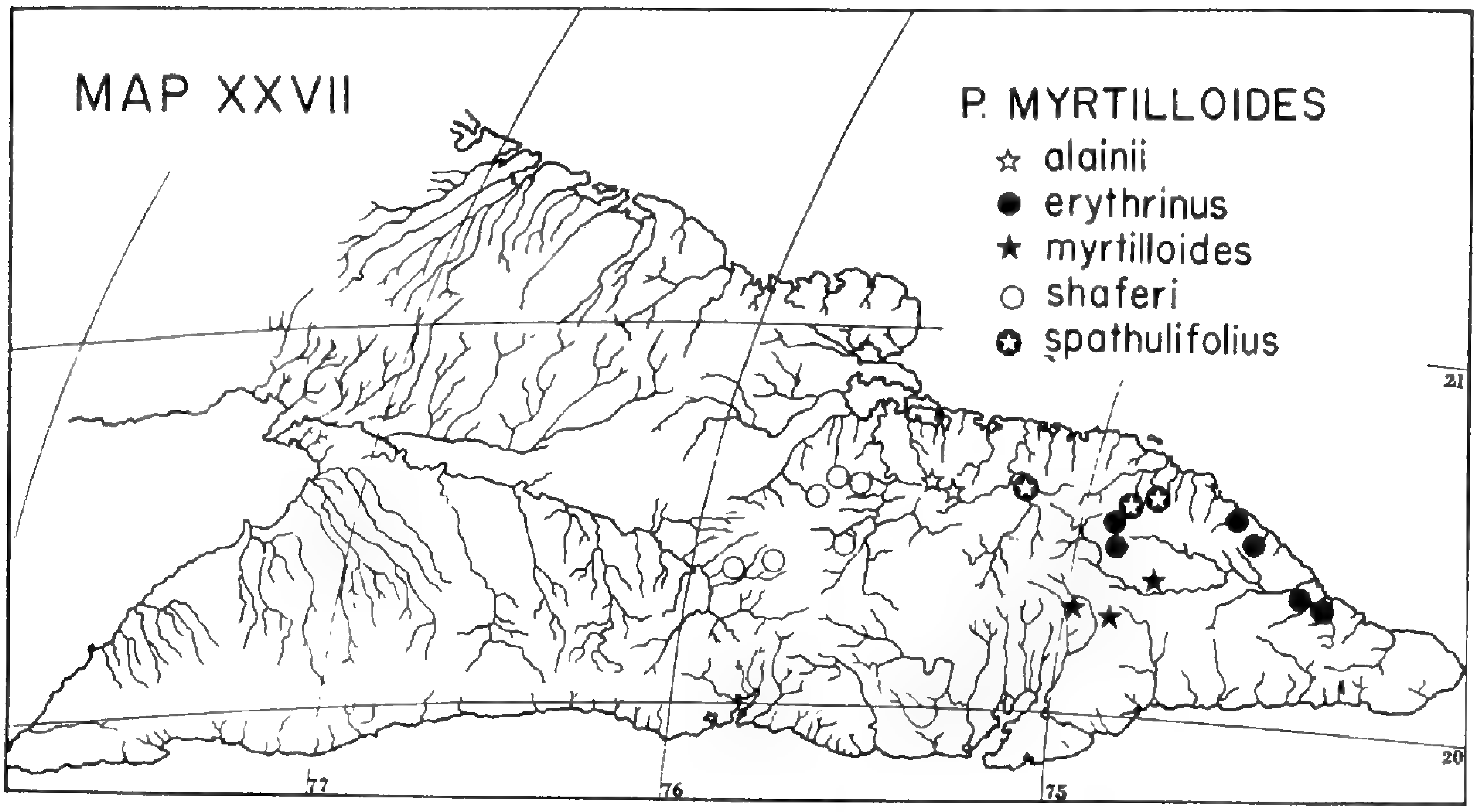
TYPE: Cuba, Oriente, *Wright 1438* ex p.

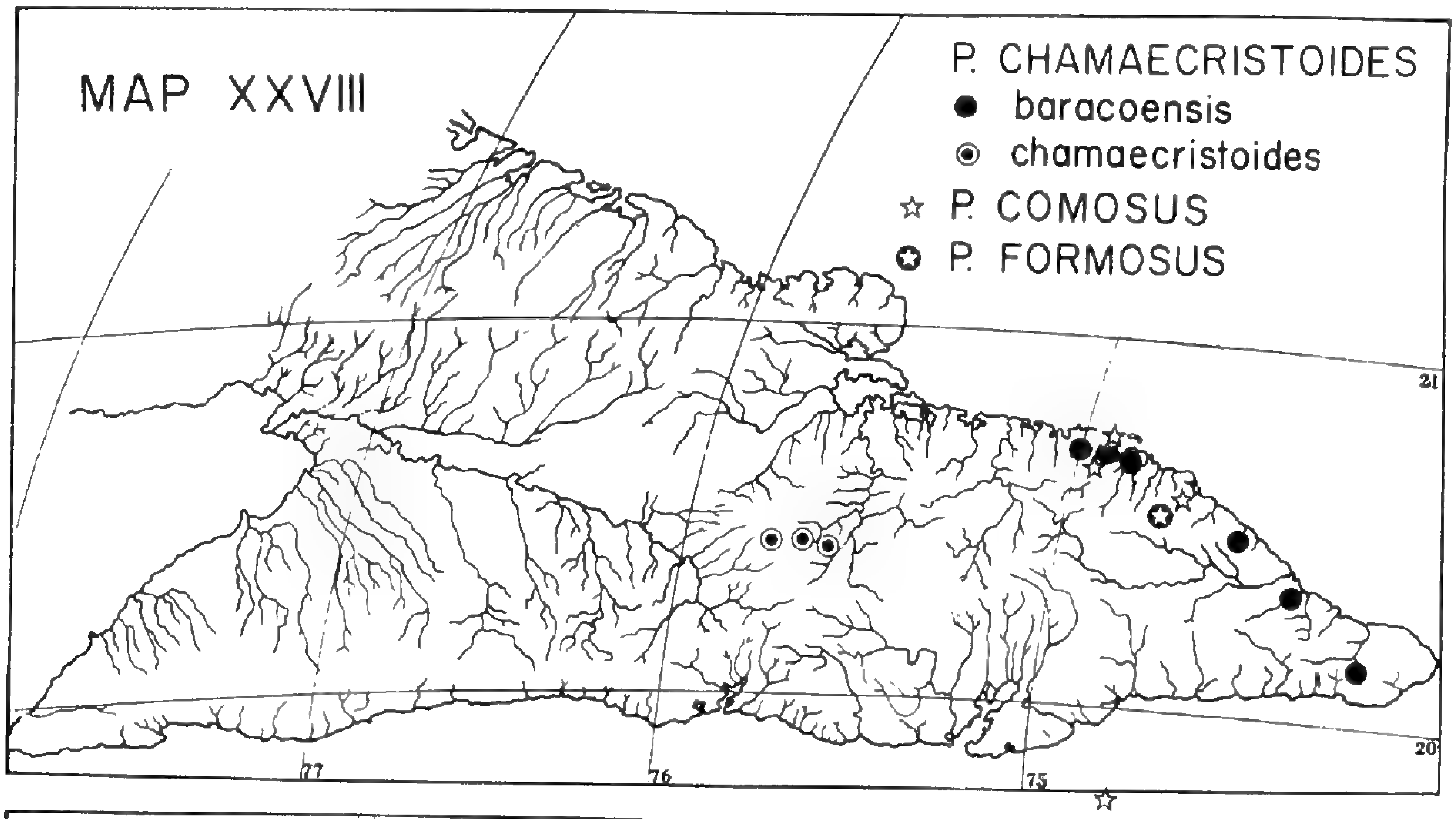
DISTRIBUTION: rain-forest, mountains of Oriente province, Cuba (MAP XXVII).

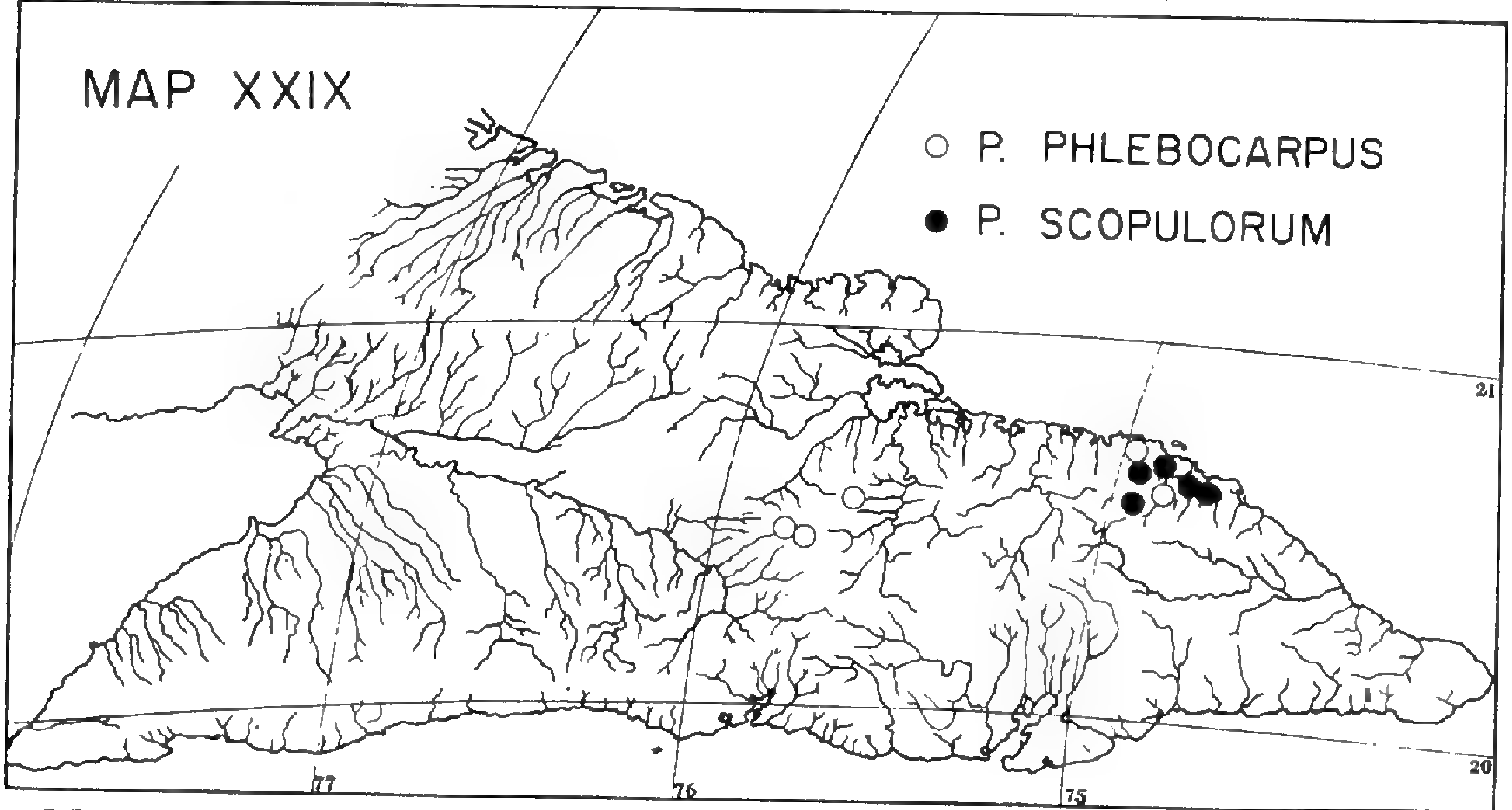
CUBA. ORIENTE: wet woods near Palenquito, Yateras region, alt. 500 m., 20 July 1953, *Alain 3073* (GH); border of Laguna del Galano, Toa, alt. 900 m., 2 Jan. 1954, *Alain 3837* (GH); woods, Monteverde, alt. 800 m., Apr. 1889, *Eggers 5110* (F, GOET, US); La Prenda, north of Guantánamo, 22 July 1921, *Hioram 4775* (MICH); Monte Verde, 23 Dec. [1858], *Wright 1438* ex p. (GOET, HOLOTYPE; BR, G, GH, NY, S, W, ISOTYPES).

In its usual phase, as in the Monteverde region, ssp. *myrtilloides* is distinguishable from the remainder of the species by the definitely stipitate anthers, the free portions of the filaments approaching the elongated condition as in *P. orbicularis*. The collection from the lake at the top of Monte Galano (*Alain 3837*) is quite atypical in having small male flowers with the anthers nearly sessile on the staminal column. However, since it agrees with ssp. *myrtilloides* in its reflexed cataphylls and short fruiting pedicel, it is classified here provisionally.

The present subspecies is certainly closely related to ssp. *erythrinus*, but clearly differs in its apiculate leaves, usually reflexed cataphylls, and lack of purplish coloration in leaves or flowers; furthermore, ssp. *myrtilloides* appears to be a more mesophytic plant. However, it is not certain that these variable morphological characters will still provide valid distinctions when additional collections become available. Another closely related plant is ssp. *alainii*, which is vegetatively similar but differs in its auriculate styles and shorter filaments.







MAPS XXVII–XXIX. Distribution of some species of sect. *Orbicularia*.

61c. **Phyllanthus myrtilloides** ssp. **alainii,** ssp. nov.[22] (PLATE XXIX, *figs. G–H*).

Shrub; cataphylls more or less spreading (not reflexed), stipules c. 1.5 mm. long, with deciduous tips, the blade c. 1.5 mm. long. Branchlets 4–8 cm. long, with c. 9–15 leaves; first internode 1.5–4 mm. long, median internodes 3–8 mm. long. Leaves: proximal stipules 2–3.5 mm. long, distal stipules c. 1 mm. long; petioles c. 1.5–2.5 mm. long; leaf-blades chartaceous, broadly elliptic or obovate, c. 10–25 mm. long and 8–15 mm. broad, the apiculum obsolete or nearly so, acute or obtuse at the base, margins plane or recurved.

Male flower: pedicel c. 10–15 mm. long; inner (larger) calyx-lobes c. 2.5–3 mm. long and 1.8–2.7 mm. broad, midrib sparsely branched; stamens 6 (rarely 4 or 5), staminal column 0.7–1.1 mm. high, anthers sessile or subsessile atop the column, the upper dehiscing vertically, the lower more or less horizontally. Female flower: pedicel 7–15 mm. long; calyx-lobes mostly 3.5–4 mm. long and 2–3 mm. broad, venation obscure; disk flat, tenuous; styles erect and connate up to the bifurcation point into a column c. 1 mm. long, style-branches reflexed from top of column, adaxially auriculate, less than 1 mm. long, revolute at the tips. Seeds c. 2.1 mm. long, 1.4 mm. radially and tangentially.

TYPE: Cuba, Oriente, *Alain et al. 5475.*

DISTRIBUTION: Sierra Cristal, Oriente province, Cuba (MAP XXVII).

CUBA. ORIENTE. Sierra Cristal: southern slopes, 2–7 Apr. 1956, *Alain, Acuña, & López Figuieras 5475* (GH, HOLOTYPE), *5478, 5579* (GH); shore of Arroyo Cristal, 2–7 Apr. 1956, *Alain, Acuña, & López Figuieras 5633* (GH); manacales at the headwaters of the Río Lebisa, alt. 600–700 m., 14 Dec. 1922, *Ekman 15939* (S; sterile).

This apparently not uncommon plant of the Sierra Cristal vegetatively resembles ssp. *shaferi* and ssp. *spathulifolius* and is, in fact, quite closely allied to the former subspecies. However, its auriculate style-branches, non-revolute leaves and large male flowers are in sum so distinctive that it merits recognition as a distinct entity. There is also a definite vegetative resemblance between ssp. *alainii* and ssp. *myrtilloides* but the leaves of ssp. *alainii* are not apiculate, the female pedicel is usually longer, and the androecium of completely connate filaments is quite different from that of ssp. *myrtilloides.*

It seems appropriate to name this plant for Brother Alain, the assiduous botanist of the Colegio de la Salle, Vedado, Habana. His recent collections

---

[22] **Phyllanthus myrtilloides** ssp. **alainii,** ssp. nov.

Frutex stipulis cataphyllorum patentibus 1.5 mm. longis; ramulis 9–15-foliatis; foliis chartaceis ellipticis obovatisve 10–25 mm. longis, nec apiculatis nec revolutis; flore masculo laciniis calycis 2.5–3 mm. longis, columna staminum 0.7–1.1 mm., antheris sessilibus; flore femineo pedicello 7–15 mm. longo, laciniis calycis plerumque 3.5–4 mm. longis, columna stylorum c. 1 mm., stigmatibus auriculatis, reflexibus, revolutis; semina c. 2.1 mm. longa.

of several species of sect. *Orbicularia* have greatly assisted in analyzing this taxonomically difficult group.

61d. **Phyllanthus myrtilloides** ssp. **shaferi** (Urb.), stat. nov.

Phyllanthus shaferi Urb. Repert. Sp. Nov. **13**: 448. 1914.

Shrub 1–3 m. high; cataphylls usually reflexed, stipules c. 1–1.5 mm. long, blade up to 1.5 mm. long but often greatly reduced. Branchlets 2–6 cm. long, with c. 10–16 (–18) leaves; first internode 1.5–4 mm. long, median internodes 2–6 mm. long. Leaves: proximal stipules c. 1–2.2 mm. long, distal stipules c. 0.5–1.3 mm. long; petioles c. 0.8–1.5 (–2.5) mm. long; leaf-blades chartaceous often becoming convex and coriaceous, broadly elliptic to obovate or sometimes suborbicular, c. 6–10 (–15) mm. long, (3–) 4–8 (–10) mm. broad, rounded at the tip, the conspicuous apiculum (of juvenile leaves) deciduous, margins usually conspicuously revolute.

Male flower: pedicel 6–15 mm. long; calyx-lobes mostly 1.7–2.1 mm. long and about as broad, midrib branched or unbranched; disk-segments rather massive, free; stamens 6 (rarely 5), staminal column 0.5–1 mm. high, anthers sessile on the column, upper dehiscing vertically, lower horizontally. Female flower: pedicel 7–15 mm. long; calyx-lobes c. 3–4 mm. long and 1.7–2.5 mm. broad, midrib branched but veins obscure; disk rather massive; styles united very nearly to the bifurcation point into a column (0.5–) 1–1.5 mm. high, style-branches sharply reflexed from the top of the column, the tips revolute. Seeds 1.9–2.2 mm. long, 1.2–1.5 mm. radially and tangentially.

TYPE: Cuba, Oriente, *Shafer 1715.*

DISTRIBUTION: serpentine regions, Sierra de Nipe, Cuba (MAP XXVII).

CUBA. ORIENTE. Sierra de Nipe: Cayo del Rey, Arroyo Canapú, Apr., May 1940, *Carabia 3603, 4086* (GH, MICH, NY); pinar de Mayarí, *Carabia 3626* (GH, MICH, NY); Salto del Sojo, *Carabia 3723* (GH, NY); along Río Piedra in pinelands, alt. c. 500 m., 3 July 1914, *Ekman 1786* (MICH, S); charrascales, at stream, 25 July 1914, *Ekman 2196* (S); Bayate prope Río Piedra, 18 F 1915, *Ekman 4671* (S, sterile); ad marginem Río Piloto, 20 Apr. 1919, *Ekman 9501* (S); La Planch, July 1941, *Howard 6181* (GH, MT, NY, US); pinelands, La Casimba, 27 July 1940, *León & Alain 19235* (MICH); pinelands, crest of Sierra Nipe, alt. 600–700 m., 16–18 Oct. 1941, *Morton & Acuña 3110* (US); near streamlet, pinales southeast of Paso Estancia, 1–2 May 1909, *Shafer 1715* (NY, LECTOTYPE; F, ISOTYPE); Arroyo del Medio, above the falls, alt. 450–550 m., 22 Dec. 1909, *Shafer 3266* (F, GH, NY, US). Sierra Cristal: border of Río Miguel, Mayarí, 2–7 Apr. 1956, *Alain, Acuña & López Figueiras 5940* (GH).

In the Sierra de Nipe ssp. *shaferi* is a very common plant along watercourses. As illustrated by Marie-Victorin (Contr. Inst. Bot. Univ. Montr. **68**: 62. 1956), it has a distinctive aspect with small convex revolute leaves and pendent long-pedicellate flowers. However, it is very closely related to ssp. *alainii*, and the auriculate style-branches and non-revolute leaves of the latter are the only really distinctive characters. Also similar to ssp. *shaferi* is ssp. *spathulifolius* of the Moa region, but that plant has narrower leaves, longer staminal column, and different styles.

61e. **Phyllanthus myrtilloides** ssp. **spathulifolius** (Griseb.), stat. nov. (PLATE XXIX, *figs. I–J*).

Phyllanthus spathulifolius Griseb. Goett. Nachr. **1865**: 169. 1865; Muell. Arg. in DC. Prodr. **15**(2): 332. 1866; Alain, Flora de Cuba **3**: *fig. 9.* 1953.
Diasperus spathulifolius (Griseb.) O. Ktze. Rev. Gen. 2: 601. 1891.
Phyllanthus myrtilloides β *spathulifolius* (Griseb.) Gomez de la Maza, Anal. Soc. Hist. Nat. Madrid **23**: 53. 1894.

Shrub 0.5–3 m. high; cataphylls deciduous, not reflexed, stipules (0.6–) 1–1.5 mm. long, blade c. 0.5–0.8 mm. long. Branchlets (2–) 3–6 (–8) cm. long, with mostly 7–12 (–15) leaves; first internode c. 2–5. mm. long, median internodes 4–8 mm. long. Leaves: proximal stipules c. 0.7–1.5 mm. long, distal stipules c. 0.4–0.7 mm. long; petioles c. 1–1.5 mm. long; leaf-blades chartaceous, obovate or spathulate, 7–13 mm. long and 5–9 mm. broad, obtuse or rounded at the tip (apiculum nearly obsolete even in young leaves), acute at the base, margins usually distinctly revolute.

Male flower: pedicel 8–16 mm. long; calyx whitish; calyx-lobes mostly 2–3 mm. long and 0.7–1.8 mm. broad, midrib distinctly branched; disk-segments free; stamens 6 (rarely 5), staminal column (1–) 1.2–1.5 (–1.7) mm. high, anthers substipitate to sessile (free portion of filament at most about as long as or slightly longer than anther). Female flower: pedicel (6–) 8–13 mm. long; calyx greenish white; calyx-lobes mostly 3–3.5 mm. long, 1.2–2 mm. broad, midrib branched but veins inconspicuous; styles erect, coherent or connate into a column c. 0.5 mm. high, free ends parted c. ½ their length, the style-branches divergent, tips revolute. Seeds 1.6–1.8 mm. long, 1.1–1.3 mm. radially and tangentially, often caruncuIate.

TYPE: Cuba, Oriente, *Wright 1438b.*

DISTRIBUTION: riparian woods, northern Oriente province, Cuba. (MAP XXVII).

CUBA. ORIENTE: Monte Grande de Centeno, south of Moa, 4 Aug. 1945, *León, Alain, & Clemente 22673* (MICH); bank of Río Moa, c. 20 km. south of Moa, 21 July 1951, *Webster 3896* (GH, MICH, NY, US), *3897* (GH, MICH); margin of Río Castro near Sagua de Tanamo, 3 Apr. 1861, *Wright 1438b* (GOET, HOLOTYPE; G, S, W, ISOTYPES).

In many respects, including its general aspect, ssp. *spathulifolius* is a very distinctive group and might be thought to merit specific distinction, although Gomez de la Maza long ago reduced it to a variety of *P. myrtilloides.* Vegetatively ssp. *spathulifolius* is not unlike ssp. *alainii* of the Sierra Cristal but its styles are much more similar to those of ssp. *myrtilloides.* In the Sierra Moa, ssp. *spathulifolius* was observed growing with *Exostema* in the bed of the Río Moa within a few miles of a small population of plants of ssp. *erythrinus.* Here the two plants appear so different from one another, both morphologically and ecologically, that they gave the impression of being distinct species. However, when the other related populations in Oriente are taken into consideration, they are seen to be merely at the opposite ends of a nearly continuous spectrum.

The locality cited for Wright's collection has been taken from a label on an isotype sheet of ssp. *myrtilloides* (GH). There is no material of the type collection of ssp. *spathulifolius* in the Gray Herbarium (due, presumably, to the vagaries of distribution), but circumstantial evidence suggests that the label cited above belongs with specimens of ssp. *spathulifolius.*

62. **Phyllanthus chamaecristoides** Urb. Symb. Ant. 9: 185–186. 1924.

Low shrub c. 1–2 m. high; branches straight, c. 1–4 mm. thick, terete, dark brown, smooth or furrowed. Cataphylls blackish, indurate, sometimes reflexed, glabrous or puberulent, deciduous: stipules lanceolate, c. 1.5–3 mm. long, acuminate, entire or denticulate; blade narrowly lanceolate, c. 1–1.5 mm. long, acuminate, entire. Deciduous branchlets ascending or spreading, c. 3–7 (–13) cm. long, 0.25–0.5 mm. thick, stramineous to reddish brown, subterete, with mostly 15–45 leaves; first internode 1–5 mm. long, median internodes 1–4 mm. long. Leaves: stipules reflexed, persistent or deciduous, triangular-lanceolate, acuminate, the proximal ones partly or entirely blackish and indurate, 1–2.5 mm. long, the distal ones brownish and scarious, 0.5–1 mm. long. Petioles 0.3–1.2 mm. long. Leaf-blades brittle-chartaceous to subcoriaceous, sometimes convex, elliptic or oblong (and sometimes falcate) to obovate or spathulate, 3–10 mm. long, 2–5 (–7) mm. broad, subacute to obtuse or rounded and obscurely to prominently apiculate at the tip, acute to obtuse (sometimes inequilateral) at the base; above olivaceous or plumbeous, dull or sublucid (sometimes glossy in age), midrib and lateral veins slightly raised, subprominent to obscure; beneath pale, sometimes whitish or yellowish, midrib and steeply ascending lateral veins (c. 5–7 on a side) slightly raised, prominent to obscure, lateral veins nearly or quite unbranched; margins plane, reflexed, or revolute.

Monoecious; flowers mostly solitary, the proximal male, occasional distal ones female; male flowers sometimes paired.

Male flower: pedicel 2.5–7 mm. long. Calyx greenish white (more or less reddish when dried); calyx-lobes normally 6, more or less membranous, biseriate, c. 1.5–2 mm. long, the outer lobes elliptic or oblong, 0.8–1.3 mm. broad, the inner lobes broadly elliptic to obovate, 1.1–1.7 mm. broad; lobes obtuse or rounded and entire or minutely denticulate at the tip, midrib simple or with steeply ascending lateral veins. Disk-segments normally 6, roundish or squarish, somewhat fleshy, entire, c. 0.3–0.5 mm. across. Stamens usually 6 (rarely 5 or 7), filaments united into a rather stout sometimes apiculate column 0.5–0.9 mm. high; anthers subsessile (the free portion of the filament usually shorter than the anther) in 2 approximate whorls atop the column, broadly ovate, rounded across the top, c. 0.2–0.3 mm. long, 0.3–0.4 mm. broad; anther-sacs divergent or divaricate, dehiscing vertically (upper whorl) or horizontally (lower whorl), the slits not confluent; pollen grains 18–23 (–26) μ in diameter.

Female flower: pedicel 0.3–2 (–2.5) mm. long, smooth, slender, angled. Calyx greenish white (drying reddish); calyx-lobes normally 6, chartaceous-scarious, subequal, elliptic-oblong to spathulate, c. 2.5–3 mm. long, 1–1.7 mm. broad, rounded or obtuse at the tip, entire or obscurely denticulate, midrib obscure and unbranched or nearly so. Disk thin and flat, 6-lobed or angled, crenulate or entire. Ovary sessile, inconspicuously sulcate or ribbed; styles erect, mostly 1.3–2.5 mm. high, united below into a column c. 0.8–1.5 mm. high, parted ⅓ to ⅗ their length; style-branches usually sharply reflexed from the point of bifurcation, c. 0.7–1.2 mm. long, divergent, narrowed to slender sometimes revolute tips.

Capsule oblate, c. 3.5 mm. in diameter (or slightly less), dark reddish brown, essentially smooth, veins obscure. Columella 1.2–1.5 mm. long. Seeds trigonous, symmetric or slightly asymmetric, 1.6–1.7 mm. long, 1–1.2 mm. radially, 1–1.3 mm. tangentially, dark greyish- or reddish-brown, with evenly spaced rows of slightly raised dots; hilum subterminal, elliptic or ovate, c. 0.2–0.3 mm. long.

The two subspecies of this rather widespread plant appear different in so many respects that some workers might be reluctant to combine them. In almost all instances, they can be distinguishd vegetatively because of the hirtellous cataphylls of ssp. *chamaecristoides*. However, the male and female flowers are nearly identical (within the usual range of variation) in both groups and the allopatric range adds support to the probability that we are here dealing with subspecies which replace one another geographically rather than with distinct "Linnaean" species. The practical task of characterizing *P. chamaecristoides* taxonomically is made more difficult by the fact that ssp. *chamaecristoides* and ssp. *baracoensis* appear to hybridize with two different species, *P. phlebocarpus* and *P. scopulorum*, respectively.

The species most closely related to *P. chamaecristoides* are probably *P. myrtilloides* and *P. scopulorum*. Subspecies *shaferi* of *P. myrtilloides* is vegetatively somewhat similar and also has connate filaments and a rather similar stylar column, although it differs in its much longer pedicels. A much greater vegetative similarity is shown by *P. scopulorum*, but that species has much shorter, free styles and also usually longer pedicels.

KEY TO THE SUBSPECIES

Cataphylls and branchlet stipules hirtellous; leaf scarcely or not apiculate, margins plane or reflexed. .... ssp. *chamaecristoides*

Cataphylls and branchlet stipules glabrous; leaf with a usually conspicuous reflexed apiculum, margins usually revolute. .... ssp. *baracoensis*

62a. **Phyllanthus chamaecristoides** ssp. **chamaecristoides**

Phyllanthus chamaecristoides Urb. Symb. Ant. **9**: 185–186. 1924.
Phyllanthus apiculatus Urb. op. cit. 184–185 (non *P. apiculatus* Merr., 1920).

Terminal cones of cataphylls conspicuously scurfy-hirtellous; cataphylls caducous. Branchlets (2.5–) 4–7 (–13) cm. long, with mostly 25–45 (–55) leaves. Leaves: stipules at first copiously hirtellous on both faces and margins, later becoming more or less glabrate; leaf-blades mostly asymmetrically elliptic or oblong, often more or less falcate, with an obscure or obsolete apiculum at the tip, more or less inequilateral at the base (one side acute, the other obtuse), c. 6–10 mm. long, 2–4 mm. broad; margins plane or reflexed, not revolute.

Female flower: pedicel 0.9–1.4 mm. long; stylar column c. 0.9–1.5 mm. high.

Collected in flower Feb., June, July, Nov.; in fruit Nov.

TYPE: Cuba, *Ekman 2127*.

DISTRIBUTION: thickets and savannas, sepentine soil, Sierra de Nipe (MAP XXVIII).

CUBA. ORIENTE: Sierre de Nipe: Loma de Estrella, *Ekman 1732* (S), *2127* (S, HOLOTYPE; A, NY, S, ISOTYPES), *9838* (S); Bayate, Arroyo Piedra, *Ekman 4655* (S); Bayate, Río Piloto, *Ekman 5908* (A, NY, S; ISOTYPES of *P. apiculatus*); Bayate, Pinalito, *Ekman 10020* (S).

This population, which can be distinguished from all others in sect. *Orbicularia* by its hirtellous cataphylls, is known (in the typical form, at least) only from the southern part of the Sierra de Nipe. The specimen of ssp. *baracoensis* collected in the Sierra de Nipe by Carabia probably comes from the northern part of the range, but it is not yet clear how close the distributional limits of the two subspecies approach one another.

The collection from the Arroyo Piedra (*Ekman 4655*), on the basis of which Urban proposed the species *P. apiculatus*, does not differ from other collections in any important respect. The leaves are somewhat less falcate and the stipules even more densely hirtellous, but the floral structure is essentially the same.

62b. **Phyllanthus chamaecristoides** ssp. **baracoensis** (Urb.), stat. nov. (PLATE XXIX, *figs. K–L*).

Phyllanthus baracoensis Urb. Symb. Ant. **9**: 186–187. 1924.
Phyllanthus coelophyllus Urb. loc. cit.

Terminal cones of cataphylls completely glabrous; cataphylls deciduous. Branchlets 2–5 (–8) cm. long, with (12–) 15–25 (–35) leaves. Leaves: stipules glabrous; leaf-blades symmetric, becoming convex, broadly rhombic-obovate to spathulate, with a usually conspicuous reflexed more or less deciduous apiculum, 3–7 (–9) mm. long, 2–5 (–7) mm. broad; margins recurved or usually strongly revolute.

Female flower: pedicel 0.3–2 (–2.5) mm. long; stylar column (0.6–) 0.8–1.1 (–1.4) mm. high.

Collected in flower and fruit Jan.-Aug.

TYPE: Cuba, *Ekman 4326*.

Distribution: pinelands, thickets, and stream-banks, serpentine areas, eastern Cuba (Map XXVIII).

CUBA. Oriente. Sierra de Nipe: Loma del Winch, *Carabia 3821* (MICH, NY). Moa region: pinares de Moa, *Acuña* (SV 13154); Moa, *Mrs. Bucher 31, 96* (SV); Río de la Sabana, Yaguaneque, near Cananova, *León, Marie-Victorin, & Clement 20706* (MICH); Cerro de Miraflores, *León 21147* (MICH); La Breña woods, *León, Clement, & Alain 22496* (MICH); Playa de Vaca, *Marie-Victorin, Clement, & Alain 21462* (MT); Centeno, bords du río, *Marie-Victorin, Clement, & Alain 21471* (MT); charrascal du Cerro de Miraflores, *Marie-Victorin, Clement, & Alain 21491* (MT); Moa, pinède, *Marie-Victorin & Clement 21748* (MT); ravines, Cerro de Miraflores, *Webster 3888* (GH, MICH); pineland between Cerro de Miraflores and Moa, *Webster 3893* (GH, MICH). Baracoa region: Minas de Iberia ad Taco Bay, *Ekman 3839* (S, isotype of *P. coelophyllus*); charrascales near Río Macaguanigua, *Ekman 4326* (S, holotype; NY, S, isotypes); Mesa de Prada, Jauco, *León 11771* (NY, SV).

In contrast to ssp. *chamaecristoides*, ssp. *baracoensis* is a much more widely distributed plant, extending from the Sierra de Nipe on the west to near the eastern tip of the island at Jauco. The Carabia collection from the Sierra de Nipe is rather surprising, since it is far disjunct from the rest of the known population, and one would rather have suspected that ssp. *chamaecristoides* would occur at the Loma del Winch. However, the collection is quite typical for ssp. *baracoensis,* although the leaves are unusually small, and there is no doubt as to its determination.

The group most closely related to ssp. *baracoensis* (besides ssp. *chamaecristoides*) is *P. scopulorum,* which has a very similar habit and which occurs together with ssp. *baracoensis* in the Moa region. In this area ssp. *baracoensis* shows an increase in female pedicel length; in *Webster 3893,* for example, the pedicels are up to 3.5 mm. long, or at the border of the size-range of *P. scopulorum,* but the long united styles of the specimen place it definitely in ssp. *baracoensis.* More nearly intermediate is *Marie-Victorin et al. 21746* (MICH, MT; not cited above), which has female pedicels 6–8 mm. long as in *P. scopulorum* but united styles as in ssp. *baracoensis.* The origin of these aberrant specimens is still not clear, but if *P. scopulorum* is really a distinct species there is certainly a strong presumption that it hybridizes with ssp. *baracoensis.*

63. **Phyllanthus scopulorum** (Britton) Urb. Symb. Ant. 9: 187. 1924. (PLATE XXIX, *figs. M-N*).

Orbicularia scopulorum Britton, Mem. Torr. Bot. Club **16**: 73. 1920.

Glabrous bushy shrub up to 1–2 m. high; branches straight, brittle, c. 1–2.5 mm. thick, terete, bark dark brown or greyish, smooth or furrowed, sometimes wax-incrusted. Cataphylls blackish, indurate, reflexed, largely persistent: stipules triangular-lanceolate, (1.5–) 2–3 mm. long, 0.5–1 mm. broad, long-attenuate at the tip, entire or obscurely denticulate; blade lanceolate, c. 1–2 mm. long, 0.5 mm. broad. Deciduous branchlets ascending or spreading, mostly 3–5 (–6) cm. long, 0.2–0.4 mm. thick, stramineous becoming greyish, subterete, with c. 15–25 (–30) leaves; first internode 1–2.5 mm. long, median internodes 1.5–3 mm. long. Leaves: stipules reflexed, lanceolate, acuminate-attenuate, entire or denticulate at the base, the proximal ones blackish, indurate, persistent, mostly 1.5–3.5 mm. long, the distal ones scarious, brownish, subpersistent, 0.5–1.5 mm. long. Petioles olivaceous or stramineous, 0.4–0.8 mm. long. Leaf-blades flexibly coriaceous, mostly obovate or obcuneate, sometimes falcate, mostly 3–6 (–7) mm. long, 1.5–4 (–5) mm. broad, broadly obtuse to rounded or subtruncate at the tip, the conspicuous attenuate apiculum of the juvenile blade reflexed and deciduous in age, acute at the base; above olivaceous, sublucid (or glossy in age), very minutely foveolate, veins somewhat raised and subprominent to quite obscure; beneath paler, greenish or whitish, often with waxy atoms or minutely scabridulous, midrib and lateral veins (c. 3–5 on a side) much more prominent than above, usually raised, veinlets obscure; margins usually conspicuously revolute (at least in older leaves).

Monoecious; cymules mostly with 1 or 2 flowers; proximal cymules male, occasional distal cymules bisexual or with a single female flower.

Male flower: pedicel 3–6 mm. long. Calyx usually pinkish-tinged; calyx-lobes 6, biseriate, membranous, 1.5–2.5 mm. long, the outer linear- to oblong-obovate, c. 0.5–0.8 mm. broad, the inner obovate or spathulate, c. 0.8–1.2 mm. broad; lobes obtuse or rounded at the tip, entire or obscurely denticulate, midrib usually unbranched or nearly so. Disk-segments 6, squarish, concave, rather fleshy, minutely pitted, c. 0.2–0.3 mm. across. Stamens 6 (rarely 7), filaments united into a slender column 0.5–0.9 mm. high; anthers sessile or subsessile in 2 approximate whorls atop the column, broadly ovate, rounded or truncate across the tip, c. 0.2–0.25 mm. long, 0.4–0.5 mm. broad; anther-sacs divergent or subparallel, dehiscing vertically (upper anthers) or horizontally (lower anthers), the slits not confluent; pollen grains c. 18–23 μ in diameter.

Female flower: pedicel becoming (3–) 4–8 (–12) mm. long. Calyx usually pinkish-tinged; calyx-lobes 6, thin, biseriate as in the male, c. 1.7–2.3 mm. long, the outer c. 0.5–0.8 mm. broad, the inner c. 0.8–1.3 mm. broad, obtuse or rounded at the tip, entire or obscurely denticulate, midrib sparsely branching but veins usually obscure. Disk undulate-lobed or divided into segments, somewhat thickened, dark. Ovary sessile, with inconspicuous sutural ribs or bands; styles free or sometimes connivent or coherent, erect, ascending, or spreading, c. 0.3–0.7 mm. high (i.e., to point of bifurcation), bifid; style-branches usually reflexed, about as long as base of style, the tips slender, inturned or revolute.

Capsule oblate, c. 3–3.5 mm. broad, dark reddish brown, smooth, with yellowish sutural stripes and rather conspicuous veins. Columella 1.2–1.5 mm. long. Seeds trigonous, slightly asymmetric, carinate on one of the lateral faces, 1.4–1.7 mm. long, 1.1–1.3 mm. radially and tangentially, reddish-brown with even rows of raised dots; hilum subterminal, roundish, c. 0.25–0.3 mm. across.

Collected in flower and fruit April through July.

TYPE: Cuba, *Shafer 4006.*

DISTRIBUTION: pinelands, northeastern Oriente province, Cuba (MAP XXIX).

CUBA. ORIENTE: Moa region: Camino Delta no. 1, *Acuña 12497* (SV, US), *12498* (US); Yagrumaje del médio, *Clément 3620* (MT); chemin du Cayo Chiquito, *Clément 3650* (GH, MT, US); Sierra de Moa, edge of creek in pine woods 15 km. southwest of Companía de Moa mill, *Howard 5854* (GH, MT, NY, US); charrascal del Coco, south of Moa, *León, Clemente, & Alain 22637* (MICH); Jicotea rivulet, pinelands, east of Moa, *León, Clemente, & Howard 20165* (MICH); pineland between Río Moa and Río Yagrumaje, *Webster 3756* (MICH); banks of Río Cayoguan c. 3–4 mi. upstream from delta, *Webster 3800* (GH, MICH, NY), *3803* (MICH); ecotone between hardwoods and pineland, Cayo Chiquita, 8 km. south of Moa, *Webster 3849* (GH, MICH); thickets near Camp Toa, alt. 400 m., *Shafer 4006* (NY, HOLOTYPE).

This species endemic to the Moa region grows both in pinelands and streambeds, although in the latter habitat it is sometimes replaced by *P. myrtilloides* ssp. *spathulifolius.* From both that plant and from *P. chamaecristoides* ssp. *baracoensis,* it is distinguished by its much shorter free styles, while in pedicel length it is intermediate between them. As previously mentioned, there is a distinct possibility that it hybridizes with ssp. *baracoensis* and it is conceivable that it may cross with ssp. *spathulifolius* as well.

In many respects *P. scopulorum* is intermediate between *P. phlebocarpus* and *P. chamaecristoides* ssp. *baracoensis*; it has the free styles and long female pedicel of the former combined with the stamen number and vegetative features of the latter. The possibility that it is in fact a hybrid population must therefore be considered. However, weighing against such an assumption is the fertility of *P. scopulorum* and the fact that in the Moa region it is much commoner and more widespread than *P. phlebocarpus.* Consequently, *P. scopulorum* is here provisionally accepted as a distinct species.

The typification of *P. scopulorum* presents additional difficulties, because the type specimen is entirely sterile and originated somewhat outside of the known range of the species as determined by the remainder of the collections. Until Shafer's type locality can be revisited, therefore, it is not certain that the name *P. scopulorum* is really applicable to the plant of the Moa region described above. However, until more evidence is forthcoming the Shafer specimen is best considered conspecific with the others.

64. **Phyllanthus nummularioides** Muell. Arg. Linnaea **32**: 5. 1863; DC. Prodr. **15**(2): 333. 1866. (PLATE XXIX, *figs. O–P*).

Diasperus nummularioides (Muell. Arg.) O. Ktze. Rev. Gen. 2: 600. 1891.

Low shrub (becoming 1 m. high, Ekman); branches erect, straight, slender (c. 1.5–3 mm. thick), smooth, subterete, reddish brown. Cataphylls blackish, indurate, reflexed, more or less deciduous: stipules lanceolate, 2–3 mm. long, 0.5–1 mm. broad, attenuate-acuminate, entire, glabrous; blade very similar, c. 2–3 mm. long. Deciduous branchlets (4–) 6–12 (–15) cm. long, 0.4–0.7 mm. thick, stramineous to reddish brown, subterete, smooth, with mostly 10–20 (–25) leaves; first internode (2–) 4–8 mm. long, median internodes (2–) 4–11 mm. long. Leaves: stipules reflexed, lanceolate, entire, the proximal ones blackish, indurate, mostly persistent, 1.5–2.5 mm. long, the distal ones scarious, brownish, subpersistent, c. 0.7–1.1 mm. long. Petiole 1–2.5 mm. long. Leaf-blades firmly chartaceous, broadly elliptic or obovate to suborbicular, mostly 10–20 (–23) mm. long and 7–17 mm. broad, rounded or subtruncate and minutely apiculate at the tip (apiculum of distal leaves not over c. 0.2 mm. long), obtuse to rounded at the base; above olivaceous, dull or sublucid, very minutely foveolate, midrib and lateral veins plane or somewhat sunken, often prominent; beneath yellowish- or greyish-green, midrib and main lateral veins (c. 4 or 5 on a side) more or less equally raised, veinlets also raised and reticulum subprominent; margins thin, scarious, plane or reflexed but not revolute.

Monoecious [but female flowers sparse and specimens thus occasionally appearing to be entirely male]; cymules mostly with 2–4 male flowers, occasional distal cymules with 1 female and 1–3 male flowers.

Male flower: pedicel capillary, 5–12 mm. long. Calyx whitish; calyx-lobes 6, membranous, subequal, elliptic to obovate, mostly 1.5–2.5 mm. long, 1–1.5 mm. broad, obtuse at the tip, subentire, midrib simple or pinnately branched. Disk-segments 6, roundish, entire, not evidently pitted, c. 0.2–0.3 mm. broad, free or united by pairs. Stamens 6 (rarely 5); filaments united into a column c. 0.5–0.9 mm. high; anthers briefly stipitate (free portion of filament c. 0.2–0.5 mm. long) or the outer subsessile, ovate, emarginate, c. 0.25–0.3 mm. long and 0.3–0.4 mm. broad; anther-sacs divergent, the slits confluent at the apex, the inner (upper) dediscing more or less vertically, the outer dehiscing more or less horizontally; pollen grains 18–26 μ in diameter.

Female flower: pedicel slender, 8–17 mm. long, terete below, angled and slightly thickened above. Calyx whitish; calyx-lobes 6, thin, subchartaceous, subequal, oblong to broadly elliptic or obovate, c. 2–3.2 mm. long, 1.2–2 mm. broad, obtuse or subacute at the tip, entire or obscurely denticulate, midrib pinnately branched. Disk entire and 6-angled or cut into distinct segments 0.4–0.5 mm. across, flat or undulate, not massive. Ovary sessile; styles free or slightly coherent at the very base, erect or ascending, bifid c. ½ their length, the undivided portion c. 0.3–0.5 mm. long, the branches slightly spreading to sharply recurving.

Capsule not seen entire (probably c. 4 mm. in diameter); valves reddish brown, smooth, not veiny, c. 2.5 mm. long. Seeds [not seen fully mature] c. 1.5 mm. long, reddish-brown, with rows of slightly raised dots.

Collected in flower and fruit Oct.-Feb.

TYPE: St. Domingo, *Bertero* (G, HOLOTYPE; MO, W, ISOTYPES).

DISTRIBUTION: pinelands, Central Hispaniola (MAP XXV).

DOMINICAN REPUBLIC. LA VEGA: pine forests on rocky slopes north of

Piedra Blanca, alt. 200–500 m., 14 Oct. & 23 Dec. 1947, 9 Jan. 1948, *Allard 16066* (GH, NY, US), *18085* (US), *18861* (S, US); Bonao, Loma Peguera, alt. c. 250 m., 8 Feb. 1929, *Ekman H11487* (A, S, US).

As the sole representative of sect. *Orbicularia* outside of Cuba, *P. nummularioides* is of particular phytogeographic interest. All of the Allard and Ekman collections are from the same mountain area north of Piedra Blanca and Ekman (in a note on a label) has suggested that Bertero may have collected the plant at the same place, since the Loma Peguera is near the road between Sto. Domingo [Ciudad Trujillo] and Santiago. The complete isolation of this small population strongly suggests its origin by long-distance dispersal from Cuba.

The relationships of *P. nummularioides* are rather difficult to determine. In a number of respects, including reflexed cataphylls and essentially free styles, it closely resembles *P. scopulorum.* However, since that plant has such a different aspect and also differs by the several characters shown in the key, it may not be the most closely related species. Much more similar vegetatively is *P. myrtilloides*, especially ssp. *erythrinus*, which differs, however, in its larger flowers, purplish coloration, and connate styles. It is possible that *P. nummularioides* should be considered only a subspecies of *P. myrtilloides* but it is retained at specific rank for the time being because its free styles, at any rate, distinguish it from all forms of that polytypic species.

65. **Phyllanthus phlebocarpus** Urb. Symb. Ant. 9: 189. 1924. (PLATE XXIX, *figs. Q–R*).

Phyllanthus breviramis Urb. op. cit. 192.
Phyllanthus estrellensis Urb. op. cit. 188.

Glabrous shrub; branches straight, slender (c. 1.5–3 mm. thick), smooth, terete, becoming dark greyish or brown. Cataphylls blackish, indurate, soon deciduous: stipules broadly triangular, c. 1–1.5 mm. long, acute, entire; blade linear-oblong, 1–1.2 mm. long. Deciduous branchlets erect or ascending, 2–6 cm. long, 0.4–0.5 mm. thick, stramineous, terete or obtusely angled, smooth, with mostly 7–12 (–20) leaves; first internode 2–8 (–10) mm. long, median internodes 2–8 mm. long. Leaves: stipules reflexed, deciduous, triangular-lanceolate, entire, the proximal ones blackish and indurate, the distal ones brown and scarious, 0.6–1 mm. long, up to 0.5–0.6 mm. broad. Petioles c. 1–2 mm. long, stramineous. Leaf-blades thinly chartaceous, broadly elliptic or obovate to suborbicular, (8–) 10–18 (–20) mm. long, (6–) 8–13 (–19) mm. broad, mostly retuse or emarginate at the tip (apiculum completely obsolete), obtuse to truncate or subcordate at the base; above olivaceous, dull to lucid, midrib, veins, and veinlets, yellowish, plane or raised, anastomosing in a fine but prominent reticulum; beneath yellowish, dull to lucid, midrib, lateral veins (c. 4–6 on a side), and veinlets prominently raised in a conspicuous reticulum; margins unthickened, plane.

Monoecious; proximal cymules with 1 or 2 male flowers, occasional distal cymules with a solitary female flower (often only one female flower on a branchlet).

Male flower: pedicel 2.5–4 (–6) mm. long. Calyx whitish; calyx-lobes normally 6 (rarely 4 or 5), membranous, biseriate, subequal, oblong or obovate (inner lobes somewhat broader than outer), 1–1.5 (–1.8) mm. long, 0.6–0.9 (–1.2) mm. broad, midrib unbranched. Disk-segments isomerous with calyx-lobes, roundish or squarish, obscurely stipitate, entire, minutely foveolate, 0.25–0.4 mm. across. Stamens 3 (rarely 2 or 4), filaments completely connate into a slender column c. 0.4–0.6 mm. high; anthers sessile atop the column, united by the connectives, ovate, c. 0.25–0.4 mm. broad; anther-sacs divergent, dehiscing obliquely or horizontally, the slits not confluent; pollen grains (14–) 16–20 (–22) μ in diameter.

Female flower: pedicel very slender, 6–9 mm. long, slightly thickened above. Calyx whitish; calyx-lobes 6, thin, biseriate, subequal, oblong to narrowly obovate, 1.5–2 mm. long, 0.8–1.2 mm. broad, rounded and entire or obscurely and minutely denticulate at the tip, midrib unbranched or nearly so. Disk 6-lobed or divided into 6 discrete, squarish, somewhat thickened, dark segments. Ovary sessile, minutely verruculose, 3-sulcate; styles very shortly basally connate into a column c. 0.2 mm. high, thence spreading, the free ends parted c. ¾ their length, the branches c. 0.2–0.4 mm. long, divergent, the narrowed tips recurved.

Capsule not seen entire; valves c. 2.5 mm. long, greenish or reddish-tinged, with a rather conspicuous reticulum of sunken veins. Columella 1.2–1.3 mm. long. Seeds asymmetrically trigonous (carinate on one face), 1.3–1.6 mm. long, 1–1.2 mm. radially and tangentially, reddish brown, with fine more or less evenly spaced reddish-brown slightly raised dots; hilum subterminal, rounded-triangular, c. 0.3–0.4 mm. across.

Collected in flower Apr.-May; in fruit May, July, Oct.

TYPE: Cuba, *Ekman 2271a.*

DISTRIBUTION: scrubland and savannas, on serpentine, northern Oriente province, Cuba (MAP XXIX).

CUBA. ORIENTE: Sierra de Nipe: Cayo del Rey, Pinar Colorado, *Carabia 3573* (GH, NY); Loma La Mensura, *Carabia 3751* (GH, MICH, NY); Cayo del Rey, Loma de Bío, *Carabia 4068* (GH, MICH, NY); Bayate, in collibus, *Ekman 2019* (S); Loma de Estrella, savanna, *Ekman 2271a* (S, HOLOTYPE; NY, ISOTYPE); charrascales ad viam Bío, *Ekman 9574* (S, HOLOTYPE of *P. breviramis*); northern slope of Sierra de Nipe, alt. 400 m., *Morton & Acuña 2984* (US). Moa region: breñales de Playa Vaca, *Acuña* (SV 13157); Mina Franklin, *Acuña 12504* (US); Moa, *Ferras 15004* (SV); charrascal, Playa de La Vaca, *Marie-Victorin, Clément, & Alain 56700* (MT).

The following more or less aberrant collections are probably also referable here:

CUBA. ORIENTE: Bayate, *Ekman 2018* (S; det. by Urban as *P. aff. norlindii ?*); Loma de Estrella, savanna, *Ekman 2271b* (S, HOLOTYPE of *P. estrellensis*), *2272* (S, NY; TYPE COLLECTION of *P. norlindii*).

As here interpreted, *P. phlebocarpus* is a rather widespread and variable plant of open vegetation on serpentine lands, extending from Sierra de Nipe to Moa. Usually the species is easily recognizable by its broad, thin leaves which are conspicuously reticulate on both sides, unlike those of any other species of sect. *Orbicularia*. The androecium of 3 stamens and the short spreading nearly free styles also sharply distinguish it. Furthermore, *P. phlebocarpus* appears to differ from other species of the section in being at least partially deciduous, the flowers and new leaves developing together on the expanding branchlets during the renewed growing season in April or May. In other species the flowers appear in sequence as each branchlet successively matures. Urban's proposed species *P. breviramis* was based on a specimen of *P. phlebocarpus* in the spring "flush" of growth. The "pistillode" described by him is merely the apiculate tip of the staminal column, and in all essential respects the specimen does not deviate from typical *P. phlebocarpus*.

Heretofore, the status of *P. phlebocarpus* has been obscured (in the literature and in herbaria) by the existence in the Sierra de Nipe of anomalous plants with narrower leaves, shorter petioles, and a variable stamen number of 3–5; on the basis of such specimens Urban described two new species, *P. estrellensis* and *P. norlindii*. However, the circumstances of the collection of these specimens casts strong suspicion on the validity of these proposed concepts as representing true species in nature. It is notable that Ekman collected the type specimens of all three "species" at the same locality (i.e., savanna at Loma Estrella) and, in fact, confounded *P. estrellensis* and *P. phlebocarpus* under the same number; this appears significant, since Ekman rarely made mixed collections of different species. The only other collection which has been referred to *P. norlindii* (*Ekman 2018*) was also taken at the same locality with *P. phlebocarpus* (*Ekman 2019*) and — judging from the consecutive collection numbers — again from adjacent plants.

The known occurrence of *P. estrellensis* and *P. norlindii* only in conjunction with *P. phlebocarpus* suggests that they may represent only some sort of modification of that species. It is possible that they represent hybrid forms between *P. phlebocarpus* and *P. chamaecristoides* ssp. *chamaecristoides*, for the latter was also collected by Ekman at both localities; and the leaf-shape, petiole and pedicel-length, and stamen-number of *P. estrellensis* and *P. norlindii* are more or less intermediate between the two putative parental species, *P. estrellensis* suggesting a back-cross with *P. phlebocarpus*, and *P. norlindii* being more truly intermediate. The type specimen of *P. norlindii* is copiously flowering and fruiting, and the pollen fertility is about 80%, but the seeds do not appear to be viable. However, it should be stated clearly that evidence of hybridity is thus far purely circumstantial and is advanced only as a working hypothesis. The situation is complicated by the intrinsic variability of *P. phlebocarpus*. For example, such specimens as *Carabia 4068*, although typical for *P. phlebocarpus* in floral characters, have leaf-shapes which match those on sheets of *P. estrellensis* and *P. norlindii*. Whatever their genetic constitution the plants to which those two names have been applied would appear to be classifiable under *P. phlebocarpus.* It does not seem necessary at the present time to designate them by formula, even if their hybrid origin could be demonstrated.

The relationships of *P. phlebocarpus* are not easy to determine, owing to its isolated position within sect. *Orbicularia.* Vegetatively it resembles some forms of *P. myrtilloides,* particularly ssp. *erythrinus,* and this is perhaps its closest definable affinity.

Sect. 19. **Omphacodes** Webster, Contr. Gray Herb. **176**: 59. 1955.

Shrubs with phyllanthoid branching; branchlets often borne on spur-shoots; leaves chartaceous, stipules subpersistent. Monoecious, cymules bisexual. Male flower: calyx-lobes 5; stamens 3 or less commonly 4, filaments united; pollen grains with large areoles. Female flower: calyx-lobes 5, often deciduous; disk shallowly cupuliform; styles free, bifid, branches rather thick. Capsule massive, the exocarp somewhat fleshy, cocci indehiscent; seeds asymmetric, smooth.

TYPE SPECIES: *Phyllanthus subcarnosus* Wright ex Muell. Arg.

The single variable species of this section occupies an isolated position in subg. *Xylophylla* and it is possible that it should be referred to subg. *Cicca* instead. The female flower resembles that of the commonly cultivated *P. acidus* (sect. *Cicca*), the subindehiscent fruit that of *P. elsiae* (sect. *Aporosella*), and the leaf venation and branch-spur formation that of *P. pseudocicca* (sect. *Ciccopsis*). Probably sect. *Ciccopsis* should be regarded as the most closely related group in subg. *Cicca.* Among the sections of subg. *Xylophylla,* perhaps the most similar is *Asterandra,* which has leaves with somewhat similar petiolar ridges, male flowers with three (or more) monadelphous stamens, areolate pollen grains, and a globose fruit which is fleshy until rather late in ontogeny.

The areolate pollen grains of *P. subcarnosus* (PL. IX, *fig. 41*) are of particular interest since they can be regarded as derived from a microspore with three confluent bordered colpi such as that of *P. acidus* (Jour. Arnold Arb. 37: 240. 1956). If the areolate grains of the other taxa in subg. *Xylophylla* can be shown to have evolved from the microspore of *P. subcarnosus,* then sect. *Omphacodes* would have to be regarded as a phylogenetically important group and possibly the most primitive group within subg. *Xylophylla.* However, the specialized fruit, reduced androecium, and peculiar styles of sect. *Omphacodes* offer rather formidable obstacles to such an evolutionary hypothesis. Furthermore, it is by no means impossible that the areolate pollen grains of sect. *Omphacodes* have been derived independently of those in the other sections of the subgenus. It is true that the areolate grains of sect. *Macraea* can be distinguished from those of subg. *Xylophylla* by the different placement of the germ-pores, while in sect. *Omphacodes* there is no such difference. Thus there is a slight presumption in favor of the idea that the pollen of sect. *Omphacodes* may be primitive within subg. *Xylophylla* but the case is by no means proved. Until some of the South American species which appear also to lie in the "neutral zone" between subgenera *Cicca* and *Xylophylla* can be critically studied, the phylogenetic position of sect. *Omphacodes* must remain somewhat uncertain.

66. **Phyllanthus subcarnosus** Wright ex Muell. Arg. in DC. Prodr. 15(2): 379. 1866. (PLATE XXX, *figs. A–B*).

Diasperus subcarnosus (Wright) O. Ktze. Rev. Gen. 2: 601. 1891.
Phyllanthus leonis Alain, Contr. Ocas. Mus. Colegio La Salle 12: 1. 1953.

Glabrous shrub or tree c. 2–4 m. high; branches straight, distally c. 3–6 mm. thick, terete or sometimes distinctly angled, smooth, dark brown or grey, lenticels inconspicuous. Cataphylls indurate, brownish, not reflexed, persistent: stipules triangular, blunt or acute at the tip, 1.5–2 (–2.5) mm. long, 1–2 mm. broad; blade linear-lanceolate, c. 1.5–2.5 mm. long. Deciduous branchlets borne scattered on main branches or clustered on lateral spur-shoots, mostly 7–15 (–25) cm. long and 1.5–2.5 mm. thick, compressed, sharply wing-angled, stramineous, smooth, with 5–12 (–15) leaves; first internode mostly 10–30 mm. long, median internodes c. 10–30 mm. long. Leaves: stipules appressed, persistent or (distally) sometimes completely deciduous, triangular-lanceolate, acuminate, 1.2–2.5 mm. long, 0.8–1.5 mm. broad, brownish, entire, the base becoming more or less indurate, the scarious tip often breaking off. Petioles 1.5–4 (–5) mm. long, brownish, with two straight or slightly undulate adaxial ridges decurrent from the blade. Leaf-blades chartaceous, elliptic or slightly ovate (less commonly obovate or suborbicular), 3–11 cm. long and 2–7 cm. broad (reduced blades at proximal nodes smaller), emarginate or obtuse to subacute and with a brownish more or less deciduous apiculum up to 0.5 mm. long at the tip, obtuse to rounded or occasionally subcordate at the base; above olivaceous to silvery, obscurely to conspicuously foveolate, the depressed or plane midrib rather conspicuous, the lateral veins obscure; beneath paler or silvery, more or less obscurely foveolate, the midrib salient (and excurrent at the apex), the lateral veins (c. 5–7 on a side) slightly raised, anastomosing short of the margin, enclosing subprominent reticula of veinlets; margin unthickened or scarcely so, plane or recurved.

Monoecious; cymules bisexual (proximal ones sometimes entirely male), of one female and several male flowers.

Male flower: pedicel capillary (slightly thickened above), c. (3–) 4–6 mm. long. Calyx whitish (in life); calyx-lobes 5, subequal, more or less spreading, suborbicular to broadly elliptic or obovate, 1.3–2.7 mm. long and 1–1.8 mm. broad (at full anthesis, somewhat smaller in mature bud stage), subentire, thickened at the junction with the fleshy receptacle but distally thin, the midrib unbranched. Disk-segments 5, free or casually united, somewhat fleshy, squarish to triangular or round, obscurely pitted, c. 0.25–0.5 mm. across. Stamens 3 or less commonly 4, filaments connate into a column (0.3–) 0.5–0.8 mm. high; anthers subsessile atop the column, more or less ascending, c. 0.25–0.3 mm. long and 0.35–0.5 mm. broad;

anther-sacs divergent, the slits apically contiguous but not confluent, dehiscing obliquely; pollen grains spheroidal, c. 20–22 μ in diameter, with large polybrochate mostly pentagonal areoles c. ⅓ the diameter of the grain.

Female flower: pedicel becoming (8–) 10–20 mm. long, terete and slender below, dilated and sharply angled above. Calyx-lobes 5, chartaceous, caducous (falling at anthesis and represented only by prominent scars) or sometimes persistent and becoming reflexed in fruit, elliptic-oblong to obovate, c. 1.8–2.5 mm. long, 1.2–1.8 mm. broad, subentire, centrally thickened with very thin scarious margins, the midrib unbranched. Disk shallowly cupuliform, tenuous, the undulate margin not pitted, c. 0.25–0.4 mm. high but always much shorter than the ovary. Ovary subglobose; styles free, spreading, bifid nearly to the base, the divergent thickened and rather fleshy branches c. 0.5–0.7 mm. long, blunt at the tips.

Capsule subglobose, when dried 6–13 mm. in diameter, the exocarp fleshy but apparently thin, drying reddish brown; cocci more or less indehiscent, the outer and inner walls firmly united. Columella not seen. Seeds asymmetrically trigonous, those of each pair often unequal, (3–) 3.5–5 mm. long, (2–) 2.7–3.3 mm. broad, shiny reddish brown, smooth (sometimes very obscurely striate); hilum subterminal, c. 0.7 mm. long; micropylar end often with a small yellowish caruncle.

Collected in flower June, July, Aug.; in fruit Feb., Mar., July, Aug.

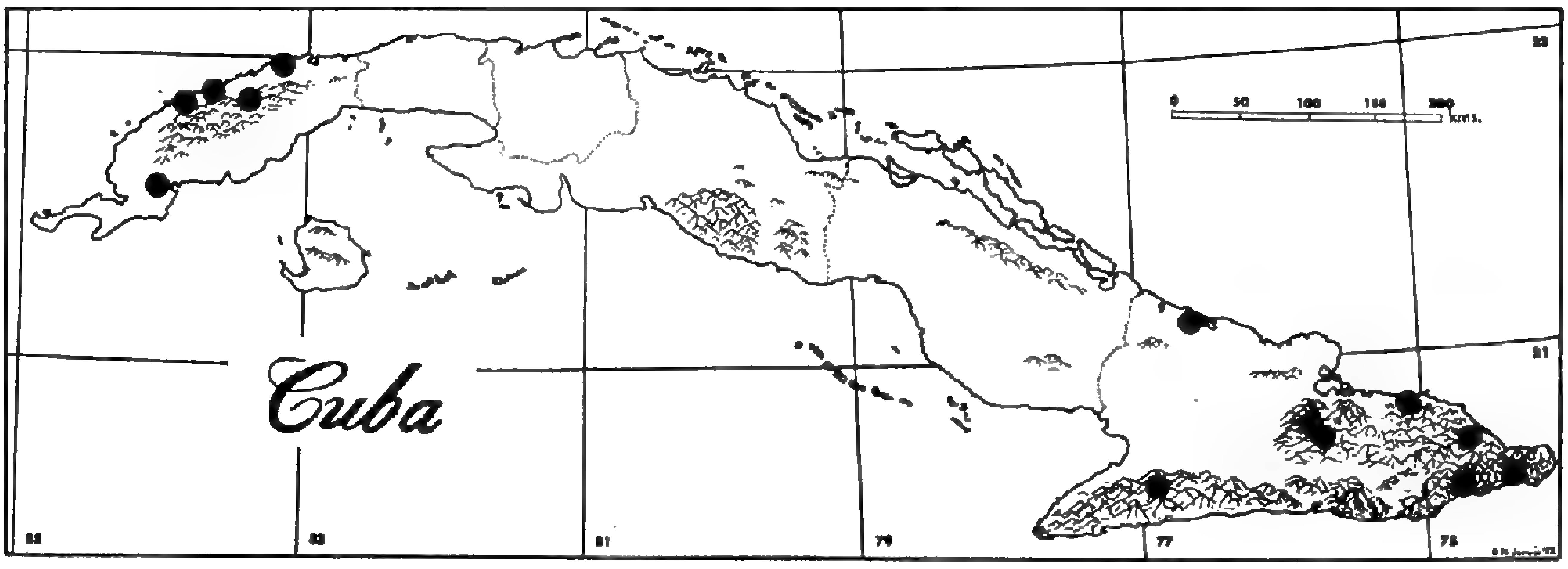
TYPE: Cuba, *Wright 1946.*

DISTRIBUTION: infra-mangrove coastal scrub and inland mountainous areas, Cuba and Hispaniola (MAP XXX).

CUBA. PINAR DEL RÍO: Mendoza, in forests at Boquerón, *Ekman 18746* (S, SV); behind manglares, halfway between Malas Aguas and San Cayetano, *Webster 4683* (GH, MICH); Sierra de los Organos, grupo del Rosario, San Diego de Tapia, at the edge of the Río Maní-Maní (= Río San Miguel), *Ekman 12665* (S); Zambumbia Hill, Rangel, *León 12715* (MICH, NY); Río San Miguel from Volador to Mal Paso, *Wilson 9374* (F, GH, NY, US); Toscano, in woods bordering manglares, *Wright 1946* (G, HOLOTYPE; F, GH, GOET, MO, P, S, ISOTYPES); Toscano, at Las Calaveras, woods bordering on manglares, *Ekman 17427* (S); Morillo, forest bordering on manglares, *Ekman 17401* (S). ORIENTE: Puerto Padre, *Curbelo X91* (NY, SV); Sierra Maestra, Río Yara, Nagua, in thickets, *Ekman 14180* (S), *León 10980* (NY); Sierra de Nipe, at base of Loma Mensura, *Ekman 3157* (S); Sierra de Nipe, El Taller, prope Río Piloto in dumetis, *Ekman 9676*; Cerro de Cananova, Sagua de Tánamo, *Clemente & Crisógono 6234* (GH, ISOTYPE of *P. leonis*); Río de la Sabana, Yaguaneque, Cananova, *León et al. 20724* (MICH); El Yunque, Baracoa, *Bucher* (SV 14556); Farallon La Perla, *Shafer 8747* (NY); woods at the foot of Sierra de Imías, Imías, *León 12137* (NY); rocky banks of Jauco River, Jauco, *León 11843* (NY, SV).

HISPANIOLA. "Saint-Domingue," *Poiteau* (A, P).

As here circumscribed, *P. subcarnosus* is a highly variable species occurring in scattered localities in Cuba and Hispaniola. Although widespread, it has been collected only rarely in the fertile condition, and its variation pattern presents many puzzling aspects. Originally it appeared that the population from Oriente province, described by Alain as *P. leonis*, could be recognized as a subspecies distinct from the Pinar del Río plants on the basis of the following features: longer branchlets (up to 30 cm.) and leaves (mostly 5–10 instead of 3–5 cm. long), larger male calyx-lobes (2 mm. long or more) and female pedicels, usually persistent rather than deciduous female calyx-lobes, and larger capsules (9–13 mm. as compared to 6–7 mm. in the very few capsules measured from Pinar del Río) and seeds (4.5–5 mm. long as opposed to 3–3.8 mm.). This would appear to be an impressive number of distinctions, but it must be remembered that the size measurements are mostly based on inadequate sampling and that, in most instances, there is either some overlap in the range of variation or else a relatively narrow gap. When the Hispaniolan plant is taken into account, the single collection of Poiteau is sufficient to erase some of the supposed distinctions, for it has the large capsules of *P. leonis* combined with the small male flowers of typical *P. subcarnosus* and is intermediate in leaf-size.



MAP XXX. Distribution of *P. subcarnosus* Wr. ex Muell. Arg.

It is still possible that when better samples are available from most areas of the range of *P. subcarnosus* it may prove feasible to distinguish two or more subspecific taxa; the leaf-shape of the Hispaniolan plants is distinctive, and the specimens from the Sierra de Nipe have unusually large leaves. However, it is outside the province of this study to base the systematic disposition on any such hypothetical prediction. Consequently, for the time being no subspecific entities are recognized within *P. subcarnosus*, with the proviso that a much more intensive study of the variation is indicated.

One of the major difficulties in the analysis of the present species is the lack of adequate floral material. It is not possible, for instance, to decide conclusively whether the variation in size of the male flowers is purely random or follows a geographical pattern. When sect. *Omphacodes* was first described, the stamen number was given as 3. This proves to be the prevalent but not the exclusive number, for a count of 50 flowers from *Webster 4683* yielded a score of 38 flowers with 3 stamens and 12 flowers with 4. This tendency toward a higher stamen number is of interest in view of the tetramerous condition of the androecium in some of the probably related sections of subg. *Cicca.* In contrast to the stamen number, no deviations were observed in the number of calyx-lobes and carpels, which were constantly 5 and 3, respectively.

The ecological behavior of *P. subcarnosus* is very interesting and merits field study. On the northern coast of Pinar del Río it occurs in the shrubby woods directly behind the mangrove zone, associated with such plants as *Eugenia axillaris* and *Comocladia dentata*; Curbelo's collection from Puerto Padre probably came from a similar habitat. However, it occurs inland both in the serpentine areas of the Sierra de Nipe and the calcareous regions of the Sierra Maestra. If it has really been derived from subg. *Cicca,* then it is probable that the original habitat of the species was in the sub-mangrove zone as in *P. elsiae* and *P. acidus.* The distribution of the present-day populations of *P. subcarnosus* may illustrate therefore, an important West Indian evolutionary phenomenon, viz., the colonization of inland areas by plants which have migrated along halophytic shoreline areas.

Sect. 20. **Asterandra** (Kl.) Muell. Arg. Linnaea **32**: 5. 1863.

Asterandra Kl. Arch. Naturgesch. **7**: 200. 1841.

Slender shrubs or trees with palm-like habit, the trunk with branchlets clustered at the apex; cataphylls inconspicuous; branchlets pinnatiform; leaves chartaceous, stipules reflexed. Monoecious; cymules mostly bisexual. Male flower: calyx-lobes 5, disk-segments coalescent into a massive ring; stamens 3–7, filaments united; anthers dehiscing horizontally or downwards; pollen grains areolate. Female flower: calyx-lobes 5 (6); disk as in male; styles erect, connate about halfway, the tips dilated, horizontally spreading. Capsule dry at maturity, cocci rather massive; seeds rounded, mottled, smooth, thick-walled.

TYPE SPECIES: *Asterandra cornifolia* (HBK.) Kl. [= *Phyllanthus juglandifolius* Willd. ssp. *cornifolius* (HBK.) Webster.]

Section *Asterandra,* although comprising only a single polytypic species, has a rather broad distribution which includes most of the West Indies and tropical South America. It is certainly very closely related to sect. *Oxalistylis,* which has very similar leaves and flowers but differs in its usually hirsutulous leaves and axes, free male disk-segments, longer styles with differently shaped stigmas, and thin-walled ridged or striate seeds. Possibly further study will show that the two sections should be combined, in which case *Oxalistylis* would have priority as a sectional epithet.

67. **Phyllanthus juglandifolius** Willd. Enum. Hort. Berol. Suppl. 64–65. 1813.

Phyllanthus grandifolius sensu Muell. Arg. in DC. Prodr. **15**(2): 329. 1866; et auct. seq., non L.

Shrub or tree 1.5–10 m. high, the slender simple or sparsely branching trunk often with branchlets clustered at the apex in the manner of a palm; axes nearly smooth (minutely scabridulous on the youngest parts) or minutely hirtellous. Cataphylls inconspicuous, reflexed: stipules chartaceous, lanceolate, c. 1.7–2.5 mm. long. Deciduous branchlets 25–120 cm. long, 2–5 mm. thick, olivaceous, smooth or minutely hirtellous, more or less angled, with c. 15–45 leaves; first internode 15–70 mm. long, median internodes 10–50 mm. long. Leaves: stipules triangular-lanceolate, soon reflexed, c. 1–2.5 mm. long, 0.8–1.5 mm. broad, chartaceous, olivaceous. Petiole glabrous or scabridulous, 2–5 mm. long, the leaf-blade margins decurrent on the adaxial side as two strongly undulate and conspicuous flanges. Leaf-blades chartaceous, elliptic- or oblong-lanceolate (proximal ones broadly elliptic to suborbicular), c. 5–20 cm. long, 2.5–6 cm. broad, abruptly short-acuminate, obtuse to cordate at the base; above olivaceous, smooth, the midrib, veins, and veinlets all evident but scarcely raised; beneath paler (sometimes glaucous), smooth or minutely scabridulous, sometimes minutely scurfy or hirtellous on the midrib and major veins, midrib salient, lateral veins (c. 6–10 on a side) and veinlets rather prominently raised, forming a conspicuous reticulum; margins unthickened, plane or recurved.

Monoecious; branchlets most often floriferous at every node; cymules simple to thrice compound, the peduncle up to 2 mm. long, more or less adnate (and flowers thus slightly supra-axillary); female flowers up to 3 or 4 in proximal axils, usually 1 or 2 in middle region of branchlet, often lacking distally (distal cymules thus entirely male); male flowers 2–10 per cymule, rarely solitary or absent.

Male flower: pedicel capillary, c. 10–20 mm. long. Calyx yellowish-green or greenish-white; calyx-lobes 5, chartaceous (rather fleshy at the base), somewhat unequal, the outer lobes elliptic or oblong and narrower, the inner lobes broadly elliptic to obovate or suborbicular, c. 1.8–3 mm. long and 1.5–2.5 mm. broad, blunt and often sparsely denticulate at the tip, otherwise entire, the scarious margin narrow and indefinite, the (1–) 3–5 nerves usually obscure. Disk annular, 5-angled, very massive, usually deeply pitted, 1.5–3 mm. across. Stamens 3–7, filaments connate into a rather massive column 1–1.5 mm. high and 0.5–0.75 mm. thick; anthers sessile atop the column, horizontal or deflexed below the umbonate top of the column, mostly c. 0.6–0.7 mm. long and 0.7–0.8 mm. broad (reduced ones smaller); anther-sacs subparallel, not confluent, dehiscing horizontally or obliquely downward; pollen grains 23–30 μ in diameter.

Female flower: pedicel slender, 5–30 mm. long, smooth or rarely scabridulous, obscurely angled. Calyx yellowish green; calyx-lobes 5, herbaceous, rather thick, subequal or distinctly unequal, elliptic or oblong to obovate, in fruit becoming 2–4 mm. long and 1.2–2.5 mm. broad, obtuse or rounded and entire or obscurely denticulate at the tip, the midrib slightly raised on both sides, the laterals obscure. Disk massive, 5-angled, closely resembling the male. Ovary smooth, carinate; styles erect, connate about halfway into a thick column, the flattened dilated tips bifid or emarginate, c. 0.5–0.7 mm. long, more or less horizontally spreading.

Capsule oblate, trigonous, deeply sulcate between the cocci, c. 7–12 mm. high and 9–17 mm. in diameter, smooth and glabrous, not veiny. Columella 4–6 mm. long, massive. Seeds plano-convex, plump, when mature 4.2–6 mm. long, 3.2–4 mm. broad, irregularly brown-and-gray mottled, smooth; hilum central, raphe linear-triangular.

It was shown previously (Jour. Arnold Arb. 37: 10. 1956) that Mueller's application of the name *P. grandifolius* to this West Indian and South American species was an erroneous adoption of horticultural practice, the true *P. grandifolius* L. being a Mexican species of subg. *Botryanthus*. As here interpreted, *P. juglandifolius* is a very widespread and polymorphic species which ranges over the West Indies and much of tropical South America.

KEY TO THE SUBSPECIES

Leaves mostly elliptic-lanceolate, obtuse to rounded at the base, c. 5–11 (rarely to 15) cm. long, glabrous beneath; stamens 3–5; fruiting pedicel 6–11 (–14) mm. long; mature capsule mostly 10–12 mm. in diameter. ...... ssp. *juglandifolius*

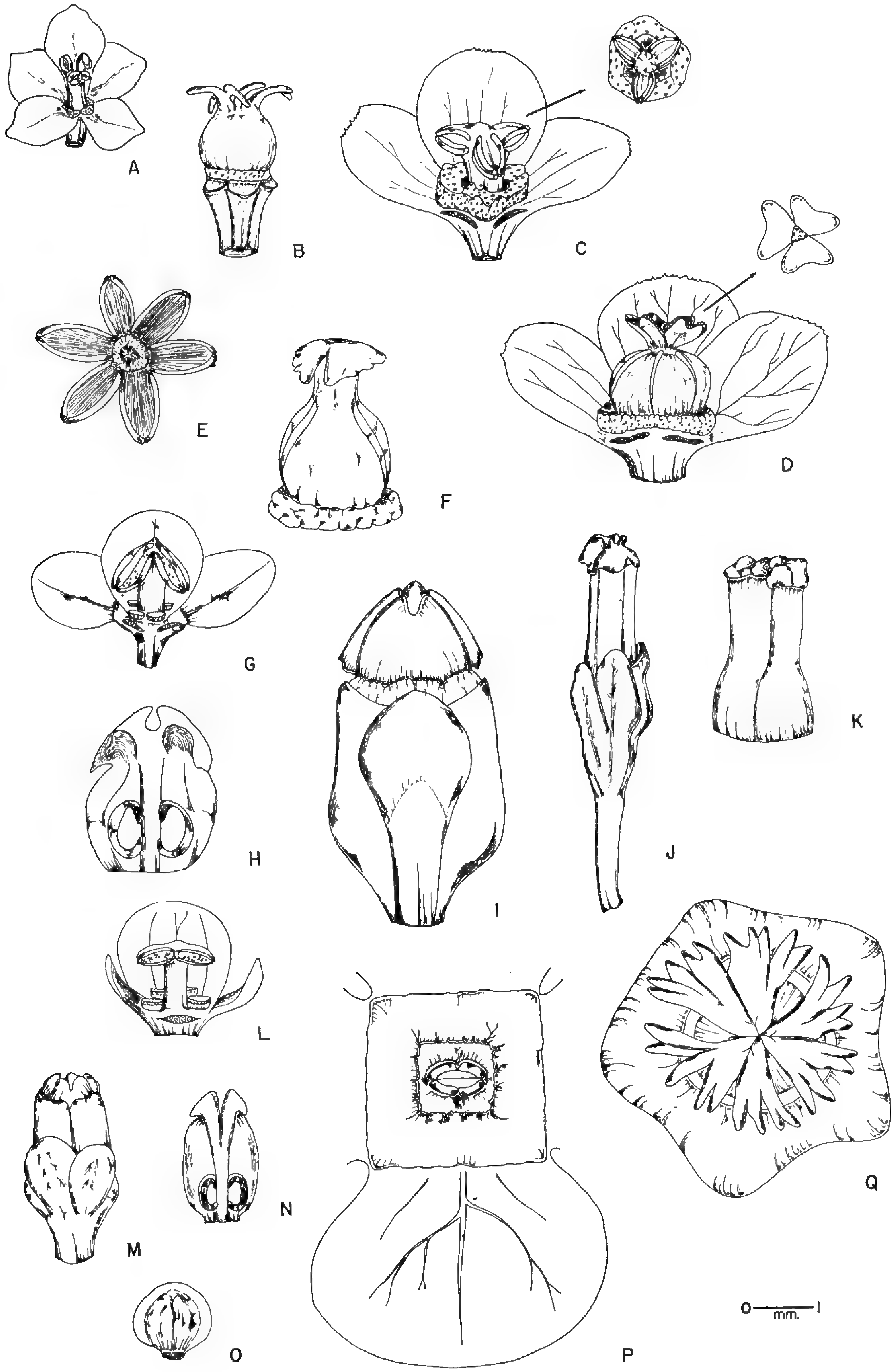
Leaves mostly oblong-lanceolate, rounded to cordate at the base, c. 12–20 (rarely only 9 or 10) cm. long, glabrous or hirtellous beneath; stamens mostly 6, less commonly 5 or 7; fruiting pedicel 15–30 mm. long; mature capsule mostly 12–15 (–17) mm. in diameter. .... ssp. *cornifolius*

67a. **Phyllanthus juglandifolius** ssp. **juglandifolius** (PLATE I, *fig. 4*; PLATE XXX, *figs. C–D*).

Phyllanthus juglandifolius Willd. Enum. Hort. Berol. Suppl. 64–65. 1813.
Agyneia berterii Spreng. Syst. Veg. **3**: 19. 1826.
Phyllanthus grandifolius γ *genuinus* Muell. Arg. in DC. Prodr. **15**(2): 329. 1866 (ex p.); non *P. grandifolius* L.
Phyllanthus quinquefidus Sesse & Moc. Flora Mex. ed. 2. 212. 1894.

PLATE XXX. FLOWERS OF SECTS. *Omphacodes*, *Asterandra*, *Epistylium*, AND *Glyptothamnus*.

FIGS. A–B. Male and female flowers of *P. subcarnosus* Wr. ex Muell. Arg. (*Webster 4683* [GH]). FIGS. C–F. Flowers of *P. juglandifolius* Willd. C, male flower of ssp. *juglandifolius* and androecium as seen from above (*Webster 4028* [GH]). D, female flower of ssp. *juglandifolius* and styles as seen from above (*Howard 6468* [GH]). E–F, androecium (as seen from above) and gynoecium of ssp. *cornifolius* (HBK.) Webster (*Haught 3067* [GH]). FIGS. G–I. Male flower, ovary in long section, and female flower of *P. cladanthus* Muell. Arg. (*Proctor 11800* [GH]). FIGS. J–K. Female flower and gynoecium of *P. cauliflorus* (Sw.) Griseb. (*Britton & Hollick 2027* [NY]). FIGS. L–O. Male flower, female flower, gynoecium in long section, and female calyx-lobe of *P. axillaris* (Sw.) Muell. Arg. (*Howard 14131* [A]). FIGS. P–Q. *Phyllanthus chryseus* Howard (*Webster 3853* [GH]). P, part of male flower, showing androecium, disk, and one calyx-lobe. Q, disk and gynoecium of female flower.



WEBSTER, WEST INDIAN PHYLLANTHUS

Shrub or treelet 1.5–3 m. high; branchlets 25–60 (–75) cm. long, smooth or minutely scabridulous, with (12–) 15–35 leaves; leaf-blades elliptic-lanceolate (less commonly oblong-lanceolate), c. 5–11 (–15) cm. long, 2.5–5 cm. broad. Male flower: calyx-lobes 1.8–2.5 mm. long, 1.2–2.5 mm. broad; disk 1.5–2 mm. across; stamens mostly 3 or 4, less commonly 5. Female flower: pedicel becoming 6–11 (–15) mm. long; fruiting calyx-lobes 2–2.8 mm. long. Capsule c. (5–) 7–8 mm. high and (9–) 10–12.5 mm. in diameter; mature seeds 4.5–5.5 mm. long, 3.2–4 mm. broad.

Collected flowering February through October; fruiting April through December.

TYPE: *Herb. Willdenow* (B, HOLOTYPE). The type sheet has no exact data, but from Willdenow's description it appears to have been taken from a plant cultivated in the Berlin Botanical Garden.

DISTRIBUTION: mainly Greater Antilles, a disjunct population occurring in Brazil (MAP XXXI).

CUBA. PINAR DEL RÍO: Sierra de Rangel, Taco-Taco, *Acuña 5950* (SV), *Wright 586* ex p. (S, US); Taco-Taco River, Aspiro, Santa Cruz de los Pinos, *Alain & Clemente 1429* (MICH). LAS VILLAS: Trinidad Mountains: San Blas to Buenos Aires, Gavinas, *Howard 6468* (GH, MO, MT, US); Buenos Aires, alt. 2500–3500 ft., *Jack 7435* (A, US), *8030* (S, US), *Webster 4771* (GH, MICH). CAMAGÜEY: potrero de La Ciega, Caobilla, *Acuña 13516* (SV). ORIENTE: Sierra Maestra, Río Yara, gravel-beds, *Ekman 14667, 14830* (S); Moa, *Bucher 11646, 14085* (SV); Los Llanos, Baracoa, *Bucher 10115* (SV); Jagüey, *Eggers 5304* (A, F, US); Mt. Liban, *Linden 1796* (BR, G, P, W); Alto Yateras, Guantánamo, *Roig 633* (SV); 20 miles south of Baracoa, alt. 2100 ft., *Webster 4028* (GH, MICH); Monte Verde, *Wright 586* ex p. (BR, C, G, GH, MO, P, S, W).

HAITI. NORD-OUEST: Bassin Bleu, road to Gros Morne, *Leonard & Leonard 14701* (GH, US); Môle River 2 miles from La Môle-St.-Nicolas, *Leonard & Leonard 13086* (US); Môle-St.-Nicolas, road through Môle gorge, *Leonard & Leonard 13125* (A, MO, US); Presqû'ile du Nord-Ouest, Port-de-Paix, Haut-Moustique, *Ekman H3670* (S). SUD: Morne de la Hotte, northeast slopes, alt. 800 m., *Ekman H212* (S); Aux Cayes, *Ekman H18* (A, S).

DOMINICAN REPUBLIC. "St. Domingue," *Bertero* (P); "Santo Domingo," *Prenleloup 524* (G, US). PUERTO PLATA: Pto. Plata, Río Mameyes, *Eggers 1652* (C, G, US). SANTIAGO: Río Amina, el Corozo, alt. 500 m., *Jimenez H15* (US); Jicomé, *Mera 2055* (US). LA VEGA: Río Yaque, near Jarabacoa, alt. 550 m., *Fuertes 1603* (A, G, L, W). SAN PEDRO DE MACORÍS: San Pedro de Macorís, *Rose, Fitch, & Russell 4208* (US); 20 km. west of San Pedro de Macorís, *Howard & Howard 9505* (GH). SEIBO: Llano Costero, Higüey, Arr. Caguero, *Ekman H12146* (S); La Romana, river basin, *Taylor 365* (US).

PUERTO RICO. *Bertero* (P; TYPE COLLECTION of *Agyneia berterii*), *Plée 848* (P), *Riedlé* (P), *Wydler 307* (F, G, P). AGUADILLA: Aguada, *Sintenis 5565* (L). ARECIBO: Manatí, Mango, *Sintenis 6611* (MO, US). SAN JUAN: Catano, limestone hill, *Britton, Britton, & Brown 6988* (F, US); Bayamon, mountains, *Sintenis 998b* (US), *Stahl 1073* (US). PONCE: El Tendal, Coamo River, *Britton, Britton, & Brown 6015* (F); arroyo near Ponce, *Britton & Britton 9562* (US). GUAYAMA: Cayey, Río Morillos, *Sintenis 2291* (G, GH, S); Cayey, La Cruz, *Sintenis 2387* (F, G, P).

VIRGIN ISLANDS. ST. THOMAS: 1798, *Riedlé* (P); Signalhill, alt. 500 m., *Eggers 374* (BR, G, GOET, W).

67b. **Phyllanthus juglandifolius** ssp. **cornifolius** (HBK.), stat. nov. (PLATE XXX, *figs. E–F*).

Phyllanthus cornifolius HBK. Nov. Gen. & Sp. **2**: 115. 1817.
Asterandra cornifolia Kl. Arch. Naturgesch. **7**: 200. 1841.
Phyllanthus grandifolius α *cornifolius* (HBK.) Muell. Arg. in DC. Prodr. **15**(2): 329. 1866.
Phyllanthus grandifolius β *salzmanni* Muell. Arg. ibid.
Phyllanthus grandifolius γ *genuinus* Muell. Arg. ibid. (ex p.).

Shrub or palm-like tree 2–10 m. high; branchlets (40–) 50–100 (–120) cm. long, smooth or hirtellous, with (25–) 30–45 leaves; leaf-blades oblong-lanceolate, (10–) 13–17 (–20) cm. long, 3–5 (–7) cm. broad, glabrous beneath or sometimes hirtellous along the midrib and main veins. Male flower: calyx-lobes 2.1–3 mm. long, 1.5–2.8 mm. broad; disk 1.8–3 mm. across; stamens mostly 6, less commonly 5 or 7 (mostly 5 in Trinidad plants). Female flower: pedicel becoming (10–) 15–25 (–30) mm. long; fruiting calyx-lobes c. 3–4 mm. long. Capsule c. 8–12 mm. high, (10–) 12–15 (–17) mm. in diameter; mature seeds 4.5–5.5 mm. long [6 mm. ex Urban], 3.5–4 mm. broad.

Collected flowering (in Trinidad) in June; fruiting in June and August.

TYPE: Ecuador, Guayaquil, *Herb. Humboldt 3850* (P, SYNTYPE).

DISTRIBUTION: widespread in tropical South America, reaching its northern limit in Trinidad (MAP XXXI).

TRINIDAD: without specific locality, *Finlay* (TRIN 2462), *Von Rohr 91* (C); Moruga, *Britton & Broadway 2463* (GH); Cedros, L'Enviense, *Broadway* (TRIN 8538); San Fernando Hill, *Lewis* (TRIN 9164); 12 mile post, Peñal Rock Road, *Williams* (TRIN 12172); Southern Watershed Reserve, *Williams* (TRIN 12179).

The following specimens are representative of the South America material studied of this subspecies:

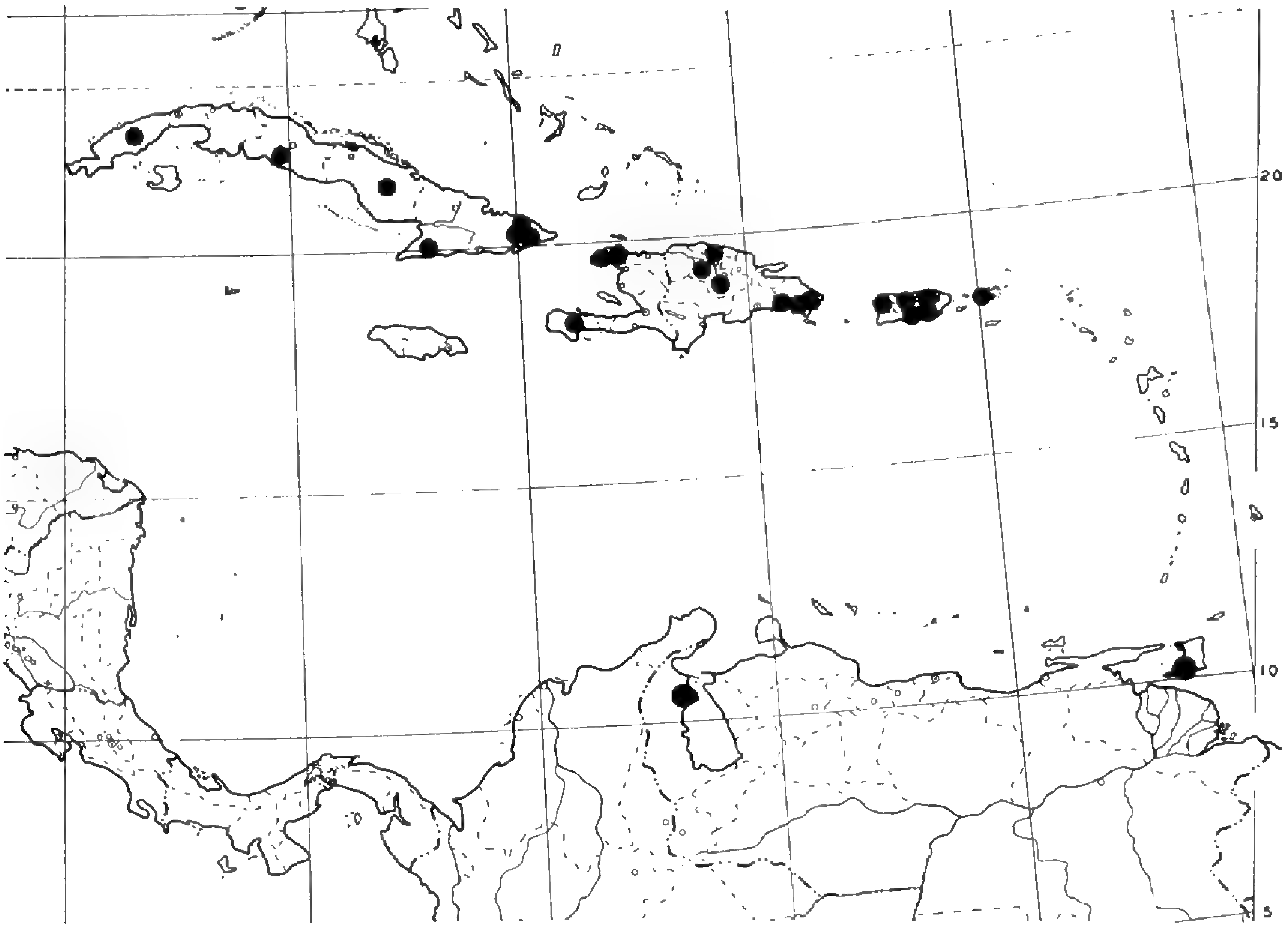
BRAZIL. BAHIA: Bahia, *Salzmann* (G, GH; TYPE COLLECTION of *P. grandifolius* var. *salzmanni*). MARANHÃO: Rio Pindare, Rapoza-Moncão, *Froes 11661* (F.) RIO DE JANEIRO: Collegio, near Campos, *Glaziou 13491* (C).

ECUADOR. GUAYAS: Balao, *Eggers 14123* (A); south of Milagro, *Hitchcock 20567* (GH). MANABÍ: near Guale, *Haught 3067* (GH).

PERU. LORETO: Lower Río Huallaga, Santa Rosa, *Williams 4880* (F).

VENEZUELA. ZULIA: Maracaybo, *Moritz 260* (GH); Perija, Maracaibo, *Karsten* (W).

Urban (Repert. Sp. Nov. **15**: 404. 1919) accepted *P. cornifolius* as a species distinct from *P. juglandifolius* on the basis of its leaf-shape, longer female pedicels, supposedly differently shaped style-tips, and larger fruit. He cited from Trinidad *Broadway 2727* (unfortunately not examined during the present study) and described the capsule as 14 mm. high, 18 mm. in diameter, and with seeds 6 mm. long. These dimensions, while presumably correctly stated, are larger than those observed in any other specimen; and the distinctive features of *P. cornifolius* as presented by Urban thus appear impressive. However, it is significant that his discussion is cautiously restricted to a comparison of the Trinidad collection with the West Indian specimens only of *P. juglandifolius*. When the variation throughout the entire range of both taxa is analyzed, the fluctuation and overlap of characters together with the complete geographical replacement of the two is strongly indicative that the populations in question are best ranked as subspecies of a single variable species.



MAP XXXI. Caribbean distribution of *P. juglandifolius* Willd.: small dots, ssp. *juglandifolius*; large dots, ssp. *cornifolius*.

Our knowledge of the variation patterns within ssp. *cornifolius* is very fragmentary in comparison with that of ssp. *juglandifolius*, which is at once homogeneous and better represented by herbarium specimens. However, although the scarcity of comparable herbarium material makes it impossible at this time to prove whether or not there is a significant overlap in measurements, it is clear that the mean values of many dimensions (e.g., height, length of branchlets and fruiting pedicels, size of leaves, and diameter of fruits) in ssp. *cornifolius* are definitely larger than those in ssp. *juglandifolius*.

The Trinidad population of *P. juglandifolius* is no better known than the South American ones with respect to the number of fertile collections available; but in any event it appears to be somewhat transitional between the two subspecies. For example, the leaves are always glabrous as in ssp. *juglandifolius*, but in size and shape they are wholly characteristic of ssp. *cornifolius*. Again, the stamen number in the Trinidad plants appears to be mainly 5, which is the number of overlap between the subspecies; and a single flower of *Von Rohr 91* had only 3 stamens. This is the only instance within ssp. *cornifolius* of a number lower than 5, so that it may simply be a completely exceptional occurrence; but the examination of a good series of male flowers from Trinidad is needed to clarify the matter.

The detailed distribution of ssp. *cornifolius* on Trinidad is interesting in that all collections have been made in the southwestern corner of the island, San Fernando Hill being the point farthest north. Judging from the vegetation map of Beard (Nat. Veg. Trinidad, *frontisp.* 1946), the plant is generally found in the semi-evergreen seasonal forest, where it presumably plays the part of a pioneer plant as ssp. *juglandifolius* was observed to do in Cuba.

Sect. 21. **Epistylium** (Sw.) Griseb. Fl. Br. W. Ind. 33. 1859.

Epistylium Sw. Fl. Ind. Occ. 1100. 1800.
Epistylium sect. *Euepistylium* Baill. Etud. Gen. Euphorb. 647. 1858.
Phyllanthus sect. *Catastylium* Griseb. ibid.

Shrubs or trees with phyllanthoid branching; branchlets pinnatiform, clustered at the apex of the more or less unbranched stem; leaves chartaceous or coriaceous, stipules persistent. Monoecious; cymules bisexual, borne on racemiform axillary or cauline thyrses. Male flower: calyx-lobes 4 or 5; disk-segments 4 or 5; stamens 2 or 3, filaments united; anthers more or less deflexed; pollen grains areolate. Female flower: receptacle and base of calyx massive; calyx-lobes 5, erect; disk tenuous, lobed or parted into 5 segments; stigmas massive, sessile atop ovary or terminating an elongated gynoecium. Capsule dry at maturity, angled; seeds 2 or possibly sometimes 1 per locule.

Type species: *Omphalea axillare* Sw. (= *Phyllanthus axillaris* (Sw.) Griseb.)

As here construed, sect. *Epistylium* comprises three species endemic to Jamaica which have the palm-like habit of sect. *Asterandra* and show a similar calciphilous habitat preference. Although the latter section differs from sect. *Epistylium* in its woodier seeds, much more massive floral disk, and very different inflorescence, its resemblance (at least to *P. cladanthus*) in habit, stipules, anthers, and styles suggests a rather close relationship. However, some of the representatives of subg. *Cicca*, especially *P. acidus* (sect. *Cicca*), also are suggestively similar to sect. *Epistylium* in the production of cauliflorous thyrses; and the tetramerous flowers, reduced female disk, and tendency to reduction in seed number in sect. *Cicca* represent a much closer approach to the condition in sect. *Epistylium* than do the corresponding features in sect. *Asterandra.* On the other hand, the tricolporate pollen grains, free stamens, and very different styles of sect. *Cicca* would appear to preclude an intimate relationship with sect. *Epistylium.* Another possibly related group is sect. *Omphacodes*, which does have areolate pollen grains and which shows some vegetative resemblance to the Jamaican plants. However, in that section cauliflory does not occur, and the stipules and styles are very different. It is most difficult to decide whether the resemblance between *Epistylium* and *Cicca* is genetically significant, or whether the various floral similarities may not rather be simply correlated with the cauliflorous condition. The multiple and seemingly contradictory affinities of sect. *Epistylium* pose a most interesting problem for further and more intensive investigation.

If the nature of the ties between *Epistylium* and its possible ancestors is obscure, the affinity in a different direction is much more clear. Undoubtedly related to sect. *Epistylium* and probably descended from it is sect. *Hemiphyllanthus*, which scarcely differs in anything more than pubescent axes and bipinnatiform branchlets. The leaf venation of the Haitian *P. maleolens* and *P. myriophyllus* is similar to that of *P. cladanthus*, and the massive receptacle and stylar column of *P. cauliflorus* is not unlike that of *P. ovatus* or *P. megapodus.* The more highly modified species of sect. *Xylophylla* are also related to sect. *Epistylium*, either directly or via sect. *Hemiphyllanthus.*

The three species of sect. *Epistylium*, although clearly differing both in floral and vegetative characters, are so obviously related that no purpose would be served in separating *P. cladanthus* into a separate sect. *Catastylium*; Mueller recognized the weakness of the distinctions but out of inertia recognized two sections. The least specialized of the three species is clearly *P. cladanthus*, which has 3 or 4 stamens and a subglobose ovary. Its reflexed stipules are much more like those of sect. *Asterandra* than are the stipules of either *P. cauliflorus* or *P. axillaris.*

KEY TO THE SPECIES

1. Stipules lanceolate, reflexed, not fused with branchlet; branchlets subterete; leaves oblong-lanceolate, chartaceous; male flower with 5 calyx-lobes and 3 stamens. . . . . 68. *P. cladanthus*
1. Stipules triangular, massive, not reflexed, more or less fused to branchlet; male flower with 4 calyx-lobes and 2 stamens.
    2. Branchlets angled, not flattened; leaves chartaceous, oblong-lanceolate; inflorescences at least partially cauline; pedicel of female flower 2–3 mm. long or more; ovary extended into a long stylar column. . . . . 69. *P. cauliflorus*
    2. Branchlets flattened; leaves coriaceous, mostly elliptic; inflorescences strictly axillary to leaves on branchlets; female flower subsessile; ovary ellipsoid (stylar column confounded with upper part of ovary). . . . . 70. *P. axillaris*

68. **Phyllanthus cladanthus** Muell. Arg. Linnaea 32: 46. 1863; DC. Prod. 15(2): 413. 1866; Fawc. & Rend. Fl. Jam. 4: 258. 1920. (PLATE XXX, *figs. G–I*).

Phyllanthus cauliflorus sensu Griseb. Fl. Br. W. Ind. 33. 1859; non *Omphalea cauliflora* Sw.

Diasperus cladanthus (Muell. Arg.) O. Ktze. Rev. Gen. 2: 598. 1891.

Slender tree c. 5–10 m. high; trunk c. 1 dm. thick or less, usually unbranched, smooth and reddish brown when young, becoming greyish. Cataphylls coriaceous, reflexed: stipules triangular or broadly lanceolate, c. 2.5–4 mm. long, 1.7–4 mm. broad, blunt, greyish; blade narrower. Deciduous branchlets steeply ascending, (15–) 20–60 cm. long, c. 2–4 mm. thick, reddish brown, smooth, terete or somewhat angled, with c. 10–20 leaves; first internode (3–) 5–8 (–12) cm. long, median internodes c. 1.5–3 cm. long. Leaves: stipules persistent, reflexed, indurate, lanceolate, 2.5–5 mm. long, 1.5–2.5 mm. broad (becoming broader with age), acuminate or blunt-tipped, dark reddish brown and polished. Petioles 4–7 mm. long, the laminar flanges adaxially decurrent. Leaf-blades chartaceous, ovate- to more commonly oblong-lanceolate, abruptly acuminate, 9–15 cm. long, 3–5.5 (–7) cm. broad, obtuse to rounded or rarely subcordate at the base; above olivaceous, the incised midrib prominent, the delicate lateral veins plane or very slightly raised; beneath paler, sublucid, the salient midrib proximally keeled, the main lateral veins (c. 8–12 on a side) and veinlets tenuous but raised, forming a conspicuous reticulum; margins plane or narrowly reflexed.

Monoecious; cymules usually bisexual, borne on naked thyrses, the latter usually fascicled at old nodes on main axis; additional thyrses sometimes produced on branchlets. Thyrses (2–) 5–20 cm. long, with c. 7–15 nodes; larger thyrses often compound, with up to 15 lateral axes and with conspicuous indurate cataphylls proximally. Cymules each with 1 female and up to c. 10 male flowers.

Male flower: pedicel slender, 3–8 mm. long. Calyx pinkish (ex Proctor); calyx-lobes 5 (rarely 6), thin and scarious, unequal: outer lobes oblong to elliptic, c. 1–1.5 mm. long and 0.8–1.2 mm. broad; inner lobes broadly obovate to suborbicular, c. 1.3–1.8 mm. long and 1.2–1.7 mm. broad; lobes rounded at the tip, entire, the midrib simple or sparingly branched above the middle. Disk-segments 5 (rarely 6), dark, roundish, thickened, pitted, crenulate, concave, c. 0.3–0.6 mm. across. Stamens 3 (rarely 4); filaments completely connate into a column c. 1 mm. high; anthers sessile atop the column, steeply deflexed (almost upside-down), (0.6–) 0.7–1 mm. long, 0.5–0.8 mm. broad; anther-sacs subparallel, dehiscing pseudo-vertically (actually obliquely downwards), the slits not confluent; pollen grains mostly 25–30 μ in diameter, with c. 15 oligobrochate areoles per amb, areoles c. 4–6 μ across.

Female flower: pedicel slender and terete (dilated only just beneath the calyx), c. 7–15 mm. long. Calyx pinkish; calyx-lobes 5, erect, strongly imbricate, somewhat unequal, fleshy with thin scarious margins, mostly broadly elliptic to suborbicular, c. 1.3–1.7 mm. long, 1–1.5 mm. broad, entire and rounded at the tip, the midrib sparsely branching. Disk a very inconspicuous membranous crenate ring (with small teeth alternating with the calyx-lobes), hidden under the ovary. Ovary subglobose, c. 1.5–2 mm. high and 2.5–3 mm. broad at (or shortly after) anthesis, shallowly sulcate; styles undeveloped, the dilated petaloid stigmas (style-tips) sessile, massive, more or less triangular, bluntly auriculate apically, crenulate along the distal margin, c. 0.5–1.5 mm. high and 1.3–2 mm. broad.

Capsule (not seen fully mature) oblate, bluntly trigonous, c. 8 mm. in diameter, smooth, not veiny. Seeds (immature) 2 per locule, c. 2.5 mm. long, brownish.

Collected flowering Mar., June, Aug.; fruiting Mar.

TYPE: Jamaica, *Wilson* (GOET, fragment of TYPE).

DISTRIBUTION: limestone hills, west central to eastern Jamaica (MAP XXXII).

JAMAICA. TRELAWNY: Cockpit country, rocky wooded hills, Tyre, 13–18 Sept. 1906, *Britton 570* (NY); Crown lands, near Troy, alt. 2000–2500 ft., 29 June, Aug., 1904, *Harris 8722* (A, F, JAM, NY, US), *8761* (F, JAM, NY). PORTLAND: John Crow Mountains, mist forest on dogtooth limestone 1.5 miles southwest of Ecclesdown, alt. c. 1000 ft., 6 Aug. 1954, *Webster & Wilson 5161* (A). ST. THOMAS: woodlands, eastern slopes of south end of John Crow Mountains, 10 Mar. 1909, *Harris & Britton* (F, JAM, NY, US); Big Level, wooded limestone hill, alt. 1500–2000 ft., 16 Mar. 1956, *Proctor 11800* (GH).

Although it was the basis for the separate section *Catastylium* established by Grisebach, *P. cladanthus* is too closely related to *P. cauliflorus* to be maintained in a distinct group. Vegetatively it so closely resembles that species that Grisebach confounded them, but Mueller was able to straighten out the confusion. However, even in the sterile condition *P. cladanthus* is ordinarily readily distinguishable from *P. cauliflorus* by its very different reflexed stipules.

Harris, in his detailed notes made on this species as he encountered it near Troy, remarked of the flowers that they were "produced along the main stem and branches, below the clusters of leaves, and extending downwards for a considerable distance. Occasionally the side branches are covered with flower fascicles." This description would appear to indicate that *P. cladanthus*, like *P. cauliflorus*, produces axillary inflorescences on the branchlets in addition to the usual cauliflorous ones.

The distribution of *P. cladanthus* parallels that of numerous other Jamaican species in the great disjunction between the western localities in the "cockpit" country at Troy and the eastern stations in the John Crow Mountains. There are no apparent differences between the specimens of the two areas, although the variation has certainly been inadequately sampled heretofore. There are no obvious habitat differences in the intervening region where the species does not occur, and such areas as Mt. Diablo, at least, are so well known that it is unlikely the species has escaped detection there.

69. **Phyllanthus cauliflorus** (Sw.) Griseb. Fl. Br. W. Ind. 33. 1859; emend. Muell. Arg. Linnaea **32**: 46. 1863; and in DC. Prodr. **15**(2): 412. 1886; Fawc. & Rend. Fl. Jam. **4**: 258. 1920.
(PLATE XXX, *figs. J–K*).

Omphalea cauliflora Sw. Prodr. 95. 1788.
Epistylium cauliflorum (Sw.) Sw. Fl. Ind. Occ. 1099, *pl. 22, figs. e, f, h.* 1800.
Diasperus cauliflorus (Sw.) O. Ktze. Rev. Gen. 2: 598. 1891.

Slender tree with usually unbranched trunk, becoming c. 5–6 m. high. Cataphylls not observed. Deciduous branchlets 25–55 cm. long, mostly 2.5–3 mm. thick, olivaceous or reddish-brown, distinctly angled, smooth, with 8–20 leaves; first internode 6–12 cm. long, median internodes c. 1.5–3.5 cm. long. Leaves: stipules persistent, not reflexed (tip appressed or spreading), indurate and rather massive, becoming more or less fused with the branchlet, triangular, c. 3–4 mm. long and 2.5–3 mm. broad on lower part of branchlet but decreasing to only 1.5 mm. long distally, blunt-tipped, greyish. Petioles 3–7 mm. long, the laminar flanges adaxially decurrent. Leaf-blades chartaceous or subcoriaceous, flexuous, ovate- to more commonly oblong-lanceolate, 7–14 cm. long, 3–6 cm. broad, abruptly short-acuminate, obtuse to rounded or subcordate at the base; above more or less lucid when dried, the midrib incised, the lateral veins and veinlets plane or slightly raised, subprominent; beneath sublucid, the midrib carinate and very prominent, the lateral veins (c. 8–10 on a side) and veinlets raised, forming a prominent reticulum; margins plane (or slightly and narrowly reflexed).

Monoecious; cymules bisexual, borne on naked thyrses, the latter usually fascicled at nodes on spur-shoots from main trunk but sometimes also produced one or two together in axils of leaves on branchlets (axis of thyrse sometimes reduced so that flowers may appear to be in axillary clusters). Thyrses c. 3–18 cm. long, with 4–20 nodes; cymules each with 1 female and several male flowers.

Male flower: pedicel slender, 3–5 mm. long. Calyx yellowish green; calyx-lobes 4, rounded at the tip, biseriate, unequal: outer lobes elliptic-oblong, c. 0.9–1.2 mm. long, inner lobes suborbicular or broader than long, 1.4–1.8 mm. long and 1.3–2.1 mm. broad; midrib of outer lobes simple, or inner lobes often sparingly branched distally. Disk-segments 4, dark, rather massive, entire, c. 0.25–0.6 mm. across. Stamens 2; filaments completely connate into a column c. 0.6–1 mm. high; anthers sessile atop the column, triangular-ovate, blunt-tipped, c. 0.5–0.7 mm. long, 0.4–0.6 mm. broad; anther-sacs subparallel, dehiscing obliquely downward or almost horizontally, the slits not apically confluent; pollen grains 15–18 μ in diameter, areoles mostly polybrochate, c. 7 or 8 per amb, c. 5–6 μ across.

Female flower: pedicel becoming 2–3.5 mm. long, slender and subterete below, rather abruptly incrassate and angled above. Calyx blood-red (ex Swartz); calyx-lobes 5, erect, strongly imbricate, massive and fleshy at the base, elliptic to suborbicular, at anthesis c. 1–1.2 mm. long and 0.9–1.2 mm. broad, later increasing up to 1.8 mm. long, rounded at the tip, entire, midrib distally sparsely branched. Disk divided into 5 thin, erect, oblong segments 0.2 mm. long or less. Gynoecium cylindrical-ellipsoidal (i.e., the massive stylar column about as long as and nearly as broad as the ovary proper); stylar column increasing to 1.5–2.5 mm. long soon after anthesis; stigmas massive, more or less triangular, bluntly auriculate and obcordate (apically channelled), subentire along the distal margin (often with a downwardly projected lateral lobe), c. 0.4–0.7 mm. high and as broad or broader.

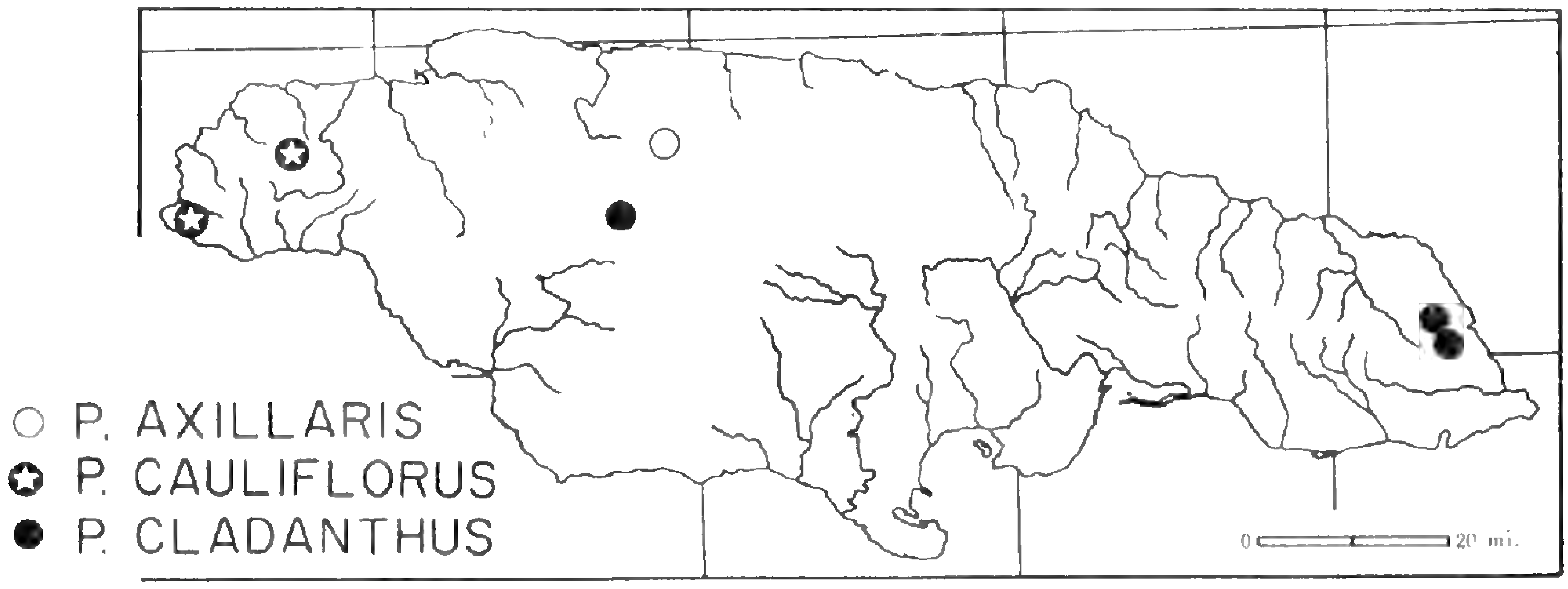
Capsule (not seen mature) ovoid, pointed, obscurely ribbed, dark, not veiny. Seeds (not seen) 2 per locule (ex Swartz).

TYPE: montane forests, western Jamaica, *Swartz* (C, G, S; SYNTYPES).

DISTRIBUTION: wooded limestone hills, western Jamaica (MAP XXXII).

JAMAICA. HANOVER: woods, summit of Dolphin Head, 17 Mar. 1908, *Britton & Hollick 2853* (F, NY). WESTMORELAND: rocky coastal thicket, Negril, 9–12 Mar. 1908, *Britton & Hollick 2027* (F, NY).

On the basis of available collections, it appears that Mueller and Fawcett and Rendle were correct in accepting Swartz's distinction between *P. cauliflorus* and *P. axillaris*. The two species are much more closely related to one another than to *P. cladanthus*, having in common the peculiar incrassate stipules, nearly indentical male flowers, and elongated gynoecia. Swartz distinguished *P. cauliflorus* from *P. axillaris* by its greater height, longer oblong leaves, cauliflorous inflorescence, more elongate gynoecium, and beaked fruit with two seeds in each locule (instead of solitary as in *P. axillaris*). In general these distinctions are still largely valid, although a few qualifications are necessary. Recent collections of *P. axillaris* show that it is not necessarily only 2–4 ft. high as stated by Swartz but may attain over 3.5 m. in height. Furthermore, *P. cauliflorus* does not produce exclusively cauline inflorescences, for they are partially axillary in *Britton & Hollick 2027*. However, this does not efface the inflorescence distinction since, as far as is known, *P. axillaris* is never cauliflorous, and *P. cauliflorus* always produces some cauline flowers.



MAP XXXII. Distribution of the species of sect. *Epistylium*.

The validity of the fruit characters suggested by Swartz must still rest on his personal observations, since herbarium material is inadequate. His descriptions are so accurate in other respects that there is no reason to doubt his ascription of paired seeds in the locules of *P. cauliflorus* and solitary ones in the locules of *P. axillaris*. However, it remains to be proved whether this distinction will hold when a large number of capsules of both species can be examined.

70. **Phyllanthus axillaris** (Sw.) Muell. Arg. in DC. Prodr. **15**(2): 412. 1866; Fawc. & Rend. Fl. Jam. **4**: 258–259. 1920.
(PLATE XXX, *figs. L–O*).

Omphalea axillaris Sw. Prodr. 95. 1788.
Epistylium axillare (Sw.) Sw. Fl. Ind. Occ. 1097. *pl. 22, figs. a–d, g, i–k*. 1800.
Omphalea epistylium Poir. Encycl. Meth. Suppl. **4**: 140. 1816.
Phyllanthus epistylium (Poir.) Griseb. Fl. Br. W. Ind. 33. 1859.
Diasperus axillaris (Sw.) O. Ktze. Rev. Gen. **2**: 598. 1891.

Glabrous shrub c. 0.5–3.5 m. high, with usually unbranched trunk topped by crown of branchlets. Cataphylls not seen. Deciduous branchlets 20–40 cm. long, c. 2–4 mm. thick, greyish and subterete proximally, reddish-brown and flattened (and more or less marginally angled) distally, with c. 15–25 leaves; first internode 6–8 cm. long, median internodes quite variable in length (successive pairs of nodes sometimes approximate). Leaves: stipules persistent, triangular, mostly 2–4 mm. long and 2.5–3.5 mm. broad (smaller at tip of branchlet), not reflexed (tip more or less spreading), massive and indurate, becoming more or less fused with the branchlet, blunt-tipped, greyish. Petioles 2.5–4 mm. long, with decurrent adaxial laminar flanges, sometimes corrugate-fissured. Leaf-blades coriaceous, sometimes quite rigid, ovate- to elliptic-lanceolate, (6–) 8–11 cm. long, (2.5–) 3–5.5 cm. broad, abruptly short-acuminate, mostly obtuse to rounded at the base; above drying dull plumbeous or brownish grey, the midrib incised but veins and veinlets distinctly raised and prominent; beneath sublucid, often coppery when dried, the midrib carinate, the lateral veins (c. 5–8 on a side) and veinlets raised, forming a very prominent reticulum; margins slightly and narrowly reflexed.

Monoecious; cymules bisexual, each usually with one female and several male flowers, borne on short naked thyrses c. 1–3 cm. long which are apparently always axillary to leaves on branchlets (i.e., flowers never cauline).

Male flower: pedicel slender, mostly 3–5 mm. long. Calyx yellowish green; calyx-lobes 4, rounded at the tip, entire, biseriate, unequal: outer lobes elliptic, c. 1–1.3 mm. long and 0.7–1.2 mm. broad; inner lobes suborbicular or broader than long, c. 1.3–1.5 mm. long and 1.7–2 mm. broad; midrib simple or sparingly branched distally. Disk-segments 4, dark, massive, rugose-crenulate, concave, c. 0.3–0.5 mm. across. Stamens 2; filaments completely connate into a column c. 0.9–1.2 mm. high; anthers sessile atop the column, nearly horizontal, triangular-ovate, blunt-tipped,

c. 0.7–0.8 mm. long and 0.5–0.6 mm. broad; anther-sacs subparallel, dehiscing horizontally or slightly obliquely downwards, the slits not apically confluent; pollen grains c. 21–25 μ in diameter.

Female flower: pedicel sub-obsolete, less than 1 mm. long. Calyx cream-colored or greenish; calyx-lobes 5, erect, strongly imbricate, massive and fleshy at base, elliptic to suborbicular, c. 1–1.3 mm. long and 0.8 (outer) to 1.3 (inner) mm. broad, rounded at the tip, entire, midrib simple or sparsely branched distally. Disk divided into 5 thin, erect, oblong segments c. 0.1–0.2 mm. long. Ovary ellipsoid, at or shortly after anthesis c. 1.5–1.8 mm. high and 1–1.3 mm. broad; styles undeveloped (confounded with ovary), the dilated stigmas sessile atop the ovary, massive, more or less triangular, bluntly auriculate and obcordate (apically channelled), subentire along the distal margin, c. 0.5–0.7 mm. high and 0.7–1 mm. broad.

Capsule trigonous, green (ex Howard); valves dark reddish brown, c. 5 mm. long. Columella c. 2.5 mm. long. Seeds solitary in each locule (ex Swartz), c. 3.5 mm. long, slightly over 2 mm. across the back, pale brown with dark brown slightly raised more or less elongated flecks; hilum submedian, triangular, c. 0.3 mm. long.

Collected in flower Apr. (Swartz), July, Sept.; in fruit July.

TYPE: mountains of western Jamaica, *Swartz* (G, SYNTYPE).

DISTRIBUTION: limestone areas, western Jamaica (MAP XXXII).

JAMAICA. TRELAWNY: Ramgoat Cave area, limestone hilltops, hillsides, and cliff-faces, 26 Sept. 1954, 4 July 1955, 19 Jan. 1956, *Howard & Proctor 14131, 14371, 14639* (A).

From the other two species of sect. *Epistylium*, *P. axillaris* is readily distinguishable on account of its shorter, thicker leaves, flattened branchlets, and axillary inflorescences. Apparently it also differs in its solitary rather than paired seeds, as pointed out by Swartz, although this requires confirmation. The gynoecium of *P. axillaris* appears to be intermediate between that of *P. cladanthus* and that of *P. cauliflorus* but this appearance may be deceptive. The complete loss of any distinction between style and ovary in *P. axillaris* might represent a further modification of the long-styled gynoecium of *P. cauliflorus*. This would appear the more probable, since in other respects — such as its more rigid leaves and flattened branchlets — *P. axillaris* appears to be the most specialized representative of sect. *Epistylium*.

Sect. 22. **Glyptothamnus** Webster, Jour. Arnold Arb. 39: 68. 1958.

Dendriform small shrub with pinnatiform branchlets; cataphylls indurate; leaves coriaceous, margins revolute, stipules indurate and persistent. Monoecious; cymules mostly unisexual. Male flower: calyx-lobes 4, disk-segments coalescent into a massive ring; stamens 2, filaments united; anthers dehiscing horizontally; pollen grains areolate. Female flower:

calyx-lobes 5; disk massive; styles dilated, lacerate. Capsule globose, not sulcate; seeds dark, fissured.

TYPE SPECIES: *Phyllanthus chryseus* Howard.

The single species of this monotypic section is so distinctive in many features, such as its small indurate cataphylls and stipules, revolute leaves golden beneath, very massive disk, and fissured seeds, that it cannot be regarded as closely related to any other group. As noted by Howard, the leaves and cataphylls show some resemblance to those of *P. subcarnosus* (sect. *Omphacodes*), but of course the flowers are completely different. The closest floral similarity is perhaps to be found in sect. *Asterandra*, where there is a very apparent resemblance in the floral disk and styles; however, the vegetative parts in sect. *Asterandra* are quite dissimilar. The Jamaican species of sect. *Epistylium* are vaguely similar but differ in many important respects, such as inflorescence, floral disk, and styles. Possibly *P. chryseus* could be regarded as a xerophytic derivative (adapted to serpentine) of the mesophytic and calciphilous *P. juglandifolius*, but if so the affinity must be indirect. *Phyllanthus chryseus* is an excellent example of a highly specialized relict species of ancient origin.

71. **Phyllanthus chryseus** Howard, Jour. Arnold Arb. **28**: 121. 1947. (PLATE XXX, *figs. P–Q*).

Glabrous shrub resembling a miniature tree, with bluish-green foliage, the erect woody unbranched stem 2–8 dm. high, 5–7 mm. thick, reddish brown and pruinose above, greyish below. Lower leaves of stem with petioles 5–10 mm. long, leaf-blades elliptic or oblong-obovate, rounded or obtuse at the tip, c. 6–8 cm. long and 2.3–4 cm. broad; upper leaves reduced to cataphylls: stipules triangular-lanceolate, acuminate, 3.5–5.5 mm. long, 2–3 mm. broad, oblique at the base, indurate, smooth, reddish brown and polished, with a single excentric keel; blade linear-lanceolate, 2.5–5 mm. long. Deciduous branchlets mostly 10–20 cm. long, 1.5–2.5 mm. thick, olivaceous, smooth, distinctly flattened but not sharply angled, with mostly 8–20 (–25) leaves; first internode (of well-developed branchlets) 25–55 mm. long, median internodes 10–35 mm. long. Leaves: stipules persistent, triangular, 1–2 mm. long, 0.9–1.8 mm. broad, bluntly pointed, shining and indurate, reddish brown. Leaf-blades rigidly coriaceous, broadly elliptic to orbicular (or sometimes broader than long), c. 2–4.5 cm. long, 1.5–3.5 cm. broad, rounded or emarginate at the tip (the minute scarious apiculum reflexed), obtuse to rounded (or sometimes truncate or subcordate) at the base; blades distinctly reddish when young, when mature bluish green above (turning olivaceous or plumbeous on drying), minutely foveolate, the midrib usually incised, other veins obscure; beneath golden-yellow (or greenish yellow) when living, turning coppery when dried, the midrib salient, laterals (c. 5 on a side) slightly raised but inconspicuous; margins thickened, conspicuously revolute.

Monoecious, cymules usually unisexual; two proximal nodes of branchlet most often with racemiform cymules of 3 (less commonly up to 7) male flowers; subsequent nodes with solitary female flowers alternating with male cymules at somewhat irregular intervals.

Male flower: pedicel slender, 4.5–7.5 mm. long. Calyx greenish or reddish-tinged, the receptacle massive; calyx-lobes 4, coriaceous, biseriate (strongly imbricate in the bud), subequal, suborbicular (mostly broader than long), 2.8–4.5 mm. long, 4.5–6 mm. broad, rounded at the tip, entire, midrib with well-developed but rather inconspicuous branches. Disk very massive, squarish in outline, surrounding the androecium (inclosing it in a hollow), deeply pitted, greenish in life but turning reddish when dried. Stamens 2; filaments completely connate into a slender column less than 1 mm. high; anthers sessile atop the column, discrete (separated by a notch on each side, the connective between the anther-sacs emarginate so that there may appear to be 4 anthers), semicircular-notched in outline, c. 0.4–0.5 mm. long, 0.7–0.8 mm. broad; anther-sacs divergent, curved, dehiscing horizontally, the slits not confluent; pollen grains 18–21 μ in diameter; areoles polybrochate, 5 or 6 per amb, 5- or 6-sided, c. 6–9 μ across.

Female flower: pedicel slender, 11–17 mm. long, terete or obscurely angled, slightly and gradually broadened upwards. Calyx greenish, the receptacle massive; calyx-lobes 5, coriaceous, spreading at anthesis, broadly ovate, c. 4–7 mm. long and broad, rounded at the tip, entire, midrib conspicuously branched. Disk massive, 5-angled, smooth, entire, yellowish at anthesis (drying reddish brown). Ovary sunken in the disk, capped by the petaloid style-tips (stigmas), these free, spreading and horizontally appressed, sessile, obcuneate, 1.5–2 mm. long, 2.3–2.7 mm. broad, yellowish, conspicuously lacerate.

Capsule spheroidal, c. 7.5 mm. in diameter, reddish brown, rugulose, not veiny. Columella slender, 4.5–6 mm. long. Seeds trigonous, symmetric, c. 4.7–5 mm. long, 2.6–3 mm. radially and tangentially, very dark reddish brown (sometimes nearly black), deeply and irregularly transversely or somewhat obliquely fissured on back and sides; hilum submedian, narrowly elliptic, c. 0.4–0.5 mm. long.

Collected in flower and fruit May, July.

TYPE: Cuba, *Howard 5829.*

DISTRIBUTION: endemic to a small area of serpentine hillsides in the Moa region, eastern Cuba.

CUBA. ORIENTE: Moa, summer 1939, *Mrs. Bucher 75* (NY); common in woods along ravine 15 km. southwest of Moa, 26 July 1941, *Howard 5829* (GH, HOLOTYPE; US, ISOTYPE); pinelands, Arroyo Jicotea, Moa, July 1941, *León, Clemente, & Howard 20169* (MICH); Moa, plateau de 400 m. entre le río Cabañas et le río Yagrumaje, 27–31 May 1943, *Marie-Victorin & Clément 21755* (A, MT); pinales c. 15 km. south of Moa, 19 July 1951, *Webster 3853* (GH, MICH, NY, US).

One of the most distinctive endemic species of the serpentine flora of Moa, *P. chryseus* appears to be confined to a very narrow range south of

Moa between the Río Cabañas and the Río Yagrumaje. In the field it presents a striking appearance due to its miniature-tree habit and stiff round leaves bluish above and yellowish beneath (cf. photograph taken by Marie-Victorin, Contr. Inst. Bot. Univ. Montreal **68**: 164. 1956). Although so restricted in range, the plant was locally quite common, associated with such characteristic Moa species as *Scaevola wrightii* and *Anastraphia recurva.*

Sect. 23. **Hemiphyllanthus** (Muell. Arg.) Muell. Arg. Flora **1865**: 370. 1865; DC. Prodr. **15**(2): 323. 1866; emend. Webster, Contr. Gray Herb. **176**: 62. 1955.

Glochidion sect. *Hemiphyllanthus* Muell. Arg. Linnaea 32: 59. 1863; Pax & Hoffm. Natürl. Pflanzenfam. **19c**: 58. 1931.

Shrubs or small trees with phyllanthoid branching; axes incrustate or tomentulose; branchlets bipinnatiform, leaves well-developed at least on ultimate axes, leaf-blades membranous to coriaceous. Monoecious; cymules unisexual or bisexual, produced only on ultimate axes of branchlet. Male flower: calyx-lobes 5; disk-segments 5; stamens 2–6, filaments free or united; anthers dehiscing obliquely or horizontally; pollen grains areolate. Female flower: calyx-lobes 5; disk cupuliform, dissected, or obscure; styles free or connate, branches erect to reflexed. Capsule trigonous, cocci fragile; seeds trigonous, verruculose or (in *P. maleolens*) smooth.

TYPE SPECIES: *Phyllanthus ovatus* Poir.

Geographically, ecologically, and morphologically, sect. *Hemiphyllanthus* is one of the most distinctive groups of West Indian *Phyllanthus.* The bicentric distribution of the section, the representatives of which occur in two widely disjunct areas (southwestern Haiti and the Lesser Antilles), raises most interesting problems regarding the past migrations of the group. All of the six species of the section agree in being rain-forest calciphiles, and they probably all have the palm-like ("schopfbaümchen") habit characteristic of pioneer plants of rain-forest areas. The bipinnatiform branchlets have a distinctive tomentum of reddish multicellular scales except in *P. maleolens*, the branchlets of which are merely incrustate.

The most specialized fern-like Lesser Antillean species, such as *P. mimosoides*, are so distinctive in appearance that they do not appear to belong with any other taxa. However, they can be related (via *P. ovatus*) to the two representatives in Hispaniola, and the latter show a definite resemblance to the Jamaican section *Epistylium*. *Phyllanthus maleolens* of the present section has leaves and stipules similar to those of *P. cauliflorus* in sect. *Epistylium*, and the flowers of *P. maleolens* are rather similar to those of *P. cladanthus*. The most important morphological gap between sects. *Epistylium* and *Hemiphyllanthus* is of course the difference between their pinnatiform and bipinnatiform branchlets. Assuming that there is a close relationship between *P. cauliflorus* and *P. maleolens*, it is easy to suggest a hypothesis of the origin of the bipinnatiform branchlets of sect.

Hemiphyllanthus. If the axillary thyrses which sometimes appear on the branchlets of *P. cauliflorus* were to become thickened, rigid, and leafy, the result would be a bipinnatiform branchlet like that of *P. maleolens,* with leaves on both orders of axes but with flowers confined to the ultimate axes. Whatever the exact course of evolution, it is apparent that the phylogenetic origin of sect. *Hemiphyllanthus* is to be sought within sect. *Epistylium.*

The disjunct distribution of the representatives of sect. *Hemiphyllanthus* is reflected in the distinct morphological differences between the Hispaniolan and Lesser Antillean species-groups, which could be defined as subsections if any formal subdivision were worthwhile. The origin of the section must have been to the west of the Lesser Antilles, possibly in Hispaniola, and the radiation in which *P. mimosoides* has taken the leading part must represent a later burst of evolution. It is notable that in sect. *Hemiphyllanthus,* in contrast to such groups as sect. *Orbicularia,* the species are much more sharply defined, only the most elementary taxonomic judgment being required to distinguish them.

Another aspect of the phylogeny of sect. *Hemiphyllanthus,* certainly of no small interest, is its relationship to sect. *Xylophylla.* It is clear that the compound phylloclade of most representatives of that group is homologous with the bipinnatiform branchlet of the present section; and it is furthermore evident that the two sections are related and that *Hemiphyllanthus* is the less specialized of the two (in vegetative characters, at least). However, this is not the same thing as saying that sect. *Xylophylla* was derived from sect. *Hemiphyllanthus.* As discussed under the former, the relationship of the two sections can perhaps best be stated as one of more or less coördinate origin.

KEY TO THE SPECIES

1. Stipules of branchlets thickened, indurate, and blackish; leaf-blades well-developed on both primary and ultimate branchlet axes; pedicel of female flower slender and terete, 3 mm. long or longer.
    2. Branchlets merely incrustate; leaves coriaceous, shiny above, 10–35 mm. long; stamens 3, filaments free, anthers dehiscing obliquely upwards. . . . . 72. *P. maleolens*
    2. Branchlets reddish-tomentulose; leaves chartaceous, dull above, 4–7 mm. long; stamens 2, filaments connate, anthers dehiscing horizontally. . . . . 73. *P. myriophyllus*
1. Stipules of branchlets scarious, neither indurate nor blackened; leaves of primary branchlet axes reduced to cataphylls; pedicel of female flower thickened and fleshy or else less than 3 mm. long.
    2. Leaves ovate or elliptic, symmetric at base, mostly 30–50 mm. long; styles undivided, united into a column 2.5–3.5 mm. high which is exserted beyond the calyx. . . . . 74. *P. ovatus*
    2. Leaves asymmetric at base, 5–30 mm. long; styles definitely bifid, column shorter and not exserted from calyx.
        3. Pedicel of female flower at anthesis dilated into an incrassate recepta-

cle usually broader than the calyx; styles fused into a massive column higher than the ovary; cataphylls of primary branchlet axis densely tomentulose when young; ultimate axes of branchlet with mostly 15–25 leaves, blades mostly 18–30 mm. long. ..... 75. *P. megapodus*

3. Pedicel of female flower more slender; styles free or shortly connate, spreading or reflexed; cataphylls of primary branchlet axis glabrous; ultimate axes of branchlet with mostly 30–60 leaves (or more), blades 5–13 mm. long.
    4. Pedicel of female flower slender, calyx-lobes 1.5–3 mm. long, spreading; styles spreading; stamens 3; leaves smooth beneath. .... 76. *P. mimosoides*
    4. Pedicel of female flower incrassate above, calyx-lobes not over 1 mm. long, erect; styles reflexed and appressed to outside of calyx; stamens usually 5; leaves minutely scabridulous beneath. .... 77. *P. acacioides*

72. **Phyllanthus maleolens** Urb. & Ekm. Ark. Bot. **22A**(8): 60. 1928. (PLATE XXXI, *figs. A–B*).

Slender tree 2–8 m. high, with unbranched trunk, evil-smelling (fide Ekman); main axis reddish-incrustate. Deciduous branchlets bipinnatiform; primary axis 25–50 cm. long, (2–) 3–4 mm. thick, leafy (but leaves often very soon deciduous), ferruginous-incrustate on younger parts (smoother and greyish in age), terete, with c. 12–30 nodes; first internode c. 3–5 cm. long, median internodes c. 1–3 (–4) cm. long. Leaf-blades of primary axis similar to those on ultimate axes but rather smaller; stipules persistent, more or less spreading or reflexed at the tip, indurate, broadly ovate-triangular (often broader than long), c. 1.5–2.5 mm. long, 1.5–3.5 mm. broad, blunt-tipped, greyish. Ultimate axes ascending, mostly 6–13 cm. long (occasional axes only 3–5 cm. long), c. 1.3–2 mm. broad, reddish brown and incrustate, more or less flattened, sharply wing-angled between the stipules, with 10–25 (–30) leaves; first internode 2.5–5 mm. long, median internodes 3.5–6 mm. long (internodes up to 10–12 mm. long on sterile axes). Leaves: stipules persistent, more or less reflexed, becoming blackish and somewhat indurate, c. 1.2–2.2 mm. long, bluntly pointed, more or less decurrent. Petioles reddish brown, plano-convex, 1–2 (–2.5) mm. long. Leaf-blades subcoriaceous, elliptic or slightly obovate, (10–) 15–35 mm. long, (5–) 10–20 (–25) mm. broad, retuse at the tip (the minute apiculum of young leaves deciduous), symmetrically acute or obtuse at the base; above olivaceous, lucid, the nerves (except the midrib) inconspicuous; beneath paler, yellowish green, the midrib conspicuous and raised, the lateral veins (c. 4 or 5 on a side) raised, somewhat crooked, giving off a few subanastomosing veinlets; margin usually narrowly revolute.

Monoecious; cymules axillary, on ultimate axes of branchlet, bisexual, of 1 female and up to 8 or 10 male flowers; bracteoles thickened and indurate.

Male flower: pedicel slender, 4–7 mm. long. Calyx yellowish, sometimes reddish-tinged; calyx-lobes 5, chartaceous, broadly elliptic or obovate, convex and sometimes cucullate, somewhat unequal, 1.2–1.5 mm. long outer lobes c. 0.75–1 mm. broad, inner lobes c. 1–1.4 mm. broad, rounded at the tip, entire, midrib sparsely branched or unbranched in smallest lobes. Disk-segments 5, suborbicular, entire, slightly thickened, c. 0.25–0.4 mm. broad. Stamens 3; filaments free, up to 0.4–0.5 mm. long or anthers appearing subsessile; anthers ovate, rounded and emarginate at the tip, c. 0.5–0.7 mm. long, 0.6–0.9 mm. broad; anther-sacs subparallel or divergent, dehiscing longitudinally (more or less obliquely), slits apically contiguous but not confluent; pollen grains c. 22.5 μ in diameter, with c. 9–11 polybrochate areoles per amb, germ-pores conspicuous.

Female flower: pedicel 6–10 mm. long, slender, terete below, angled above, straight or curved. Calyx-lobes 5, chartaceous, spreading at anthesis (more or less reflexed in fruit), unequal, oblong to obovate, 1–1.2 mm. long, 0.6–1 mm. broad, obtuse at the tip, entire, midrib inconspicuously branched. Disk somewhat fleshy, 5-angled, crenulate. Ovary oblate, sulcate; styles free or slightly connate at the base, erect, 0.7 mm. high, bifid, sharply bent at the crotch, style-branches somewhat dilated and flattened, one or both toothed or again bifid.

Capsule oblate, trigonous, c. 5 mm. in diameter, dark reddish brown, obscurely rugulose. Columella stout, c. 1.3–1.5 mm. high and nearly as broad. Seeds asymmetrically trigonous (plano-umbonate), c. 2.5–2.7 mm. long, 1.7–2 mm. radially and tangentially, light brown, smooth; hilum submedian, ovoid, partly extending onto the lateral face, c. 0.6–0.7 mm. long and 0.4–0.5 mm. broad.

Collected in flower June-Sept.; in fruit July, Sept.

TYPE: Haiti, *Ekman H6849.*

DISTRIBUTION: mountains, southwestern Hispaniola (Map XXXIII).

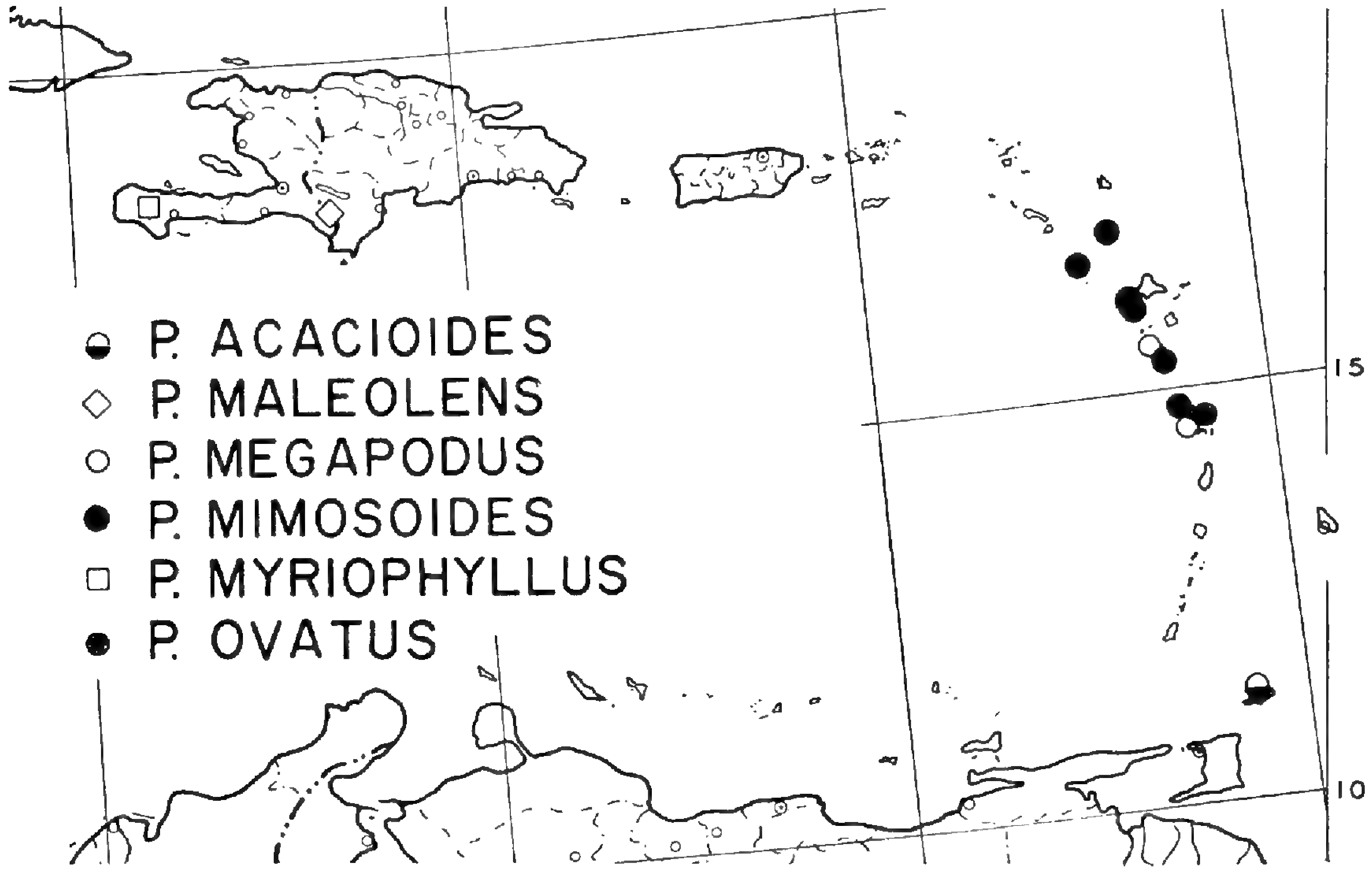
HAITI. OUEST: Morne des Commissaires: Grand-Gosier, Morne Sincilio, alt c. 1300 m., 3 Sept. 1926, *Ekman H6849* (S, HOLOTYPE); Grand-Gosier, Ravine-Fanchon, alt. c. 1675 m., 4 Sept. 1926, *Ekman H6880* (A, S); Boucan Chat, alt. 1600 m., 10 June 1942, *Holdridge 1266* (GH, MO); Mare Sal, alt. 1600 m., 28 July 1942, *Holdridge 1381* (GH, MICH, MO, US).

DOMINICAN REPUBLIC. BARAHONA: Cordillera de Bahoruco, Sierra de los Comisarios, above Gros-Figuier, alt. 1500 m., 29 Sept. 1926, *Ekman H6782* (S).

The offensive odor from which this species takes its name was noted by Ekman only for the plant encountered in Barahona, and was not mentioned by Holdridge. Since the production of a distinct odor by the vegetative part of the plant (Ekman's specimen bears no flowers) is a distinctly unusual, if not unique, character in *Phyllanthus*, Ekman's observation needs to be confirmed. The formation of an unpleasant odor at night has been reported for *P. epiphyllanthus*, but this appears to be associated with flowering.

The citation of specimens from both Hispaniolan republics is somewhat misleading, for the total range of *P. maleolens* is apparently confined to the Morne des Commissaires, and it barely crosses the international line into the Dominican Republic. According to the collectors' notes, the species grows in "Laubwald" (broadleaf forest) on calcareous soil at higher altitudes than those known for any other West Indian species of subg. *Xylophylla*.

The closest relative of *P. maleolens* is certainly its counterpart in the Massif de la Hotte, *P. myriophyllus*. That plant, however, not only differs in its smaller flowers with shorter pedicels, dimerous androecium, and reflexed styles, but vegetatively — by virtue of its smaller leaves and tomentulose axes — resembles the Lesser Antillean species. Distinctly similar to *P. maleolens* in several respects is *P. ovatus* of Martinique, which has however, completely different female flowers with highly modified styles.



MAP XXXIII. Distribution of the species of sect. *Hemiphyllanthus*.

Since in many respects — notably its lack of tomentum, large leaves, free stamens, and unmodified female flower — *P. maleolens* is the least specialized of the members of section *Hemiphyllanthus*, its extra-sectional affinities are of particular interest. There is no doubt that these affinities are all with the Jamaican sect. *Epistylium*, despite the fact that all three species of that group have simply pinnatiform branchlets. Each one of the three species shows some similarity to *P. maleolens*, *P. cauliflorus* in its stipules, *P. cladanthus* in its comparatively long pedicels, and *P. axillaris* in the flattened branchlets. It would appear, therefore, that *P. maleolens* evolved from the common ancestor of the three living species of sect. *Epistylium*.

73. **Phyllanthus myriophyllus** Urb. Ark. Bot. 17(7): 36. 1921. (PLATE XXXI, *figs. C–D*).

Slender shrub or tree c. 2–3 m. high, with unbranched trunk. Deciduous branchlets bipinnatiform; primary axis 30–80 cm. long, 3–4 mm. thick, leafy (leaves subpersistent), densely scurfy with ferruginous tomentum (becoming glabrate on older parts), terete, with 40–110 nodes; first internode 10–25 mm. long, median internodes 5–10 mm. long. Leaf-blades of primary axis precisely as on ultimate axes; stipules at first broadly triangular and reddish brown, c. 1.5–2.5 mm. long, the tip deciduous, the blackish, massive, indurate base persistent, c. 1.5–2.5 mm. broad. Ultimate axes ascending or spreading, (5–) 7–14 cm. long, 0.7–1 mm. broad, chestnut-brown, conspicuously fluted with obtuse ribs decurrent from the stipule-bases, tomentulose between the ribs with simple pale to dark ferruginous hairs, with 25–70 leaves; first internode c. 1 mm. long, median internodes 1.5–2.5 mm. long. Leaves: stipules persistent, decurrent at the base, at first ovate-lanceolate and c. 1 mm. long (with denticulate margin), later the tip inflexed and base incrassate, blackish, indurate, c. 0.7–1 mm. broad. Petioles reddish-brown, 0.3–0.4 mm. long. Leaf-blades firmly chartaceous, smooth on both sides, broadly elliptic-oblong or ovate-oblong, (4–) 5–7 mm. long, (2.5–) 3–4.5 mm. broad, obtuse or bluntly apiculate at the tip, symmetrical and obtuse to truncate or subcordate at the base; above dark olivaceous, dull, the nerves completely obscure or the plane midrib visible; beneath pale green, lucid, the midrib raised, the lateral veins (c. 4 or 5 on a side) ascending, inconspicuous, veinlets not visible; margins slightly thickened and subrevolute.

Apparently monoecious (possibly sometimes dioecious); cymules axillary, on ultimate axes of branchlet, the proximal with 3–5 male flowers, the distal with some male and some bisexual cymules (each of the latter with a single female flower).

Male flower: pedicel capillary, 2–4 mm. long. Calyx yellowish white; calyx-lobes 5, thin and scarious, obovate or suborbicular, unequal, c. 1–1.2 mm. long, 0.7–1.1 mm. broad (the outer narrower), obtuse or acute, entire or obscurely crenulate, midrib simple or sparsely branched. Disk-segments 5, oval, thin and flattened, entire, c. 0.25 mm. across. Stamens 2; filaments connate into a column c. 0.3 mm. high; anthers subsessile, broadly ovate, rounded and minutely emarginate at the tip, c. 0.3 mm. long and 0.5 mm. broad; anther-sacs divergent, dehiscing more or less horizontally, the slits not apically confluent; pollen grains c. 16–18 μ in diameter, with c. 5–7 polybrochate areoles per amb.

Female flower: pedicel 3–3.5 mm. long at anthesis, slender, only very slightly and gradually broadened upwards, terete, smooth, reddish brown. Calyx yellowish white; calyx-lobes 5, membranous, more or less spreading, unequal: outer lobes obovate-oblong c. 1 mm. long and 0.6–0.7 mm. broad; inner lobes suborbicular, c. 1.2 mm. long and broad; lobes entire, midrib unbranched. Disk conspicuous, fleshy, 5-angled, crenulate. Ovary oblate, shallowly sulcate; styles slightly connate at the base, flattened, dilated, c. 0.7 mm. long, parted c. ¾ to ⅘ their length, the branches reflexed over the ovary (but remaining inside the outspread calyx), tapering to acute tips. Fruit unknown.

Collected in flower May, Nov.

TYPE: Haiti, *Ekman H140.*

DISTRIBUTION: mountains, western end of southern peninsula of Haiti (MAP XXXIII).

HAITI. SUD, Massif de la Hotte: along stream, northwest slopes, montane forest, alt. c. 800 m., 10 May 1917, *Ekman H140* (S. HOLOTYPE); Camp-Perrin, northern slope of Morne Vandervelde, in "Jardins Coutard", laterites on eruptive, alt. c. 900 m., 29 Nov. 1925, *Ekman H5185* (S, US); Pestel, rocky ridge of M. Delcour, alt. 1000 m., 27 Aug. 1927, *Ekman H9007* (S).

Not only is *P. myriophyllus* interesting as yet another example of the remarkable endemism of the Massif de la Hotte, but it is phylogenetically significant in being transitional between the large-leaved species *P. maleolens* and the "mimosoid" species of the Lesser Antilles. It seems unlikely, however, that *P. myriophyllus* can be regarded as directly ancestral to *P. mimosoides* or its relatives; it rather illustrates a parallel reduction in leaf-size to that which can be traced from *P. ovatus* to the small-leaved Antillean species.

74. **Phyllanthus ovatus** Poir. in Lam. Encycl. Method **5**: 297. 1804 (as *P. ovata*); Muell. Arg. in DC. Prodr. **15**(2): 323. 1866. (PLATE XXXI, *figs. E–F*).

Phyllanthus grandifolius sensu Spreng. Syst. Veg. **3**: 22. 1826; non L.
Glochidion ovatum (Poir.) Muell. Arg. Linnaea **32**: 71. 1863; Pax & Hoffm. Natürl. Pflanzenfam. **19c**: 58. 1931.
Diasperus ovatus (Poir.) O. Ktze. Rev. Gen. **2**: 600. 1891.

Shrub 1–4 m. high, with usually unbranched trunk; stem ferruginous-tomentulose at the apex, becoming more or less glabrate below. Cataphylls inconspicuous, indurate, very similar to those of main axis of branchlet. Deciduous branchlets bipinnatiform; primary axis (8–) 10–25 cm. long, c. 2.5–3 mm. thick, distally ferruginous-tomentulose, proximally sparsely hairy or glabrate, subterete, with 10–20 (–35) leaves; first internode 20–60 mm. long, median internodes mostly 10–20 mm. long. Leaves of primary axis reduced to cataphylls: stipules persistent, spreading or somewhat reflexed, indurate, ovate-triangular, 1–2 mm. long, 1.3–2.3 mm. broad, obtusely pointed, brownish or greyish; blade narrower, 1–1.2 mm. long. Ultimate axes ascending, when well developed c. 5–15 cm. long, 1–1.5 mm. broad, olivaceous, angled or somewhat flattened, smooth and glabrous, with mostly 5–20 (–30) leaves; first internode mostly 5–15 mm. long, median internodes mostly 5–20 mm. long. Leaves: stipules persistent, sometimes reflexed, indurate, triangular-lanceolate, mostly 1–1.5 mm. long, acuminate, entire. Petioles not sharply set off from blade, c. 0.5–1.5 mm. long. Leaf-blades chartaceous, smooth on both sides, symmetrically or asymmetrically elliptic or ovate, mostly 30–50 mm. long and 20–35 mm. broad, sometimes (especially on distal part of branchlet) only 15–30 mm. long and 10–20 mm. broad, acute or subacute at the tip, acute or obtuse at the base; above olivaceous or plumbeous, minutely foveolate, midrib incised and prominent but other veins obscure; beneath paler, more or less smooth, the midrib conspicuous and raised, the lateral veins (c. 5–7 on a side) somewhat raised, ascending, straight, veinlets obscure; margins unthickened, plane or narrowly recurved.

Monoecious; cymules axillary, on ultimate axes of branchlet; proximal cymules male and distal ones bisexual (of 1 female and c. 6–8 male flowers), or all bisexual.

Male flower: pedicel thickened upwards, 1.5–3.5 mm. long. Calyx drying reddish brown; calyx-lobes 5 (rarely 6), chartaceous, oblong-obovate to suborbicular, subequal, c. 1.5–1.8 mm. long, 1.1–1.6 mm. broad, obtuse or rounded at the tip, entire with narrow pale scarious margins, midrib unbranched. Disk-segments 5, more or less reniform, entire, somewhat thickened, inconspicuously pitted, c. 0.4–0.6 mm. across. Stamens 3 (rarely 4); filaments completely connate into a column c. 0.4–0.6 mm. high; anthers sessile atop the column, fused by their connectives (androecium plane on top, 3-lobed), triangular-ovate, obtuse, c. 0.4–0.6 mm. broad; anther-sacs discrete, divergent, dehiscing horizontally; pollen grains c. 22–25 μ in diameter, with c. 15 oligobrochate areoles per amb.

Female flower: subsessile at anthesis, the thick fleshy obpyramidal pedicel lengthening in fruit up to 1.5–2.2 mm. long. Calyx-lobes 5, coriaceous, erect at anthesis (spreading or reflexed in fruit) strongly imbricate, more or less unequal, ovate or elliptic, 2–2.7 mm. long, 1.5–2.5 mm. broad, obtuse at the tip, midrib apparently unbranched. Disk somewhat fleshy, crenulate or notched, dark reddish brown. Ovary oblate; styles completely united into a thick fleshy urn-shaped column c. 2.5–3.3 mm. high (far exceeding the ovary); stigmas (undivided style-tips) triangular, obtuse, more or less spreading, subentire, c. 0.4–0.7 mm. long.

Capsule not seen entire; valves c. 4 mm. long, dark reddish brown, not veiny. Columella 2.7 mm. long. Seeds (not seen fully mature) somewhat asymmetrically trigonous, c. 4 mm. long and 2.5 mm. radially and tangentially, light brown with irregular rows of slightly raised dark reddish-brown dots; hilum ovate-triangular.

Collected in flower Feb., Mar., July, Aug.; in fruit, Feb., July.

TYPE: Martinique, *Herb. Poiret.*

DISTRIBUTION: forested regions, Martinique (MAP XXXIII).

MARTINIQUE: without specific locality, *Herb. Lamarck* (G, P); *Herb. Poiret* (P, TYPE COLLECTION); *Sieber Fl. Martin. 224* (F, GOET, MO, P, W); Hauteurs de la Grand-Rivière, de Case-Pilote, Morne-Rouge, 1880, 1899, *Duss 53* (F, GH, MO, NY, US), *4057* (NY, US); Hauteur de la Case-Pilote, July 1870, *Hahn 323* (K, P); Case-Naoire, collines peu buisées, Feb. 1868, *Hahn 406* (A, G, P); same locality, Feb. 1869, *Hahn 643* (P); taillis a lisiers forestiers et alturales, Morne Vert, Bernadette, alt. 560 m., 17 July 1942, *Stehlé 5065* (F).

In its occurrence in moist forested regions of northern Martinique, *P. ovatus* conforms with the ecological preference of other species of the section. According to Stehlé it is found at the margin of the forest, and is thus heliophilous as well as mesophytic. The species is certainly very distinct but is perhaps most closely related to *P. maleolens,* from which it differs in its tomentulose axes, thinner more pointed leaves, thickened female pedicel, and connate nearly entire styles. Also related to *P. ovatus* is *P. megapodus,* which has somewhat similar female flowers but which vegetatively is much closer to *P. mimosoides* and *P. acacioides.*

As was pointed out previously (Contr. Gray Herb. 176: 62. 1955), the referral of *P. ovatus* to *Glochidion* by Pax and Hoffman on the basis of its undivided styles is unjustified, since it contradicts all other indications of affinity. Mueller was correct in reversing himself as to the generic disposition of this species, even though he did not place it in the proper circle of relationship. There is indeed a certain similarity between the stylar column of *P. ovatus* and the much shorter one of *P. botryanthus* (the species associated with it by Mueller), but the two species are only distantly related, and the gynoecial resemblance must be ascribed to parallel evolution.

75. **Phyllanthus megapodus** Webster, Contr. Gray Herb. 176: 62–63. 1955. (PLATE XXXI, *figs. G–H*).

Phyllanthus mimosoides [lusus] *macrophyllus* Muell. Arg. in DC. Prodr. **15**(2): 381. 1866; non *Phyllanthus macrophyllus* Muell. Arg. Flora **1865**: 370. 1865.

Shrub or small tree up to 3–5 m. high, presumably with the habit of *P. mimosoides.* Cataphylls indurate, densely tomentulose: stipules and blade triangular-lanceolate, recurving, c. 2.5–3 mm. long. Deciduous branchlets bipinnatiform; primary axis 20–40 cm. long, 2–3 mm. thick, sparsely tomentulose and soon glabrate, smooth, terete, with (6–) 10–18 nodes; first internode 50–130 mm. long, median internodes mostly 15–40 mm. long. Leaves of primary axis reduced to cataphylls: stipules persistent, appressed or reflexed, subindurate, triangular-lanceolate, c. 2.5–4 mm. long, 1.5–2.5 mm. broad, acuminate (but tip often broken off), auriculate at the base, densely reddish-tomentulose (when young; more or less glabrate in age); blade lanceolate, usually spreading or reflexed, reddish-tomentulose, c. 2–3 mm. long. Ultimate axes ascending, (5–) 7–15 (–18) cm. long, 0.8–1.3 mm. broad, olivaceous or stramineous, flattened ventrally (above) and angular-convex dorsally (beneath), with ribs decurrent from stipules on both sides, smooth and glabrous, with (13–) 15–25 (–27) leaves; first internode (1–) 3–7 mm. long, median internodes 4–9 mm. long. Leaves: stipules more or less deciduous, not reflexed, scarious, lanceolate, c. 1–1.8 mm. long, reddish, more or less ciliate at apex and on margins (tomentulose when young), decurrent at the base. Leaf-blades subsessile (petioles ill-defined, c. 0.5 mm. long or less), chartaceous, smooth on both sides, asymmetrically broadly oblong or obovate, subfalcate, (12–) 18–30 mm. long, (5–) 8–15 mm. broad, obtuse or rounded and apiculate at the tip, at base oblique on adaxial side; above olivaceous, minutely foveolate, veins inconspicuous; beneath midrib conspicuously raised, lateral veins (c. 7 or 8 on a side) straight and slightly raised, veinlets completely obscure; margins not especially thickened, plane or recurved.

Monoecious; cymules axillary, on ultimate axes of branchlet; proximal cymules with 1–5 male flowers; distal cymules either male or of a solitary female flower, or sometimes bisexual (with 1 female and 1 or 2 male flowers).

Male flower: pedicel slender, 3–5 mm. long. Calyx whitish; calyx-lobes 5, membranous, somewhat spreading, broadly elliptic to obovate, subequal, c. 1.8–2.5 mm. long, 1.3–2.1 mm. broad, obtuse or rounded at the tip, entire, midrib unbranched. Disk-segments 5, roundish, rather thin, entire, c. 0.3–0.5 mm. across. Stamens 3; filaments connate into a column c. 0.5–0.8 mm. high; anthers subsessile atop the column, discrete, emarginate, c. 0.3 mm. long and 0.6–0.7 mm. broad; anther-sacs spheroidal, divaricate, dehiscing horizontally, slits not apically confluent; pollen grains c. 21–24 μ in diameter, with c. 15 areoles per amb.

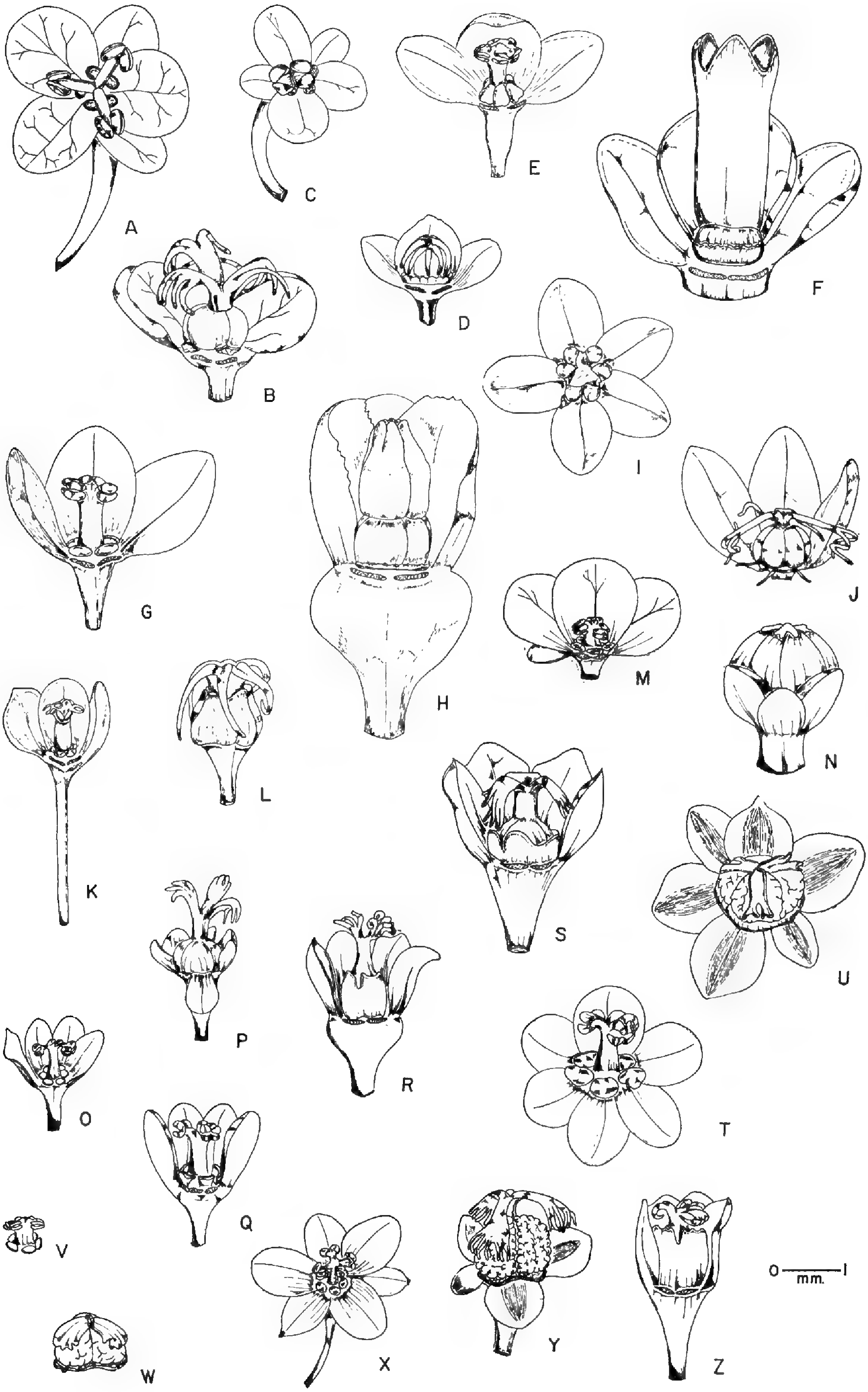
Female flower: pedicel at anthesis c. 1.5–2 mm. long, terete and slender at the very base but above greatly dilated, obpyriform, fleshy, as broad as or broader than the calyx; fruiting pedicel c. 3–4 mm. long and 1.3–2.2 mm. broad (when dried). Calyx-lobes 5, thick and fleshy, at anthesis stiffly erect and imbricate-connivent around the ovary, elliptic to ovate (becoming obovate-oblong in fruit), c. 1.8–2.5 mm. long and 1.2–2 mm. broad, obtuse at the tip, entire, midrib unbranched. Disk nearly obsolete (scarcely 0.1 mm. high, or less, with 5 small points alternating with the calyx-lobes). Ovary oblate-spheroidal, smooth; styles erect, united into a massive column c. 2 mm. high and nearly as broad; style-branches reduced to blunt apical projections or becoming up to 1 mm. long.

Capsule not seen entire; valves c. 5.5 mm. long. Columella massive,

---

PLATE XXXI. MALE AND FEMALE FLOWERS OF SECT. *Hemiphyllanthus* AND SECT. *Xylophylla.*

FIGS. A–B. *Phyllanthus maleolens* Urb. & Ekm. (*Ekman H6849* [S]). FIGS. C–D. *Phyllanthus myriophyllus* Urb. (*Ekman H5185* [S]). FIGS. E–F. *Phyllanthus ovatus* Poir. (*Duss 53* [GH]). FIGS. G–H. *Phyllanthus megapodus* Webster (male flower, *Hodge & Hodge 2841* [GH]; female flower, *Sieber 396* [MO]). FIGS. I–J. *Phyllanthus mimosoides* Sw. (*Hodge & Hodge 3439* [GH]). FIGS. K–L. *Phyllanthus acacioides* Urb. (*Broadway 4189* [MO]). FIGS. M–N. *Phyllanthus montanus* (Sw.) Sw. (*Proctor 11594* [GH]). FIGS. O–P. *Phyllanthus latifolius* Sw. (*Webster 4875* [A]). FIGS. Q–S. *Phyllanthus arbuscula* (Sw.) Gmel. Q–R, male and female flowers of Race A (*Harris 9191* [US]). S, female flower of Race C (*Stearn 387* [JAM]). FIGS. T–U. *Phyllanthus angustifolius* (Sw.) Sw. (*Webster 5558* [A]). FIGS. V–W. *Phyllanthus proctoris* Webster (*Macfadyen* [K]). FIGS. X–Z. *Phyllanthus epiphyllanthus* L. X–Y, male and female flowers of ssp. *epiphyllanthus* (*Nash & Taylor 875* [NY]). Z, female flower of ssp. *dilatatus* (Muell. Arg.) Webster (*Ekman 10271* [S]).



WEBSTER, WEST INDIAN PHYLLANTHUS

2–2.8 mm. long. Seeds (not seen mature) slightly over 3 mm. long, with evenly spaced slightly raised reddish-brown dots.

TYPE: Martinique, *Sieber Fl. martin. 396.*

DISTRIBUTION: Dominica and Martinique, probably in upper montane rain-forest (MAP XXXIII).

DOMINICA: forest clearings or along river, Fon Pays, a lesser peak of the western ridge of Morne Diablotin, alt. c. 1000 m., 14 Apr. 1940, *W. & B. Hodge 2841* (GH); forest, Hampstead, 1903, *Lloyd 640* (F, NY).
MARTINIQUE: *Sieber Fl. martin. 396* (W, HOLOTYPE; BR, G, L, MO, P, ISOTYPES).

In Dominica *P. megapodus* is apparently a rare plant of the upland rain forests, where it appears to replace the much more common lowland species, *P. mimosoides*. It is not yet clear, however, whether the replacement is so complete that the two species are allopatric. The record from Martinique requires confirmation, since it is not certain that all the plants distributed by Sieber under the "Flora Martinicensis" or "Flora Trinitatis" labels were actually collected on those two islands. Of course, if *P. megapodus* is as uncommon on Martinique as on Dominica it may have escaped detection since the visit of Sieber's collector, Kohaut.

Although in aspect it resembles *P. mimosoides* so markedly that Mueller interpreted it as merely a large-leaved form, *P. megapodus* has very different female flowers which are much more like those of *P. ovatus*. Vegetatively *P. megapodus* is well distinguished from *P. mimosoides* having fewer than 20 ultimate axes per branchlet instead of 30–60 or more, tomentulose branchlet cataphylls, and larger leaves. From *P. ovatus, P. megapodus* differs in its non-exserted stylar column, smaller asymmetrical leaves, and especially in its hypertrophied female pedicel. In the last feature *P. megapodus* appears to represent the generic extreme, although it is somwhat approached by the thickened pedicel of *P. acacioides*.

76. **Phyllanthus mimosoides** Sw. Prodr. 27. 1788; Fl. Ind. Occ. 1101–1102. 1800; Muell. Arg. in DC. Prodr. **15**(2): 380–381. 1866. (PLATE XXXI, *figs. I–J*).

Diasperus mimosoides (Sw.) O. Ktze. Rev. Gen. **2**: 600. 1891.

Shrub c. 1–5 m. high, with a slender usually unbranched trunk and a terminal crown of leafy branchlets; stem apex ferruginous-tomentulose, older parts glabrate. Cataphylls indurate: stipules triangular, recurving, c. 2–2.5 mm. long, becoming acropetally displaced to flank the base of the branchlet; blade c. 1.5 mm. long. Deciduous branchlets bipinnatiform; primary axis (20–) 30–70 (–100) cm. long, 2–4 mm. thick, more or less ferruginous-tomentulose (proximally becoming glabrate), terete, with (20–) 30–60 (–100) nodes; first internode (25–) 40–100 (–130) mm. long, median internodes (5–) 7–15 (–20) mm. long. Leaves of primary axis reduced to cataphylls: stipules persistent, not reflexed, more or less indurate, lanceolate, (2–) 2.5–4 mm. long, 0.7–1.3 mm. broad, acuminate, stramineous or reddish, with a dark sharply demarcated subtriangular fleshy basal area; blade thinner, scarious, linear-lanceolate, attenuate-acuminate, sometimes obscurely marginally ciliate below, mostly 2–3.5 mm. long and 0.2–0.5 mm. broad. Ultimate axes ascending, (3–) 5–10 (–12) cm. long, 0.5–0.9 mm. broad, olivaceous, flattened and angled with sharp ridges decurrent from stipules, smooth and glabrous (except for one or few tufts of hairs often present on internodal part of dorsal ridge), with (20–) 30–60 (–80) leaves; first internode c. 1–1.5 (–2) mm. long, median internodes c. 1–3 mm. long. Leaves: stipules persistent, not reflexed, scarious, lanceolate, mostly 1–1.5 (–1.8) mm. long, acuminate, decurrent at the base (adaxial margin running down center of the axis as a ridge). Leaf-blades subsessile (petioles only 0.2–0.4 mm. long), thinly chartaceous, smooth on both sides, asymmetrically oblong or oblong-obovate and often falcate, c. 5–11 (–13) mm. long, 2–4 (–6) mm. broad, mostly rounded or subtruncate and apiculate at the tip, at base abruptly oblique on adaxial side and straight on abaxial side; above olivaceous, minutely foveolate, veins obscure; beneath pallid, midrib slightly raised and running out into apiculum, lateral veins (4–6 on a side) ascending, straight, inconspicuous or quite obscure; margins unthickened, plane or slightly revolute.

Monoecious; cymules axillary, on ultimate axes of branchlet; proximal cymules with usually 1 or 2 male flowers; distal cymules male or a few with a single female flower, this solitary or accompanied by 1 or 2 males; bracteoles fimbrillate.

Male flower: pedicel capillary, 1–3.5 mm. long. Calyx whitish; calyx-lobes 5, thin and scarious-membranous, spreading, oblong-elliptic to broadly elliptic (outer lobes narrower), (0.8–) 1–1.5 mm. long, c. 0.5–1.3 mm. broad, obtuse at the tip, entire, midrib unbranched (or branches very obscure), usually somewhat raised on ventral surface. Disk-segments 5, roundish, flattened, smooth, entire, c. 0.2–0.3 mm. across. Stamens 3; filaments connate into a stout or slender column 0.2–0.8 mm. high; anthers subsessile atop the column, discrete, very broadly ovate, obtuse, emarginate, 0.2–0.3 mm. long, 0.3–0.6 mm. broad; anther-sacs divaricate, dehiscing horizontally, the slits apically contiguous, discrete or confluent; pollen grains 16–18 μ in diameter, with c. 7–10 polybrochate areoles per amb.

Female flower: pedicel scarcely evident at anthesis, in fruit becoming 0.5–1.5 (–2) mm. long, smooth, terete, not markedly dilated above. Calyx whitish; calyx-lobes 5, thin and membranous or scarious, spreading from anthesis onwards, subequal, elliptic-oblong to obovate or spathulate, c. 1.5–2.5 mm. long (or up to 3 mm. long in fruit), 0.4–1.5 mm. broad, obtuse and entire at the tip, midrib unbranched. Disk divided into 5 reddish-brown linear to filiform segments 0.2–0.5 mm. long (or the smaller one or two reduced to short points). Ovary spheroidal, deeply sulcate; styles united below into a column 0.3–0.8 mm. high (or sometimes nearly free), ascending or spreading, the free ends c. 1.5–2 mm. long, divided ½ to 4/5 their length into two slender divergent, often twisted terete branches with bluntly pointed tips.

Capsule oblate-spheroidal, c. 4–5 mm. in diameter, olivaceous or dark reddish-brown, not veiny. Columella slender, 1.2–2.5 mm. long. Seeds trigonous, sometimes rather asymmetric, 1.5–2.5 mm. long, 1.2–2 mm. radially and tangentially, light brown with evenly spaced slightly raised reddish-brown dots; hilum rounded-triangular, 0.7–1 mm. across.

Collected in flower Feb.–Oct.; in fruit Feb.–Aug.

TYPE: Antigua, *de Ponthieu* (ex Swartz, 1788). The type collection is probably represented by the Ponthieu collection in the herbarium of the Conservatoire Botanique (G), and by a fragment in Swartz's herbarium (S); but neither of these has any definite indication of locality. A sheet collected by Ponthieu on Dominica and cited by Swartz in the "Flora Indiae Occidentalis" was examined at the British Museum; but this can hardly be considered the type. Since the sheet at Geneva has been annotated as "peut-etre l'echantillon dulequel Swartz a fait la description" and since it is a more ample specimen than that at Stockholm, it is here chosen as the lectotype.

DISTRIBUTION: rain-forest areas, Lesser Antilles (MAP XXXIII).

ANTIGUA: *de Ponthieu* (G, LECTOTYPE; S, ISOTYPE; both presumably from Antigua).

MONTSERRAT: *Ryan* (BM, C); Fergus Mountain, *Shafer 340* (F, NY); *West* (W).

GUADELOUPE: without specific locality, *Duchassaing* (C, GOET, P), *L'Herminier* (P), *Perrottet* (G), *Quentin 389* (P), *Richard* (P); Bassin Bleu, *Duss 208* (P); Bois des Bains-Jaunes, du Matouba, de Bouillante, etc., alt. 450–990 m., *Duss 2445* (F, GH, NY, US); Matouba, *Forsstrom* (S); Sofaya, above Ste. Rose, alt. 700 m., *Holdridge 449* (NY); Ste. Rose, alt. 20 m., *Questel 852* (US); Plateau du Palmiste, *Rodriguez 4669* (A, P); mornes basaltiques, Honelmont, *Stehlé 205* (US); hauteurs de Vernon, Petit-Bourg, alt. 450 m., *Stehlé 266* (A, S, US); Comperon près Font arabe, alt. 200 m., *Stehlé 2630* (US).

DOMINICA: without specific locality, *Bryant* (NY), *Fishlock 35* (NY), *Imray 315* (GOET), *de Ponthieu* (BM), *Ramage* (BM); St. Hilaire Trace, alt. 300 m., *J. S. Beard 645* (A, US), *P. Beard 1460* (S); Sugarloaf prope Prince Ruperts, *Eggers 770* (G, GOET, P, W), *1064* (US); bank of St. Mary's River, at mouth of Pegoua River, Hatton Garden Estate, near sea level, *W & B. Hodge 3075* (GH); along stream 1 mile north of Calibishie, *W. & B. Hodge 3172* (GH); Carib trail from Salybia to Hatton Garden, *W. Hodge 3219* (GH); Pegoua River, Deux Branches, Concorde Valley, *W. & B. Hodge 3439* (GH); Hampstead River, c. 2 miles from mouth, La Chaudière, alt. 100 m., *W. & B. Hodge 3558, 3662* (GH).

MARTINIQUE: dans le haut de la rivière de la Grande-Rivière, *Duss 2045* (NY).

TRINIDAD: *Sieber Fl. Trinitatis 153* (MO, P, W).

By far the commonest and most widespread species of the section, *P. mimosoides* is apparently the only one which has been taken into cultivation, where it has attracted the interest of morphologists; illustrations showing its distinctive habit have been published by Goebel (Organogr. Pflanz. 84. 1898) and Troll. The species is abundant on Guadeloupe, where it is called "batard de fougere", and Dominica, where it is referred to as "tamarind grand bois". According to Beard (Nat. Veg. Windward & Leeward Isl. 106. 1949) it forms an extensive ground stratum in the secondary rain-forest on Montserrat. On Martinique, in contrast, Duss (Fl. Phanerogam. Ant. Fr. 23. 1897) found it very rare; and the species has presumably become extinct on Antigua. The record of Wickström (Kgl. Vet. Acad. Handl. [Stockholm] **1825**: 423. 1826) from St. Barthélemy, based on a Forsstrom collection, is surely erroneous and perhaps was based on misdetermined specimens of *P. amarus* which are preserved in the Riksmuseet, Stockholm. One would in any event not expect a mesophytic species such as *P. mimosoides* to occur on a low barren island such as St. Barthélemy. The collection from Trinidad, *Sieber 153*, offers greater difficulties. It is possible that this record is correct, but unless the collection was made from a cultivated plant it represents a remarkable range extension. The failure of subsequent collectors to encounter the plant on Trinidad suggests that Sieber's locality may be erroneous, and in any event the record needs confirmation.

In view of its wide distribution, it is not surprising that *P. mimosoides* is a rather variable species; the populations on each island tend to be somewhat different from those on neighboring islands. The plants of Dominica are perhaps the most divergent, differing from those of Guadeloupe and Montserrat in their somewhat larger leaves, flowers, and seeds. Some characters, such as the size of male flowers and degree of stylar union, appear to be intrinsically variable in all populations. However, even those which show some geographical correlation are not sufficiently well-marked to justify the recognition of subspecific taxa.

Although *P. acacioides* is vegetatively quite similar to *P. mimosoides*, its female flowers (as noted in the key) are so different that there can be no doubt the two species are perfectly distinct. There is also an obvious resemblance between *P. mimosoides* and *P. megapodus*, but the latter is not only vegetatively different but also has female flowers which are even more dissimilar than are those of *P. acacioides*. It is possible that the larger size of vegetative and floral parts in the Dominican population of *P. mimosoides* may be partly attributable to hybridization with *P. megapodus*, although there is no direct evidence for this, but in any event this would not prove that *P. megapodus* is the most closely related species. The sum of the evidence would appear to suggest that *P. mimosoides* is closest to *P. acacioides* in morphological characters, but is distinctly isolated even from that species.

77. **Phyllanthus acacioides** Urb. Symb. Ant. 3: 287–288. 1902. (PLATE XXXI, *figs. K–L.*)

Slender shrub with habit of *P. mimosoides*, up to 4 m. high; stem densely reddish-tomentulose near apex, glabrate below. Cataphylls indurate: stipules triangular, appressed, acuminate, c. 2 mm. long; blade lanceolate, convex, nearly 2 mm. long. Deciduous branchlets bipinnatiform; primary axis c. 30–50 cm. long, 1.5–2 mm. thick, reddish- or purplish-tomentulose, becoming more or less glabrate, scabridulous, terete, with c. 40–70 nodes; first internode 15–25 mm. long, median internodes 5–9 mm. long. Leaves of primary axis reduced to cataphylls: stipules persistent, not reflexed, more or less indurate, triangular or triangular-lanceolate, c. 1.2–1.8 mm. long, 1–1.7 mm. broad, acuminate, stramineous or reddish, entire and glabrous, with dark fleshy basal area as in *P. mimosoides*; blade about as long as stipules, lanceolate, long-acuminate, strongly convex on back. Ultimate axes ascending, 5–11 cm. long, 0.5–0.6 mm. broad, purplish-brown to olivaceous, more or less flattened and bluntly angled with ridges decurrent from the stipules, glabrous (occasionally with a few deciduous tufts of hair proximally), usually scabridulous, with 35–60 leaves; first internode 1.5–2.5 mm. long, median internodes 1.5–3 mm. long. Leaves: stipules persistent, not reflexed, scarious, lanceolate, 1–1.3 mm. long, 0.2–0.3 mm. broad, acuminate, marginally ciliate when young (otherwise glabrous), adaxially decurrent at the base. Petioles 0.3–0.5 mm. long. Leaf-blades subchartaceous, asymmetrically oblong- or obovate-falcate, c. 6–11 mm. long, 2–4 mm. broad, obtuse or abruptly subacute at the tip (apiculum more or less deciduous), at base oblique on adaxial side and straight on abaxial side; above olivaceous, smooth, veins obscure; beneath pallid (albescent), finely and densely scabridulous, midrib raised and running to tip, lateral veins obscure; margins somewhat thickened, plane or reflexed.

Monoecious; cymules axillary, on ultimate axes of branchlet; cymules mostly bisexual, of 1 female and 1 or 2 male flowers, but perhaps sometimes unisexual; leaves subtending flowers at branchlet tip sometimes reduced to scales.

Male flower: pedicel capillary, c. 2.5–5 mm. long. Calyx-lobes 5, chartaceous, elliptic or obovate, c. 1–1.3 mm. long, 0.7–1 mm. broad, obtuse or rounded at the tip, entire, midrib unbranched. Disk-segments 5, roundish to cuneate, somewhat fleshy, smooth, entire, c. 0.25–0.4 mm. across. Stamens usually 5 (rarely 4 or 6); filaments completely connate into a stout column 0.3–0.5 mm. high; anthers subsessile, one or two slightly displaced in rare androecia of 6 stamens, anthers in two superposed whorls, discrete, ovate, obtuse, c. 0.2 mm. long, 0.2–0.3 mm. broad; anther-sacs divaricate, flattened, dehiscing horizontally, slits apically contiguous but discrete; pollen grains c. 13–14 μ in diameter, with c. 5 or 6 polybrochate areoles per amb.

Female flower: pedicel c. 0.7–1.3 mm. long at anthesis, broadly dilated above. Calyx-lobes 5, thick and fleshy, at anthesis stiffly erect and imbricate-connivent around the ovary, broadly elliptic or ovate to suborbicular, c. 0.5–0.8 mm. long and broad, rounded at the tip, entire, midrib unbranched. Disk nearly obsolete (reduced to a tenuous ring with minute projections at angles). Ovary smooth, subspheroidal; styles united at the base into a very short and stout column, bifid c. 4/5 their length, in bud erect and slightly protruding above the calyx, at maturity greatly elongating; stylar branches flattened, becoming 2–2.5 mm. long, tapering from base to the acute tips, sharply reflexed on outside of calyx.

Capsule not seen entire; valves c. 3 mm. long, reddish-brown. Seeds trigonous, c. 1.5 mm. long, light brown.

TYPE: Tobago, *Eggers 5840.*

DISTRIBUTION: endemic to Tobago (MAP XXXIII).

TOBAGO: near Lot 42, shaded cool places, 21 Apr. 1913, *Broadway 4189* (F, G, GH, MO, W); in sylvis Montis Morne d'or, alt. 500 m., *Eggers 5840* (K, LECTOTYPE); St. George–Castara Road, 27 May 1930, *Marshall* (TRIN 12384).

Broadway described this plant as a gregarious single-stemmed shrub with the appearance of *Jacaranda caerulea* and growing in shaded cool places. The female flowers are remarkable for the great change in stylar configuration associated with anthesis; in the bud the styles are erect and protrude slightly above the calyx, but at anthesis they elongate greatly and recurve abruptly so that they are appressed to the outside of the rather fleshy calyx.

Although not all the diagnostic characters cited by Urban are dependable, *P. acacioides* clearly differs from *P. mimosoides* not only in its distinctive styles but also in its reduced female disk, pentamerous androecium, and whitened scabridulous undersurface of leaf-blade. Because of its distribution, *P. acacioides* might be taken for an outlying species derived from a disjunct population of *P. mimosoides.* However, the fact that the female flower of *P. acacioides* shows a greater resemblance to that of *P. ovatus* than it does to that of its "sister" species shows that great caution must be observed in proposing phylogenetic speculations. Thus although *P. mimosoides* is overall the species most similar to *P. acacioides*, it should not be regarded as necessarily its direct ancestor.

Sect. 24. **Xylophylla** (L.) Baill. Etud. Gen. Euphorb. 623. 1858.

Xylophylla L. Mant. 2: 147–148. 1771.
Genesiphylla L'Hérit. Sert. Angl. 29. 1778.
Hexadena Raf. Sylva Tellur. 92. 1838.
Lomanthes Raf. ibid.
Phyllanthus b. *Xylophylla* Endl. Gen. Pl. 1120. 1840 (without indication of rank).
Phyllanthus sect. *Typophyllanthus* subsect. *Genesiphylla* (L'Hérit.) O. Ktze. Lex. Gen. Phaner. 434. 1904.

Shrubs or small trees with phyllanthoid branching; axes smooth and glabrous; cataphylls of main stem indurate, clustered at the apex in a scaly cone; branchlets bipinnatiform with ultimate axes transformed into usually leafless phylloclades, or (in *P. epiphyllanthus*) entire branchlet converted into phylloclade; nodes represented by marginal notches, leaves usually all reduced to scales, occasionally well-developed. Monoecious;

cymules unisexual or bisexual, produced at notches of phylloclades. Male flower: calyx-lobes 6 (rarely 5); disk-segments usually 6 and discrete; stamens normally 3 or rarely 4 (very rarely 5), filaments united at least at the base; anthers dehiscing more or less horizontally; pollen grains globose, areolate. Female flower: calyx-lobes 6 (rarely 5); disk of discrete segments or cupuliform to urceolate; styles free or connate below, style branches often again lobed or bifid. Capsule oblate, smooth to tuberculate; seeds trigonous or sometimes (when only 1 per locule) ovate and flattened, verruculose.

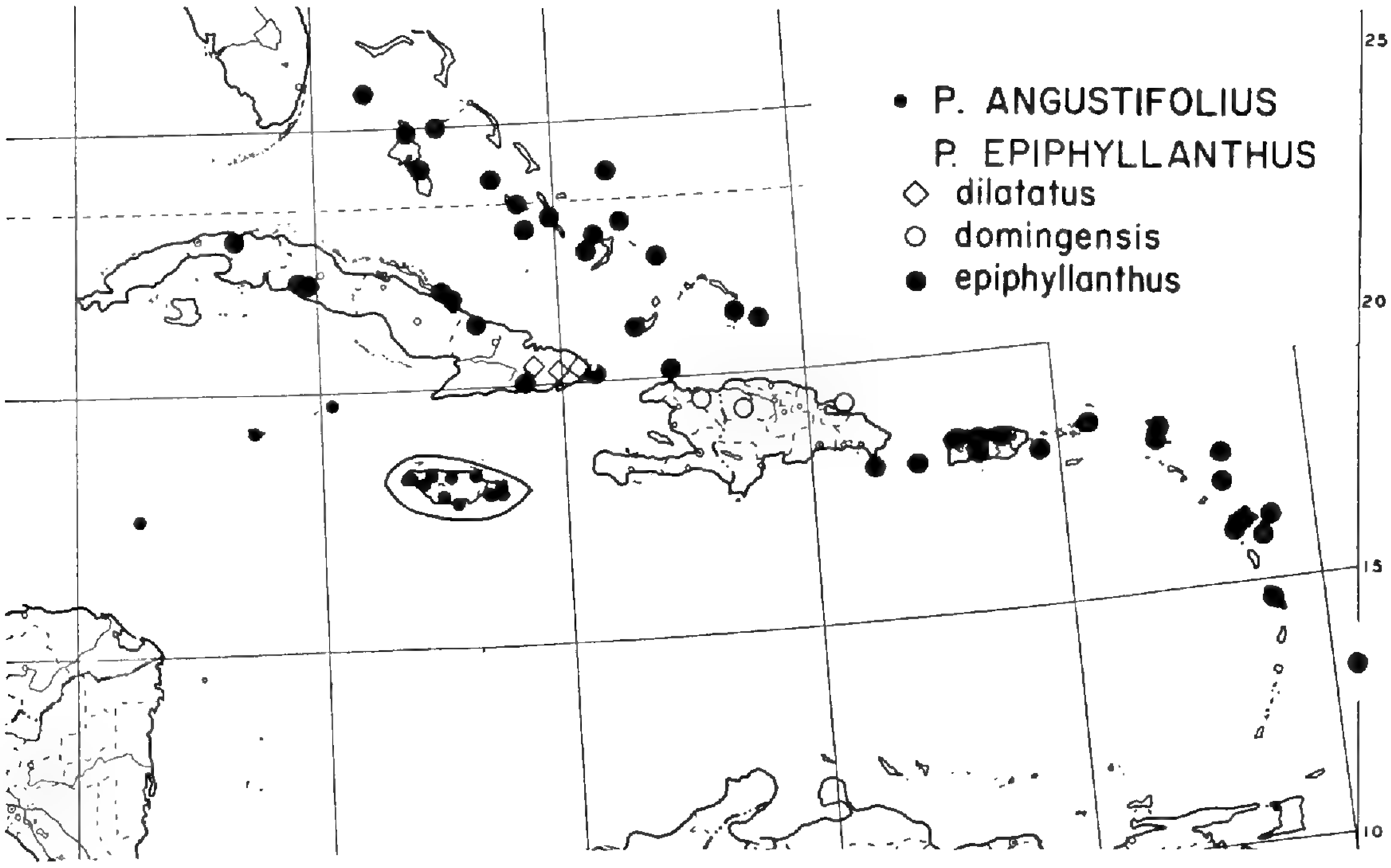
TYPE SPECIES: *Phyllanthus epiphyllanthus* L. (*Xylophylla latifolia* L., ex p.).

This West Indian section of about 10 specific and subspecific taxa includes some of the most familiar representatives of the genus; the type species, *P. epiphyllanthus*, was the first American member of the genus to become well-known in Europe. Because of their unusual morphological features, plants of sect. *Xylophylla* have received considerable attention from both horticulturists and morphologists, but except in the little-quoted work of Dingler (Flachsprosse der Phanerogamen. 1885) few attempts have been made to understand the evolution and relationships of the phylloclade-bearing species of *Phyllanthus*.

As here construed, sect. *Xylophylla* has a circumscription narrower than that of Mueller (DC. Prodr. **15**[2]: 427–432. 1866) or Pax and Hoffman (Naturl. Pflanzenfam. **19c**: 64–65. 1931). These authors included, in addition to the West Indian species, four or five phyllocladiferous Brazilian species such as *P. klotzschianus* and *P. flagelliformis*. Convergent evolution has progressed so far that on superficial inspection certain forms of *P. klotzschianus* and *P. montanus* might almost appear to be conspecific. However, an attentive examination of the flowers belies this impression, for the flowers of the Brazilian species differ in many details, including their deeply emarginate anthers, and their tricolporate coarsely reticulate pollen grains are completely different from the areolate grains of the West Indian species. It therefore appears certain, as suggested earlier in this study (Jour. Arnold Arb. **37**: 111. 1956), that the Brazilian species have evolved phylloclades quite independently of the West Indian ones; they are to be transferred to sect. *Choretropsis*.

As emended, sect. *Xylophylla* comprises only West Indian species, all except two of which are confined to Jamaica. At the present time sect. *Xylophylla* gives the appearance of a successful group in which evolution is probably actively in progress. Several of the species, particularly *P. epiphyllanthus* and *P. angustifolius*, occur in large and conspicuous populations, which show signs of incipient speciation. The representatives of the section afford a most interesting epitome of the evolutionary process as it occurs in many groups of higher plants on the Caribbean islands, and merit more intensive study than has been accomplished here.

The relationships of sect. *Xylophylla* are plainly closest to sects. *Epistylium* and *Hemiphyllanthus*, the former appearing to be the group from which both sect. *Xylophylla* and sect. *Hemiphyllanthus* were derived. An hypothesis of the probable origin of bipinnatiform branchlets has already been mentioned under the latter group. The peculiar branchlet structure of sect. *Xylophylla* is thus a specialization involving the replacement of the original leaves of a bipinnatiform branchlet by the expanded axes themselves. However, the relationship of *P. montanus*, the most primitive species of sect. *Xylophylla*, to *P. cauliflorus* and *P. axillaris* of sect. ***Epistylium*** is so striking that it seems possible that sect. *Xylophylla* may have arisen from sect. ***Epistylium*** coördinate with, rather than derived from, the less specialized sect. *Hemiphyllanthus*.



Map XXXIV. Distribution of sect. *Xylophylla*; heavy black line indicates limit of range of species other than *P. angustifolius* and *P. epiphyllanthus*.

In order to make clear the homology between the branchlets in the present section and those in sect. *Hemiphyllanthus*, the terminology used for vegetative structures in the species descriptions has been slightly modified from that presented in the introductory section of this study. The compound phylloclade, as illustrated in *text-fig. 5*, is here described as a branchlet with the ultimate axes transformed to phylloclades, the branchlets of all species of sect. *Xylophylla* being regarded as modifications of bipinnatiform branchlets as in sect. *Hemiphyllanthus*. In *P. montanus*, which is the most primitive species of sect. *Xylophylla*, the primary branchlet axis is unmodified and the term phylloclade is applicable only to the lateral ultimate axes. In *P. angustifolius* the primary axis is flattened and as green as the ultimate axes, so that the branchlet of this species can be regarded as a truly compound phylloclade. Finally, in the most specialized species, *P. epiphyllanthus*, the lateral axes are suppressed and the dilated primary axis of the branchlet serves directly as a simple phylloclade.

Although it cannot be used as a key character, due to its relative infrequency of occurrence, the production of leaves on the usually leafless phylloclades of sect. *Xylophylla* is a phenomenon of some taxonomic interest; the tendency toward suppression of leaves parallels, as might be anticipated, the trend toward an increasingly leaf-like character of the branchlet axes. In *P. montanus* leaves commonly occur on seedling phylloclades and sprout-shoots and, in a diminutive form, may sometimes be produced on normal branchlets. In *P. latifolius* and *P. angustifolius* leaves normally occur on seedlings and also appear on wound-shoots, and this is probably true of *P. proctoris* as well. In *P. arbuscula* and *P. epiphyllanthus*, on the other hand, leaves have never been observed at any stage in ontogeny.

The identification and taxonomic analysis of the Jamaican species of sect. *Xylophylla* is beset with a number of practical difficulties due to the high percentage of sterile specimens; flowering in some species appears to be erratic and infrequent. The key has been constructed with this in mind and should be workable even for sterile specimens as long as they are not sprout-shoots or unusual modifications.

KEY TO THE SPECIES

1. Phylloclades borne distichously on main axis of deciduous branchlet.
   2. Branchlet slow-growing, rather long-persistent, main axis greyish or brownish, not colored as the phylloclades; pedicel of female flower 0.5–1.5 mm. long. . . . . 78. *P. montanus*
   2. Branchlets expanding rapidly, not long-persistent, main axis greenish and of consistency of lateral axes (phylloclades).
      3. Pedicel of female flower only 0.5–1.5 mm. long; disk of female flower dissected into lobes or segments; phylloclades more or less rhombic-lanceolate, with mostly 20–50 nodes; apical cone 10–15 mm. broad, cataphylls scarcely or not ciliate. . . . . 79. *P. latifolius*
      3. Pedicel of female flower mostly 2 mm. long or more; disk of female flower entire; phylloclades elliptic- to obovate-lanceolate.
         4. Cataphylls of main axis remaining brown or grey, ciliate (if at all) only toward the base; phylloclades mostly 1–2 cm. broad with 20–40 nodes; ovary smooth. . . . . 80. *P. arbuscula*
         4. Cataphylls of main axis becoming dark or blackish-brown, copiously ciliate on margins at least when young; phylloclades mostly 0.5–1 cm. broad with 10–25 nodes, often subopposite at end of branchlet axis.
            5. Phylloclades (floriferous axes) lanceolate, mostly well over 3 mm. broad, with (8–) 10–20 (–24) nodes; styles not dilated, the ends 3–5-fid into slender tips. . . . . . 81. *P. angustifolius*
            5. Phylloclades (floriferous axes) narrowly linear, only 1–3 mm. broad, with 7–10 (–13) nodes; styles dilated and flattened, ends merely crenulate, forming a sort of calyptra over the ovary. . . . . 82. *P. proctoris*
1. Phylloclades each representing an entire branchlet, borne scattered directly on main stem. . . . . 83. *P. epiphyllanthus*

78. **Phyllanthus montanus** (Sw.) Sw. Fl. Ind. Occ. 1117. 1800; Muell. Arg. in DC. Prodr. **15**(2): 429. 1866; Fawc. & Rend. Fl. Jam. **4**: 261–262. 1920. (PLATE XXXI, *figs. M–N*).

Xylophylla montana Sw. Prodr. 28. 1788.
Diasperus montanus (Sw.) O. Ktze. Rev. Gen. 2: 600. 1891.

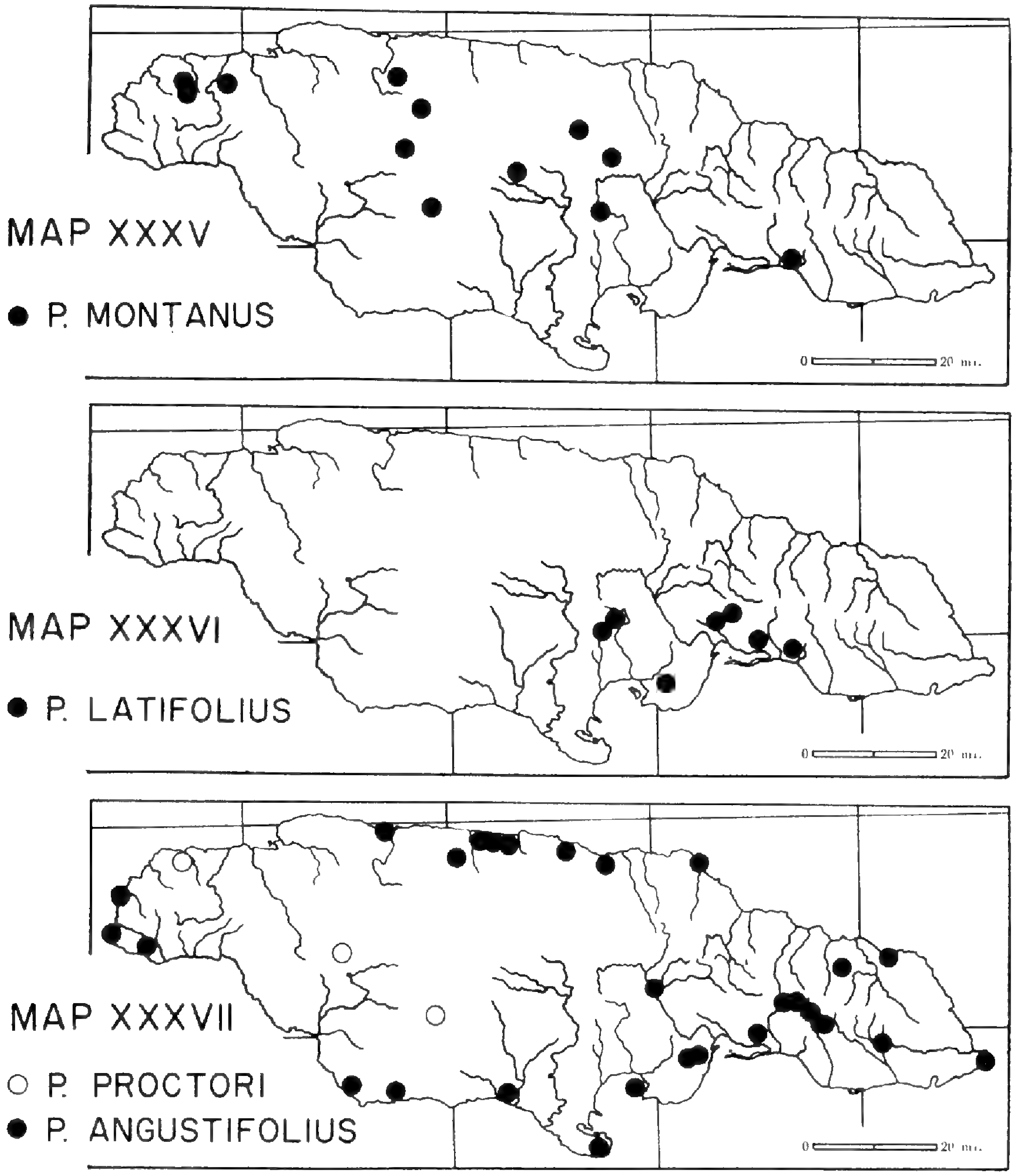
Shrub or small tree, usually c. 2–5 m. high; branches 2–8 mm. thick, terete, smooth, greyish-brown. Apical cone inconspicuous, c. 2 mm. long and 2–2.5 mm. broad; cataphylls deciduous, pale, thickened, deltoid, not over c. 1.5 mm. long, blunt, entire; blade about as long, massive. Branchlets ascending, bipinnatiform, ultimate axes transformed into phylloclades; primary (penultimate) axis 5–30 (–40) cm. long, 1.5–3 mm. broad, proximally terete, distally often flattened, greyish or brownish, with 7–20 (–30) lateral axes; first internode (0.5–) 1.5–4 cm. long, median internodes mostly 0.5–2 cm. long. Cataphylls of primary axis subpersistent or deciduous; stipules ovate, thickened, mostly 1–1.5 mm. long, blunt, entire or sparsely ciliate; blade shorter or about as long. Phylloclades flexible or rather stiff, elliptic to lanceolate (rarely linear-lanceolate), obtuse to long-attenuate at the tip, 3–20 cm. long, 0.5–3 cm. broad, with 10–30 (–50) slightly notched nodes; midrib conspicuous, more or less plane or salient beneath, veins tenuous and not very prominent; margins slightly (if at all) differentiated. Euphylls rarely produced except on sprout-shoots, blade elliptic, up to 11 mm. long and 6 mm. broad, obtuse or subacute at the tip, acute at the base, distinctly paler beneath, midrib prominent but veins and veinlets rather obscure. Cataphylls of ultimate axes reddish brown, scarious with often narrow, paler margins; stipules suborbicular-ovate, auriculate, 0.5–1.3 mm. long, 0.4–0.8 mm. broad, subentire or denticulate; blade subulate, less than 1 mm. long.

Monoecious; cymules usually bisexual, pulviniform, each with a single (rarely 2) female flower and c. 3–12 male flowers.

Male flower: pedicel slightly thickened, stiff, 1–3 mm. long. Calyx usually reddish-tinged; calyx lobes 5, chartaceous or hard-scarious, erect to somewhat spreading, unequal, one or two outer lobes usually elliptic to ovate, less than 1 mm. long, inner lobes suborbicular, c. 1.5 mm. long and broad, blunt-tipped, midrib simple or very sparsely branched above. Disk-segments 5, rather massive, roundish concave, c. 0.4–0.5 mm. across. Stamens 3; filaments completely connate into a column c. 0.5 mm. high; anthers sessile atop the column, broadly deltoid, blunt or emarginate, c. 0.2–0.25 mm. long and 0.3–0.4 mm. broad; anther-sacs dehiscing horizontally; pollen grains 17–21 μ in diameter.

Female flower: pedicel stout, c. 0.5–1.5 mm. long. Calyx greenish or (ex Swartz) dark purplish; calyx-lobes 5 or 6, at anthesis somewhat fleshy and erect, becoming scarious and spreading in fruit, subequal (outer lobes narrower), c. 1–1.5 mm. long, 0.8–1.5 mm. broad, more or less denticulate, midrib unbranched. Disk divided into distinct thin, petaloid segments c. 0.2–0.3 mm. long. Ovary ellipsoid or oblate, smooth, shallowly sulcate; styles free, spreading or ascending, sometimes slightly recessed into the top of the ovary, c. 0.3–0.5 mm. long, bifid, the tips blunt, sometimes dilated.

Capsule oblate, rounded-trigonous, c. 4 mm. in diameter, reddish brown, sometimes somewhat glaucous, rugulose, not veiny. Columella c. 1.8 mm. long. Seeds asymmetrically trigonous (plano-umbonate), 1.7–1.9 mm. long, 1.2–1.4 mm. broad, reddish, verruculose with rather densely spaced slightly raised dots; micropylar end sometimes carunculate.



MAPS XXXV–XXXVII. Distribution of some Jamaican species of sect. *Xylophylla*.

Collected in flower Dec., Feb.–May; in fruit Feb., July, Oct.

TYPE: western Jamaica, *Swartz* (S, HOLOTYPE).

DISTRIBUTION: wooded hills, western and central Jamaica (MAP XXXV).

JAMAICA: without specific locality, *Purdie* (A), *Swartz* (S, HOLOTYPE, G, K, ISOTYPES). HANOVER: Dolphin Head, *Britton 2211* (NY), *Harris 9251* (JAM, NY); hills near Kempshot, *Britton 2422* (NY); Shepherds Hall, 1 mi. east of Great Valley, *Proctor 7255* (JAM). TRELAWNY: near Troy, *Harris 8736* (NY); Sherwood Content, hilltop, *Proctor 11064* (GH); Ramgoat Cave area, *Howard & Proctor 14412* (A). MANCHESTER: Somerset, northwest of Mandeville, limestone cliff, *Proctor 11594, 11595* (GH). ST. ANN: Hollymount, Mt. Diablo, *Harris 8986* (A, JAM, NY, S), *Maxon 1906* (US); Pedro district, *Purdie* (K); Ramble Estate, 2.5 mi. SW of Claremont, *Webster & Proctor 5637* (A). CLARENDON: Peckham Woods, *Harris 10991, 11013* (NY), *12797* (JAM, NY), *Proctor 8430* (GH), *Stearn 15* (A), *Webster & Proctor 5431* (A). ST. CATHERINE: Lluidas Vale, *Hunnewell 19766* (GH). ST. ANDREW: cascade of Falls River, Kingston, *Prior* (K).

Phyllanthus montanus is a species with most interesting features, since it clearly is the most primitive living representative of sect. *Xylophylla* and furthermore is obviously related to the species of sect. *Epistylium.* The primary axis of the branchlet of *P. montanus* is so similar to the branchlet of *P. axillaris,* even to the stipules, that a reasonably close affinity between the two species seems undeniable. One difficulty in assessing the relationships of *P. montanus* is that it is an extraordinarily variable species in its vegetative features. Specimens from Peckham Woods, which have short, often twisted branchlets with short lateral axes, scarcely suggest any relationship to a species of sect. *Epistylium,* but two unusual collections made near Somerset by Proctor have long primary axes with an unmistakable resemblance to those of *P. axillaris.* Despite these differences, intraspecific variability of *P. montanus* does not appear to show any definite geographic correlation, and there is no necessity to describe subspecific taxa.

Although it is the most isolated species in the section, *P. montanus* shows certain points of resemblance to *P. latifolius* — specifically, the short pedicels and dissected female disk — which suggest that the latter is its closest relation within the section. However, *P. latifolius* is vegetatively much more like the other species of the section in having a definitely modified primary branchlet axis, and its relation is certainly not very close.

79. **Phyllanthus latifolius** Sw. Fl. Ind. Occ. 1109. 1800. (PLATE XXXI, *figs. O–P*; PLATE XXXII).

Phyllanthus 1. Foliis latioribus, &c. Browne, Hist. Jam. 188. 1756.
Xylophylla latifolia L. Mant. 2: 221. 1771 (ex p.; excl. typ.).
Lomanthes latifolia Raf. Sylva Tellur. 92. 1838.
Diasperus latifolius (Sw.) O. Ktze. Rev. Gen. 2: 599. 1891.
Phyllanthus isolepis Urb. Symb. Ant. 3: 290. 1902.

Shrub or small tree c. 1–4 m. high; branches of current year's growth 3–5 mm. thick, terete, brownish or greyish. Apical cone conspicuous, c.

10–15 mm. long and broad, irregular in outline. Cataphylls of main axis deciduous, scarious-indurate; stipules lanceolate, (4–) 6–10 mm. long, acuminate, squarrose; blade 3.5–11 mm. long. Branchlets ascending, bipinnatiform, ultimate axes transformed into phylloclades; primary axis (5–) 8–20 cm. long, (1–) 1.5–2 mm. broad, flattened, edges obtuse, olivaceous, smooth, with (4–) 7–12 (–15) lateral axes (phylloclades); first internode (1–) 2–4 (–8) cm. long, median internodes mostly 1–2 cm. long. Cataphylls of primary axis deciduous; stipules and blades linear-lanceolate, attenuate-acuminate, c. 1–2 mm. long, reddish brown, not ciliate. Phylloclades usually rigid, most often rhombic- or obovate-lanceolate but sometimes (especially on sprout-shoots) narrowly lanceolate, (3.5–) 5–8 (–10) cm. long, (0.7–) 1.5–3 cm. broad, narrowed (often abruptly so) to a blunt or sometimes caudate tip, with (15–) 20–50 (–60) nodes; midrib more or less prominent, veins steeply ascending, tenuous or subprominent; margins not differentiated. Euphylls occasional on sprout-shoots: blade obovate, c. 3–5 mm. long, acute at the tip and base, midrib rather prominent beneath but veins otherwise obscure. Cataphylls of ultimate axes suborbicular, convex, trifid, not over c. 0.5 mm. long, reddish brown, ciliate.

Monoecious; cymules male or (more often) bisexual, with 1 female and several (up to c. 10) male flowers.

Male flower: pedicel c. 1–3.5 mm. long. Calyx reddish; calyx-lobes 6, scarious-membranous, spreading (at least at the tips), subequal, obovate, c. 0.7–1.3 mm. long and 0.4–0.9 mm. broad (occasional outermost lobes greatly reduced), entire, midrib unbranched. Disk-segments 6, not pitted, c. 0.2–0.3 mm. broad. Stamens 3; filaments (0.5–) 0.7–0.9 mm. long, united below into a stout column c. 0.3–0.7 mm. high; anthers broadly ovate, emarginate, c. 0.2–0.3 mm. long, 0.4–0.5 mm. broad; anther sacs dehiscing more or less horizontally, pollen grains 15–19 μ in diameter.

Female flower: pedicel 0.5–1.5 mm. long. Calyx reddish; calyx-lobes 6, scarious or chartaceous, spreading, obovate or suborbicular, 0.5–0.8 mm. long, 0.4–0.7 mm. broad, entire, midrib unbranched. Disk separated into 6 lobes or segments c. 0.2–0.4 mm. across. Ovary oblate or turbinate, sulcate, smooth; styles basally connate into a short column 0.2–0.4 mm. high; style-tips spreading, c. 0.6–0.8 mm long, with mostly 3–5 lobes (occasional style-tips merely bifid).

Capsule oblate, c. 4 mm. in diameter, reddish brown, rugulose, not veiny. Columella c. 1 mm. long. Seeds asymmetrically trigonous, c. 2 mm. long, 1–1.2 mm. broad, reddish brown, verruculose with slightly raised dots.

Collected in flower June, July, Sept.; in fruit July.

TYPE: Jamaica, *Browne* (Herb. Linn. 1105-1 LINN; HOLOTYPE).

DISTRIBUTION: dry rocky areas, southern Jamaica (MAP XXXVI).

JAMAICA: without specific locality, *Browne* (LINN), *Jacquin* (BM), *March* (GH), *Masson, Shakespeare* (BM). ST. CATHERINE: near Salt Island, Healthshire Hills, *Britton 3058* (NY), *Harris & Britton 10532* (JAM, US); 2 mi. NNW of Guanaboa Vale P.O., 900 ft., *Proctor 7151* (MICH); Horse Cave, Hellshire Hills, *Proctor 7602* (GH); near Bartons, c. 5 mi. north of Old Harbor, alt.

Habit of *Phyllanthus latifolius* Sw., growing on limestone hilltop near Barton's, St. Catherine Parish, Jamaica (*Webster & Wilson 4862*). Left-hand figure, × 1/10; right-hand figure, × 1/4.

c. 1000 ft., *Webster & Wilson 4862* (A). ST. ANDREW: Ferry River, *Britton 2828* (NY); Ferry Pen, *Campbell 6280* (NY; type collection of *P. isolepis* Urb.); Fresh River north of Ferry, *Proctor 8276* (GH), *Webster & Wilson 5129* (A); Red Hills, *Britton 3469* (NY), *Grant & Barkley 22J080* (GH, MICH); Long Mountain, *Barry* (JAM, MICH), *Harris 8843* (NY), *8845* (NY), *Maxon 10531* (NY, US), *Webster & Wilson 4875* (A, MICH); Mona, *Barry* (JAM); Cane River Valley, alt. 250–400 ft., *Harris 9631* (US, NY), *10065* (JAM, NY, US).

Phyllanthus latifolius has a relatively restricted distribution, being known thus far only from dry hills in St. Catherine and St. Andrew parishes, although it may eventually be found to overlap into Clarendon and St. Thomas. It is perhaps the most xerophytic species in the section, although some forms of *P. angustifolius* and *P. epiphyllanthus* also occur in similarly dry habitats. The detailed distribution of *P. latifolius* offers some interesting problems with regard to the interaction between species. On Long Mountain, it was found to occupy the dry, lower southwestern slopes, while *P. angustifolius* occupied the northeastern slopes of the relatively mesophytic woods on top. This suggests an ecological separation between the species, but in some areas (e.g., Portland Ridge) *P. angustifolius* grows in habitats which are the sort occupied by *P. latifolius*. It is striking that the two species have never been observed growing side by side, even where (as at Long Mountain) their populations are in close proximity; this mutual exclusiveness, which suggests the effects of competition, deserves to be investigated critically from the ecological point of view.

As has been mentioned above, *P. latifolius* approaches closer to *P. montanus* than any other species of the section. The characters which suggest such a relationship — the dissected female disk and short pedicel — are also the ones which serve to separate *P. latifolius* from its close relative, *P. arbuscula*. These two species have the same kind of cataphylls and rather similar phylloclades, but those of *P. latifolius* are often thicker, more rhombic, and with denser clusters of flowers. The plants of *P. angustifolius* which occur within the range of *P. latifolius* may usually be easily distinguished from "narrow-leaved" forms of the latter by their blackish, ciliate cataphylls and phylloclades with fewer nodes which are often paired at the branchlet-tip.

80. **Phyllanthus arbuscula** (Sw.) Gmel. Syst. 2: 204. 1791.
(PLATE XXXI, *figs. Q–S*).

Xylophylla arbuscula Sw. Prodr. 28. 1788.
Xylophylla angustifolia b. *linearis* Sw. ibid.
Phyllanthus speciosa Jacq. Collect. **2**: 360. 1788; Ic. Pl. Rar. *pl. 616.* 1792.
Phyllanthus linearis (Sw.) Sw. Fl. Ind. Occ. 1113. 1800.
Xylophylla speciosa (Jacq.) Sweet, Hort. Brit. ed. 1. 360. 1827.
Genesiphyla speciosa (Jacq.) Raf. Sylva Tellur. 92. 1838.
Phyllanthus linearis α *genuinus* Muell. Arg. in DC. Prodr. **15**(2): 430. 1866 (excl. descr.).
Diasperus speciosus (Jacq.) O. Ktze. Rev. Gen. **2**: 601. 1891.

Phyllanthus inaequaliflorus Fawc. & Rend. Jour. Bot. **57**: 66. 1919.
Phyllanthus coxianus Fawc. & Rend. ibid.
Phyllanthus swartzii Fawc. & Rend. ibid. 67.
Phyllanthus dingleri Webster, Jour. Arnold Arb. **37**: 4. 1956.

Shrub or small tree up to 7 m. high, usually with a single main trunk and a few erect branches, these c. 3–5 mm. thick, smooth, light brown or greyish. Apical cone as broad as long, c. 5–10 mm. across, outline irregular due to exsertion of phyllocladar cataphylls; cataphylls deciduous, pale, thickened: stipules deltoid to lanceolate, 2.5–7 (–9) mm. long, 1–3 mm. broad, obtuse to acuminate, entire (rarely ciliate toward the base); blade deltoid to lanceolate, acuminate, about as long as the stipules. Branchlets ascending, bipinnatiform, ultimate axes transformed into phylloclades; primary axis (2.5–) 5–25 (–30) cm. long, 1–2.5 mm. broad, compressed and obtusely angled, adaxially sulcate, greyish green, with 4–16 lateral axes (phylloclades); first internode 1.5–5 (–6) cm. long, median internodes 0.5–2.5 mm. long. Cataphylls of primary axis mostly deciduous (occasional ones more or less persistent): stipules linear-lanceolate, (1.5–) 3–6 (–8) mm. long, acuminate, entire (or rarely sparsely ciliate toward the base), pale brown, basally auriculate; blade linear-lanceolate, about as long as the stipules. Phylloclades thin and flexible to somewhat rigid, elliptic to lanceolate, (2.5–) 4–11 cm. long, (0.5–) 1–2 (–2.7) cm. broad, tapering (sometimes abruptly) to an acute or acuminate tip, often paler (yellowish) beneath, with (10–) 20–40 (–50) conspicuously notched nodes; midrib and veins very often conspicuous and raised on both sides; margins usually with a distinctly differentiated rim running between notches. Euphylls never observed, even on seedlings. Cataphylls of phylloclades reddish brown, fragile and readily breaking off at the base, trifid (stipules united to the blade), tips acuminate, c. 0.5–1 mm. long; base auriculate, auricles ciliate-dentate.

Monoecious; cymules bisexual, of 1 female and c. 3 or 4 males, or proximal cymules male.

Male flower: pedicel capillary, (1.5–) 2–5 (–8) mm. long. Calyx cream-colored or greenish to scarlet; calyx-lobes 6 (rarely 5), membranous to coriaceous, more or less unequal, outer lobes obovate to elliptic and inner lobes ovate, or all lobes ovate, 1–2 mm. long, 0.8–1.8 mm. broad. Disk-segments 6, roundish, entire, thin, flat, c. 0.3–0.6 mm. across. Stamens 3; filaments 0.3–0.6 (–0.8) mm. high, united into a massive column 0.2–0.5 mm. high; anthers emarginate, 0.25–0.4 mm. long, 0.4–0.6 mm. broad; anther-sacs dehiscing horizontally; pollen grains c. 18–21 μ in diameter.

Female flower: pedicel thicker than in male, stiff, (2.5–) 3.5–10 (–14) mm. long at anthesis, increasing to 6–15 mm. long in fruit. Calyx-lobes cream-colored or greenish,* membranous to coriaceous, erect to spreading, c. 1–1.5 (–3) mm. long and broad (reduced outer lobes often smaller), obtuse (outer lobes sometimes with a brownish scarious tip), entire, midrib unbranched. Disk annular or shallowly cupuliform to urceolate and

---

* or scarlet in western populations.

enclosing the ovary, up to c. 1 mm. high. Ovary oblate, smooth; style free and spreading or basally united and then more or less erect, stylar column up to 1 mm. long; style-ends often twice bifid, tips with 3 or 4 lobes.

Capsule oblate, trigonous, c. 4–5 mm. in diameter, dark reddish brown, rugulose, not veiny. Columella 2–2.2 mm. long. Seeds asymmetrically trigonous (plano-umbonate), 2.7–3.3 mm. long, 2–2.5 mm. radially and tangentially, with irregular longitudinal lines of slightly raised reddish-brown dots.

Collected in flower Feb., Apr., June–Nov.; in fruit Apr.–July.

TYPE: Jamaica, Catherine Hill, *Swartz* (BM, HOLOTYPE; S, ISOTYPES).

DISTRIBUTION: upland areas, Jamaica (MAP XXXVIII).

This species consists of some distinctive populations but no clear-cut subspecies. The specimens are cited according to these races, which are lettered but not named; the proposed species to which each race roughly corresponds is given in parentheses.

Race A. Calyx scarlet, fleshy or coriaceous, lobes erect; disk of female flower urceolate, enclosing the ovary; styles united into a column as high as or higher than the ovary; (*P. dingleri*).

JAMAICA: sea-coast, *Swartz* (BM, S; TYPE COLLECTION of *P. swartzii*). HANOVER: Dolphin Head, woods on summit, *Britton & Hollick 2850* (NY), *T. Farr* (GH), *Proctor 7276* (GH, MICH); Kempshot, alt. 550 m., *Britton 2428* (NY). ST. JAMES: Lapland, alt. c. 2000 ft., *Harris 9191* (A, JAM, US). MANCHESTER: Somerset, northwest of Mandeville, alt. 2300 ft., *Proctor 11605* (GH).

Race B. Calyx scarlet, more or less coriaceous; disk of female flower partially enclosing the ovary; styles united into a definite column; seeds often 1 per locule; phylloclades often small and thick; (*P. coxianus*).

JAMAICA. TRELAWNY: Kimloss, *Howard 14136* (A); Stonehenge, *Howard 14156* (A); Ramgoat Cave, *Howard & Proctor 14394, 14401, 14407* (A); Troy, *Britton 596* (NY), *Harris 9368* (A, JAM, NY), *8565* (A, NY), *Proctor 7998* (JAM). MANCHESTER: 1 mile west of Christiana, alt. 3000 ft., *Howard & Proctor 14336* (A). ST. ANN: St. Anns, 1850, *Prior* [*Alexander*] (GOET, K, NY; TYPE COLLECTION of *P. coxianus*); 2 mi. west of Albion, alt. 2500 ft., *Howard et al. 14617* (A); Ramble, Claremont, alt. 1700 ft., *Fawcett & Harris 7025* (BM, US); Union Hill, near Moneague, *Britton & Hollick 2743* (NY, US). CLARENDON: Peckham Woods, alt. 2500 ft., *Proctor 8432* (GH), *Webster & Proctor 5404* (A, JAM, MICH).

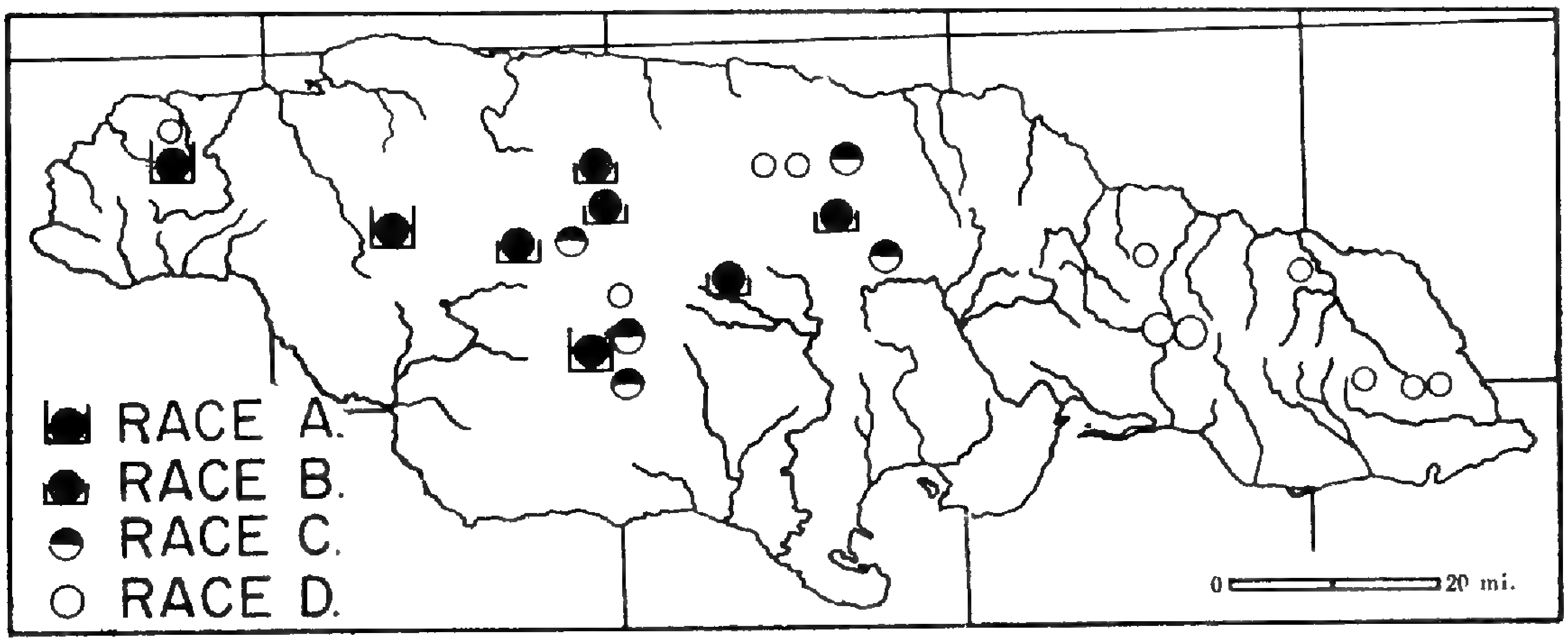
Race C. Calyx whitish, or partly pinkish-tinged, thin-textured; disk of female flower covering c. ½ ovary or less; styles slightly united or nearly free; phylloclades broad and thin; (*P. inaequaliflorus*).

JAMAICA. TRELAWNY: near Troy, alt. 2000–2500 ft., *Harris 8714* (NY, S, US), *8771* (JAM, NY), *Maxon 2891* (US), *Webster et al. 5380* (A, MICH). MANCHESTER: Marshall's Pen, alt. 2300 ft., *Stearn 387* (A, JAM); Mandeville, *Brown 135* (NY, US); Fairfield, *Wullschlaegel 1012* (GOET, M, W; data ex M). ST. ANN: Lydford (Golden Grove), *Howard & Proctor 13982* (A); Mt. Diablo, *Hunnewell 15306, 15307* (GH); Holly Mount, Mt. Diablo, *Harris 8988* (BM, JAM, NY; TYPE COLLECTION of *P. inaequaliflorus*), *Webster & Wilson 5012* (A, JAM, MICH); Grier Mount, *Webster & Proctor 5627* (A, JAM, MICH).

Race D. Calyx whitish or greenish, membranous; disk of female flower covering less than ½ the ovary; styles free or very nearly so, spreading; phylloclades usually broad and thin; (*P. speciosus*).

JAMAICA: without locality (probably St. Andrew), *March* (GOET), *Swartz* (S, probably ISOTYPE), *Wright* (W). ST. ANDREW: John Crow Peak, *Bancroft* (*J.P. 1263*) (JAM); Silver Hill, *Hylton* (JAM); Catherine Hill, *Swartz* (BM, HOLOTYPE). PORTLAND: Haycock Mt., above Balcarres, alt. 2750–3500 ft., *Proctor 8074* (JAM); Spring Bank, 2.5 mi. WSW of Port Antonio, *Proctor 6722* (MICH). ST. THOMAS: House Hill to Cuna Cuna Gap, alt. 550–725 m., *Maxon 8966* (NY, US); Corn Puss Gap, *Webster & Wilson 4893* (A, JAM, MICH); Mansfield, near Bath, alt. 300–500 m., *Maxon 2404* (NY, US); Big Level, alt. 2200–2500 ft., *Webster & Proctor 5517* (A, JAM, MICH).

The long synonymy of *P. arbuscula* is a good indication of the extraordinary variability of this common Jamaican species. For a long time an attempt was made by the writer to distinguish the species proposed by Fawcett and Rendle, first on the specific level and then on the subspecific. After prolonged consideration, however, any attempt to distinguish subspecific taxa within *P. arbuscula* has been abandoned, for although "subspecies" could be recognized and grouped in a key, this would give a misleading impression of permanence and solidity to what are more probably clines, rather than geographically delimited subspecies. If one compares a flowering specimen of the Dolphin Head race (A), with one from the Blue Mountains race (D), it appears at first glance that two different species are at hand; but if the specimens are taken instead from the area in the center of the island, between Troy and Mt. Diablo, serious difficulties immediately arise. All combinations of the characters mainly concerned (flower color and texture, female disk size, and stylar configura-



MAP XXXVIII. Distribution of *P. arbuscula* (Sw.) Gmel., showing variation in floral characters according to races described in text. Small circles indicate sterile specimens.

tion) can be found within a relatively small area. Thus, in Manchester parish, *Proctor 11605* from Somerset represents "good" *P. dingleri,* with red flowers, urceolate female disk, and united styles; but the *Brown* and *Wullschlaegel* collections from Mandeville and Fairfield are, despite their peculiar phylloclade shape, scarcely different from the typical form of the species in the Blue Mountains; and *Stearn 387,* with whitish flowers but united styles, is transitional to the Dolphin Head type. Similar examples could be added if it seemed necessary to elaborate the point, that the characters which appear so distinct at the two extremities of the island undergo "dissolution" in the center. The situation might possibly be interpreted as representing that of two extensively hybridizing subspecies, but the area of intermediates would probably be so large that such a classification would serve no useful purpose. The variation is so evidently clinal in character that it would be extremely interesting to map it in detail but, unfortunately, the large number of sterile specimens makes a thorough analysis impracticable at this time.

A character of especial interest is the common occurrence in plants of the Cockpit Country race (B) of capsules in which all or some of the locules produce only a single seed. As is usual in the Phyllantheae, the single seeds are so differently shaped that they look quite unlike the paired ones. Unfortunately, it is not yet possible to estimate the taxonomic importance of this feature because seeds are not known from the other three races. Thus far it appears that the production of solitary seeds is confined (in sect. *Xylophylla*) to *P. arbuscula.*

The name *Xylophylla arbuscula*, the basis for that here accepted for this species, was reduced by Swartz himself to the synonymy of *P. speciosus* Jacq., a course subsequent writers have followed. It has been assumed that Swartz withdrew his own name because of Jacquin's priority in publication, but Mr. William Stearn (personal communication) has discovered evidence that Swartz's name was actually the earlier. Swartz may have withdrawn his proposed name out of modesty or perhaps because Jacquin's was published under the correct genus; but in any event, the plant collected by Swartz in the Blue Mountains must take the name of *P. arbuscula.*

Phyllanthus arbuscula is rather closely related to *P. latifolius* but, as has been discussed under that species, it clearly differs both in floral and vegetative characters. More closely related is the species from the John Crow Mountains which must unfortunately remain undescribed because of lack of floral material. In contrast, *P. angustifolius* is much less similar morphologically since it has dark, ciliate cataphylls, usually narrower indistinctly veined phylloclades with fewer nodes, and a rugulose ovary. However, at least one specimen (*Webster & Proctor 5517*) has characteristics intermediate between *P. arbuscula* and *P. angustifolius,* suggesting that it may represent a hybrid. The peculiar plant named *P. linearis* by Swartz may possibly represent a cross between *P. proctoris* and *P. arbuscula*; but narrow-leaved forms of the latter sometimes occur normally (e.g. *March,* GOET), so that in this case the situation is not entirely clear.

81. **Phyllanthus angustifolius** (Sw.) Sw. Fl. Ind. Occ. 1111. 1800 (as *P. angustifolia*); Fawc. & Rend. Fl. Jam. **4**: 262. 1920.
(PLATE XXXI, *figs. T–U*).

Phyllanthus 2. Foliis angustis longioribus, &c. Browne, Hist. Jam. 188. 1756.
Xylophylla angustifolia Sw. Prodr. 28. 1788.
Phyllanthus cognatus Spr. Syst. **3**: 23. 1826.
Hexadena angustifolia (Sw.) Raf. Sylva Tellur. 92. 1838.
Phyllanthus angustifolius α *genuinus* Muell. Arg. in DC. Prodr. **15**(2): 430–431. 1866.
Phyllanthus linearis β *cognatus* (Spr.) Muell. Arg. op. cit. 430.
Diasperus angustifolius (Sw.) O. Ktze. Rev. Gen. **2**: 598. 1891.
Xylophylla contorta Britton, Bull. Torr. Bot. Club **37**: 353–354. 1910.

Shrub up to c. 3 m. high; branches 2.5–5 mm. thick, reddish brown or greyish. Apical cone usually rounded in outline (cataphylls with tips parallel or inflexed) and c. 3–4 mm. in diameter, but sometimes up to 5 or 6 mm. in diameter and irregular, the cataphyll tips somewhat divergent (but not squarrose); cataphylls deciduous, light brown to blackish brown, scarious-indurate: stipules usually broadly ovate, c. 1.5–2 mm. long and about as broad, less commonly lanceolate and up to 5 mm. long, margins always copiously ciliate when young (becoming more or less glabrate in age); blade ovate to lanceolate, about as long. Branchlets bipinnatiform, ultimate axes transformed into phylloclades; primary axis 3–12 (–14) cm. long, 1.2–2.5 mm. broad, flattened with acute edges, pale green as phylloclades, with 4–8 (–12) lateral axes; first internode (1–) 2–5 (–6) cm. long, median internodes mostly 0.5–2 cm. long. Cataphylls of primary axis usually with deciduous tips: stipules and blade lanceolate, not fused, c. 0.7–1.5 mm. long, copiously ciliate when young, becoming dark reddish brown and glabrate with a narrow whitish margin. Phylloclades usually flexible, elliptic- or oblong- to obovate-lanceolate, c. 3–10 (–13) cm. long, (0.2–) 0.5–1 (–1.2) cm. broad, obtuse to bluntly acuminate at the tip, with (8–) 10–25 nodes; veins occasionally distinct but more often obscure and phylloclades merely longitudinally furrowed or channelled; margins not differentiated.

Monoecious; cymules male or bisexual, of mostly 1 or 2 (rarely 3) female and c. 2–5 male flowers.

Male flower: pedicel (1–) 2–6 mm. long. Calyx reddish or cream-colored; calyx-lobes 6 (rarely 5), membranous, more or less spreading, subequal or sometimes unequal (outer lobes then narrower), elliptic to broadly obovate, (0.8–) 1–1.5 (–2.3) mm. long, entire, midrib unbranched. Disk-segments usually 6, thin, flat, entire, roundish, c. 0.2–0.5 mm. across, sometimes united in pairs or obsolete. Stamens 3 or less commonly 4 (rarely 5); filaments 0.4–0.8 (–1) mm. long, united for usually ½ their length or more into a column 0.3–0.7 mm. high, free ends spreading; anthers emarginate, c. 0.2–0.3 mm. long, 0.4–0.5 mm. broad; anther-sacs rounded, dehiscing more or less horizontally; pollen grains c. 18–25 μ in diameter.

Female flower: pedicel (1–) 2–4 (–7) mm. long. Calyx yellowish-green to pinkish; calyx-lobes 6, scarious, subequal or distinctly unequal, elliptic to obovate, 1–1.5 (–2.2) mm. long, 0.7–1.5 (–2) mm. broad, entire, midrib unbranched. Disk plane or shallowly cupuliform, c. 0.25 (–0.5) mm. high, rim undulate or crenulate. Ovary sulcate, rugulose; styles c. 0.6–1 mm. long, free or basally united into a very short column not over c. 0.3 mm. high, somewhat flattened, shallowly to deeply 3–4-lobed, lobes slender.

Capsule oblate, 3–4 mm. in diameter, reddish brown, rugulose, not veiny. Columella 1–1.8 mm. long. Seeds trigonous, 1.4–2.6 mm. long, 1–2 mm. radially and tangentially, reddish brown to fuscous, with finely raised dots.

Collected in flower and fruit throughout the year, but many collections sterile.

Type: Jamaica, *Browne* (LINN, holotype).

Distribution: seacoasts and lower altitudes inland, usually on limestone, Swan Islands, Cayman Islands, and Jamaica (Maps XXXIV and XXXVII).

SWAN ISLANDS: Eastern Swan Island, *Moyne 6, 12* (K); Larger Island, *Nelson 103, 104, 105* (GH); "Crane Island", 1897, *Sharples* (GH).

CAYMAN ISLANDS. Grand Cayman: Georgetown, 1888, *Fawcett* (K); 1891, *Hitchcock* (MO); 1 mi. SE of Georgetown, *Kings G.C.–202* (BM, NY); east end, *Kings G.C.–116* (BM, NY); Grape Tree Point, *Proctor 11974, 11976* (GH). Cayman Brac: 1888, *Fawcett* (K); 1924, *Matley* (BM); east end, *Kings C.B.–70* (BM, NY).

JAMAICA: without specific locality, *Bertero* (MO; type collection of *P. cognatus*), *MacFadyen* (K), *Shakespeare* (BM), *Swartz* (BM, S), *Wolle* (GH). Hanover: Orange Bay Point, *Harris 10262* (JAM); Lucea, 1891, *Hitchcock* (MO). Westmoreland: Negril, near lighthouse, *Britton & Hollick 2075, 2075a* (NY), *M. Farr* (GH), *Harris 10233* (JAM, P, US), *Webster & Wilson 5062* (A, JAM, MICH); Negril Hills, 0.5 mile east of Little Bay, *Proctor 11150* (GH). St. Elizabeth: Yardley Chase, *Britton 1157* (NY), *Harris 9666* (JAM, US); Merriman's Point, *Proctor 15335* (GH). Trelawny: Jackson Town, *Hunnewell 19767*; 1 mi. NW of Stewart Town, *Pierce 24* (MICH); Florida Beach, Falmouth, *West & Arnold 808* (GH). St. Ann: east of Rio Bueno, *Patrick 306* (JAM); Discovery Bay (Dry Harbour), *Dignum 86* (JAM), *T. Farr* (GH), *Hunnewell 15304, 18845* (GH); Runaway Bay, *Orcutt 6119* (MO, US); St. Ann's Bay, Gully Road, *Britton 2515* (NY, holotype of *Xylophylla contorta*); Ocho Rios, *Hunnewell 18843* (GH), *Proctor 9566, 15533* (A). Clarendon: Round Hill, *Proctor 9481* (GH); Portland Ridge, *Howard 12007* (A), *von der Porten* (JAM), *Webster 5111* (A, JAM, MICH). St. Catherine: Bog Walk, *Crawford 817* (NY); Great Goat Island, *Britton & Hollick 1891* (NY, US), *Harris 9334* (JAM, NY), *9339* (A, NY, US); Lazaretto, *Proctor 9968* (GH); Port Henderson Hill, *Webster & Wilson 4925* (A, JAM, MICH). St. Mary: Cabarita Island, off Port Maria, *Proctor 7549* (GH), *7550* (JAM). St. Andrew: Cinchona, *Harris 8592* (MO, NY); between Pleasant Hill and Green Valley, *Maxon & Killip 1058* (A, GH, NY, US); Long Mountain, *Davis* (MICH), *Proctor 7338* (JAM), *7387* (GH), *Webster 4857* (A, JAM, MICH). Portland: Uncommon Hill, *Proctor 8558* (JAM); Port Antonio, *Britton 879* (NY), *910* (NY, US), *Fredholm 3187* (US), *Hitchcock* (MO). St. Thomas: road to Hagley Gap, *Harris 5830* (NY, US); Sheldon Road, *Harris 12889* (GH, JAM, NY, US); Yallahs River, *Purdie* (K); Plantain Garden River, near Whitehall, *Proctor 7421, 11778* (GH); Morant Point, *Bengry* (GH), *Britton 4105* (NY), *Webster 5558* (A, JAM, MICH).

The following collections include plants which presumably were cultivated or naturalized:

FLORIDA. DADE CO.: Deering Hammock, Cutler, 1921, *Small et al.* (NY). MONROE CO.: Key West, *Blodgett* (NY), *Small et al. 10201* (NY). CUBA: *Ramon de la Sagra* (A, P). HAITI: OUEST: garden, Petionville, collected by Barker, *Ekman H9965* (S). DOMINICAN REPUBLIC: garden, Santiago, *Jiménez 1624* (US). VIRGIN ISLANDS: St. Thomas: Dec. 1880, *Eggers 358* (GH); July 1882, *Eggers 769* (G); Oct. 1882, *Eggers* (US).

Few species of *Phyllanthus* have a more interesting distribution than does *P. angustifolius*; the occurrence of the plant outside of Jamaica only on the Swan and Cayman Islands is an indication that the migrational history of this species may provide the key to some of the Pleistocene biogeographical problems of the Caribbean. Typically, *P. angustifolius* is a xerophytic species of dry littoral areas, often on cliffs or platforms of dogtooth limestone near the sea; however, it occurs inland at a number of localities (notably in the Blue Mountains) and thus shows some adaptability to colonizing different habitats. In the southeastern end of the John Crow Mountains it may at the present time be interbreeding with *P. arbuscula*.

Morphologically, *P. angustifolius* and its sister species *P. proctoris* are distinguished by their dark ciliate cataphylls, often in a distinctly small apical cone, and by the narrow phylloclades which are often paired at the end of the primary branchlet axes. Although closely related, *P. proctoris* appears to be sufficiently distinct by virtue of the floral characters mentioned below.

Phyllanthus angustifolius is a rather variable species and individual specimens often look distinctive. A form with narrow, elongated and often twisted phylloclades sometimes occurs and was the basis for the proposed *Xylophylla contorta* of Britton. In the vicinity of Port Antonio occurs a form with unusually large flowers, but it does not diverge sufficiently to warrant taxonomic recognition. The specimens from the Cayman Islands and Swan Islands are quite typical for the species and show no unusual features; this may indicate that the migration of the species there took place relatively recently.

82. **Phyllanthus proctoris**, nom. nov. (PLATE XXXI, *figs. V–W*).

Phyllanthus linearis sensu Griseb. Fl. Br. W. Ind. 35. 1859; Muell. Arg. in DC. Prodr. **15**(2): 430. 1866 (excl. *β cognatus*); et Fawc. & Rend. Fl. Jam. **4**: 266. 1920; non *P. linearis* (Sw.) Sw.

Shrub up to 3 m. high; branches of current year's growth c. 1.5–2.5 mm. thick, terete, greyish-brown. Apical cone roundish, c. 2.5–3 mm. long and 2–2.5 mm. broad, smooth in outline; cataphylls of main axes deciduous, blackish and scarious: stipules triangular-lanceolate, c. 0.8–1.7 mm. long, blade lanceolate, about as long. Branchlets pinnatiform, ultimate axes transformed to phylloclades; primary axis (3–) 5–13 cm. long, 1–2 mm. broad, flattened, edges obtuse, pale green as ultimate axes, with c. (4–) 6 or 7 lateral axes; first internode (1–) 2–6 cm. long, median internodes mostly 0.7–1.5 cm. long. Cataphylls of primary axis deciduous; stipules lanceolate, c. 1 mm. long, basally auriculate, densely ciliate marginally (when young; soon glabrate), reddish brown; blade about as long as the stipules. Phylloclades thin and flexuous, linear-lanceolate, c. (3–) 4–11 cm. long, 0.1–0.35 cm. broad, attenuate to the tip, finely striate or sulcate longitudinally (veins obscure) with 7–10 (–13) nodes; margins not differentiated. Euphylls not observed. Cataphylls of ultimate axes basally auriculate, c. 0.5–0.8 mm. long, prominently ciliate on margins (when young).

Monoecious: cymules male or bisexual, of 1–3 male flowers and/or 1 female flower.

Male flower: pedicel 2–3.5 mm. long. Calyx presumably greenish; calyx-lobes 6, membranous, more or less spreading, subequal, elliptic to obovate, 0.8–1 mm. long, 0.6–1 mm. broad, entire, midrib unbranched. Disk segments 6, roundish, c. 0.2 mm. across. Stamens 3; filaments united into a column 0.2–0.25 mm. high; anthers subsessile atop the column, c. 0.15 mm. long and 0.25 mm. broad; anther-sacs dehiscing horizontally; pollen grains 14–17 μ.

Female flower: pedicel mostly 2–3 mm. long. Calyx presumably greenish; calyx-lobes 6, unequal, the outer one or two usually brownish and scarious, only 0.7–0.9 mm. long; inner lobes chartaceous, broadly obovate, c. 1–1.2 mm. long, 0.8–1.2 mm. broad, entire, midrib unbranched. Disk shallowly cupuliform, irregularly notched, c. 1.2 mm. across. Ovary subglobose, smooth; styles divergent, dilated, obcuneate with crenulate distal margin, c. 0.5–0.9 mm. long, 0.5–0.8 mm. broad, horizontally spreading or reflexed over the ovary and forming a calyptra. Fruit and seeds unknown.

Collected in flower Jan.

TYPE: Jamaica, *Purdie*.

DISTRIBUTION: seacoast and inland hills, western Jamaica (MAP XXXVII).

JAMAICA. HANOVER: Lucea, *Hitchcock* (MO); Eton, alt. 100 ft., *Harris 12871* (JAM, MO, NY, US). WESTMORELAND: seacoast, Jan. 1844, *Purdie* (K, HOLOTYPE). ST. JAMES: Cinnamon Hill, in garden, 1897, *Fawcett* (NY). ST. ELIZABETH: Mulgrave, alt. 1300 ft., *Harris 12382* (MO, NY, US). MANCHESTER: Fairfield, *Wullschlaegel 1011* (G, GOET, M). Parish not designated: *Macfadyen* (GOET, K).

This species has long been misunderstood, owing to the fact that Swartz's type represents a peculiar plant which has not been recollected. It is clear from details of his description (such as pedicels 4 lines long and styles bifid) that Swartz's *P. linearis* (Fl. Ind. Occ. 113–114. 1800) cannot be the same as the plant described above and accepted as *P. linearis* by Grisebach, Mueller, and Fawcett and Rendle. The long pedicels suggest an affinity of Swartz's plant with *P. arbuscula* which has been confirmed by examination of the type specimen of *P. linearis*. The latter is not typical for *P. arbuscula* and may possibly be a hybrid, but in any event Swartz's name cannot be applied to the present plant.

Since a new name is required, it seems appropriate to name the plant for Mr. George Proctor of the Institute of Jamaica. Although he has not collected this species, his extensive gatherings of representatives of sect. *Xylophylla* and of other Jamaican groups of *Phyllanthus* have supplied valuable data during this study.

The closest relative of *P. proctoris* is certainly *P. angustifolius*, with which it agrees in having darkened ciliate cataphylls and often paired phylloclades at the end of the main branchlet axis. However, the phylloclades of *P. proctoris* are consistently narrower than all except a few aberrant forms of *P. angustifolius*, and no specimen of the latter has such highly modified styles. Thus although the two species are certainly very closely related, they nevertheless appear to be quite distinct.

83. **Phyllanthus epiphyllanthus** L. Sp. Pl. 981. 1753.

Shrub or small tree generally 1–3 m. high, trunk slender, erect, sparsely to considerably branched; branches of current year's growth 2.5–10 mm. thick, reddish brown becoming greyish, smooth, lenticels very inconspicuous. Apical cone usually small, c. 2–4 mm. in diameter. Cataphylls persistent, reddish brown becoming greyish, indurate, massive, the stipules fused with the blade in the lower half or entirely coalescent into a deltoid scale, c. 2.5–5 mm. long, more or less marginally ciliate when young but later often appearing entire. Phylloclades flexible to rigid, borne c. 0.5–1 cm. apart on terminal branches, or densely clustered on lateral spur-shoots, simple, often extremely variable in size and shape: linear to oblanceolate, straight to markedly falcate, (3–) 5–25 (–32) cm. long, (0.3–) 0.5–2.3 cm. broad, long-attenuate to truncate at the tip, with 7–40 nodes, these mostly in the distal half; midrib raised and rather conspicuous on both sides, lateral veins departing at an acute angle, tenuous, neither raised nor conspicuous; nodes mostly conspicuous along the margin, forming distinct notches, each with a dense cushion of persistent bracteoles. Euphylls never observed; cataphyll blade partially to completely united with its stipules, c. 0.8–1 mm. long, copiously ciliate along the margin, reddish brown, delicate and evanescent (scarcely evident except on young expanding phylloclades).

Monoecious; cymules usually bisexual, each with 1–3 female and several to many male flowers.

Male flower: pedicel capillary to thickish, 1–2.5 mm. long. Calyx usually reddish- or pinkish-tinged; calyx-lobes usually 6, subequal to very unequal, erect or spreading, sometimes connate below, oblong to ovate or obovate (sometimes broader than long), c. 0.8–1.3 mm. long, outer lobes often with dark brownish scarious fimbriate tips. Disk-segments usually 6, discrete or sometimes united in pairs, tenuous to massive, sessile to pedicellate, more or less foveolate-pitted, 0.25–0.5 mm. broad. Stamens 3 (rarely 4 or with the rudiment of a fourth); filaments partially to wholly united into a slender to massive column; anthers stipitate to sessile atop the column, broadly deltoid, more or less emarginate, 0.15–0.25 mm. long and 0.25–0.5 mm. broad; anther-sacs rounded, dehiscing horizontally or slightly deflexed; pollen grains c. 16–20 μ in diameter.

Female flower: pedicel rather stout, curved, often greatly thickened above, 0.5–2.5 mm. long. Calyx usually reddish- or pinkish-tinged; calyx-lobes 6, chartaceous, erect or spreading, equal or unequal, oblong to obovate (or broader than long), 0.7–1.5 mm. long, 0.5–1.5 mm. broad, entire or outermost lobes with dark brownish scarious ciliate tips, midrib unbranched. Disk variable, patelliform to urceolate and enclosing the ovary. Ovary smooth to conspicuously tuberculate, sulcate; styles free or shortly united into a column; style-ends spreading or deflexed, mostly dilated and irregularly 5–8-lobed.

Capsule oblate, trigonous, c. 3.5–4 mm. in diameter, dark reddish brown, not evidently veiny, smooth to incrustate-tuberculate; valves 2.5–3.2 mm. long. Columella c. 1.5 mm. long. Seeds asymmetrically trigonous, 1.4–2.1 mm. long, 1–1.6 mm. broad, smooth, dark reddish brown.

Collected in flower and fruit throughout the year.

Phyllanthus epiphyllanthus, vegetatively the most specialized species of sect. *Xylophylla*, is also the most widespread. It clearly appears to be closely related to and presumably has been derived from *P. angustifolius*, its simple phylloclades corresponding to the main axis of the branchlet of that species. In floral characters the two plants are very similar but *P. epiphyllanthus* usually has shorter pedicels and a greater number of stylar branches. The extensive populations of *P. epiphyllanthus* may be grouped into three distinctive and rather sharply defined subspecies which can be separated by the following key.

KEY TO THE SUBSPECIES

1. Stipules of cataphylls completely fused with the blade into an entire scale (rarely the extreme tips free); female disk c. 1/4 the height of the ovary or less (rarely to 1/3); calyx-lobes free to base, spreading at anthesis. .... *ssp. epiphyllanthus*
1. Stipules of cataphylls only partially fused with the blade at base, the tips free; disk covering 1/3 or more of the ovary; calyx-lobes more or less erect.
    2. Disk covering c. 1/3 to 1/2 of the ovary; calyx-lobes definitely connate below, forming a cup in which the disk is concealed. . *ssp. domingensis*
    2. Disk urceolate, entirely enclosing the ovary; calyx-lobes only barely, if at all, united at base. .... *ssp. dilatatus*

83a. **Phyllanthus epiphyllanthus** ssp. **epiphyllanthus** (PLATE XXXI, *figs. X–Y*).

Phyllanthos americana planta, flores e singulis foliorum crenis proferens Herm. Par. Bat. Prodr. 385. 1689 [nom.]; Commelin, Hort. Med. Amstel. Rar. 199–200, fig. 102. 1697.

Phyllanthus foliis lanceolatis serratis: *crenis floriferis* L. Hort. Cliff. 439. 1738 [excl. ref. Sloan.].
Phyllanthus epiphyllanthus L. Sp. Pl. 981. 1753.
Xylophylla falcata Sw. Prodr. 28. 1788.
Phyllanthus falcatus (Sw.) Gmel. Syst. Nat. ed. 13. 2: 204. 1791.
Phyllanthus epiphyllanthus β genuinus Muell. Arg. in DC. Prodr. **15**(2): 428. 1866; in part [excl. ref. Linden et Schomb.].
Diasperus epiphyllanthus (L.) O. Ktze. Rev. Gen. **2**: 599. 1891.
Xylophylla epiphyllanthus (L.) Britton in Small, Fl. Florida Keys 76. 1913.
Exocarpus epiphyllanthus (L.) Merr. Interpr. Rumph. Herb. Amb. 208. 1917 (as to type only).

Shrub 0.5–2.5 m. high; cataphylls of branches with stipules and blade completely fused into a deltoid scale (rarely the extreme tips becoming free) (1.5–) 2.5–4 (–5) mm. long. Phylloclades flexible to rigid, linear to oblanceolate, often falcate, 2.5–20 cm. long, 0.3–2 cm. broad, truncate to attenuate at the tip, with (7–) 9–30 (–35) nodes.

Male flower: pedicel slender, 1–3 mm. long. Calyx-lobes spreading, usually in two dissimilar whorls, the outer oblong to obovate, c. 0.5–1 (–1.5) mm. long and 0.5–0.9 (–1.3) mm. broad, the inner ovate to orbicular or broader than long, 0.7–1.5 mm. long and broad. Filaments mostly united ⅓ to ⅘ their length into a column 0.2–0.6 (–0.9) mm. long.

Female flower: pedicel becoming 0.5–2 mm. long. Calyx-lobes spreading, similar to the male, the outer c. 0.5–1 mm. long and broad, inner c. 0.8–1.3 mm. long and broad. Disk patelliform or shallowly cupuliform, at most not over 0.2 mm. high, usually enclosing the basal ¼ of the ovary (rarely to ⅓). Ovary rugulose to conspicuously tuberculate, at least above; styles nearly free or less commonly united into a column up to 0.5 (rarely to 1.3) mm. high, style-tips spreading, distally lacerate, 0.5–1 mm. long. Capsule apically rugulose to conspicuously tuberculate, 3–4.2 mm. in diameter, valves 2.2–3 mm. long. Seeds 1.4–2.1 mm. long, 1–1.6 mm. broad.

TYPE: *Herb. Hort. Cliffort.* (BM). The specimen was probably collected in the Bahamas by Catesby and given to Linnaeus by Miller.

DISTRIBUTION: widespread in the West Indies, mostly on limestone rock, often near the sea (MAP XXXIV).

BAHAMAS. BIMINI: North Bimini, *Howard & Howard 10086* (GH, NY, US), *Millspaugh 2375* (NY); South Bimini, *Millspaugh 2411* (NY). ANDROS: Mangrove Cay, *Brace 4864* (NY, US); Mastic Point, *Brace 7096* (NY); Nicols Town, *Northrop & Northrop 325* (A, G, GH), *Small & Carter 8954* (NY, US). NEW PROVIDENCE: Blue Hills Road, *Britton 14, 57* (NY); Farringdon Road, *Britton & Brace 223* (NY, US); Adelaide, *Britton & Brace 520* (NY); Nassau, *Britton & Millspaugh 5357* (NY), *Curtiss 4* (A, G, GH, MO, P, US), *Earle 57* (NY), *Northrop & Northrop 146* (NY); Mt. Vernon Estate, *Coker 31* (NY); *Cooper 48* (NY); Hog Island, *Eggers 4059* (US), *Wilson 8255* (NY); *von Reis 227* (MICH, US); Grantstown, *Wight 18* (GH, NY), *Wilson 8184* (NY). EXUMA: Little Galiot Cay, *Britton & Millspaugh 2837* (NY); Great Guana Cay, *Britton & Millspaugh 2866, 2919* (NY); Great Exuma, Haynes Road, *Britton & Millspaugh 3034, 3038* (NY). WATLING'S ISLAND: Columbus Monument, *Britton & Millspaugh 6179* (NY); *Hitchcock* (MO); southeast end, *Wilson 7266* (GH, NY). LONG ISLAND: *Britton & Millspaugh 6294* (NY); Water Cay, *Coker 524* (NY). CROOKED ISLAND: *Brace 4538* (NY). ATWOOD CAY: *Wilson 7381* (GH, NY). GREAT RAGGED ISLAND: *Wilson 7816* (GH, NY). LONG CAY (Fortune I.): *Brace 4026, 4216* (NY), *Hitchcock* (MO). MAYAGUANA (Mariguana): 10 mi. west of Abraham Bay, *Wilson 7431* (GH, NY). GREAT INAGUA: Matthewtown, *Harshberger 13* (US), *Nash & Taylor 875* (NY). CAICOS ISLANDS: South Caicos, *Wilson 7662* (GH, NY). TURKS ISLANDS: *Hjalmarsson* (GOET); Grand Turk, *Lewis* (GH), *Nash & Taylor 3766* (NY), *Proctor 8764* (GH).

CUBA. MATANZAS: Pan de Matanzas, *Ekman 16454* (S). LAS VILLAS: Calicita, *Combs 502* (GH, MO, NY, P, US); Cienfuegos Bay, *Britton & Wilson 5724* (NY), *Fernando 734* (NY), *Howard 5462* (NY), *Jack 4190* (A), *5110* (A, NY, US), *7559* (A, US); Trinidad Mts., *Ekman 13904* (S), *Webster 4784* (GH); La Vigia Hill, *Britton & Wilson 5532* (NY); Río Toyaba, *Britton et al. 557* (NY). CAMAGUEY: Jatovieja, Cayo Sabinal, *Shafer 1059* (NY, US); Cayo Paredon Grande, *Shafer 2747* (NY, P, US); Cayo Guajaba, *Shafer 728* (NY), *2813* (NY, US); Pastelillo, near Nuevitas, *Ekman 15401* (S). ORIENTE: Las Salinas, Puerto Padre, *Curbelo X60* (NY); Santiago, mouth of Río Aguadores, *Ekman 9232* (S); Jauco, *Jervis 3381* (GH); *Leon 11851, 11767* (NY).

HAITI. ILE DE LA TORTUE: Embouchure de la Rochelle, *Ekman H4190* (US).

DOMINICAN REPUBLIC. SEIBO: Isla Saona, *Taylor 506* (NY).

PUERTO RICO. MONA ISLAND: *Britton et al. 1748* (NY), *Noble 2827* (NY, US), *Stevens 6447* (NY). AGUADILLA: Quebradillas, *Britton et al. 1955* (NY, US), *Sargent 720* (US), *Stevens & Hess 5146* (NY); Camuy, *Hess 2583* (NY). ARECIBO: Vega Baja, *Britton et al. 6925* (NY). MAYAGUEZ: Guayanilla, *Britton & Shafer 1833* (NY, US); Yauco, *Garber 120* (GH). PONCE: west of Ponce, *Britton & Britton 7354* (NY), *Heller 6317* (A, G, GH, MO, NY, P, US). SAN JUAN: Bayamon, *Britton et al. 1518* (NY, US), *Heller & Heller 398* (NY, US), *Johnston* (NY, US), *Sintenis 1028* (GH, US), *Stahl 1074* (US), *Stevenson 382* (US). VIEQUES ISLAND: 1876, *Eggers* (GH); Campo Asilo, *Eggers* (MO); *Eggers 769* ex p. (P); Cayo Puerto Real, *Shafer 2757* (NY, US).

LESSER ANTILLES. VIRGIN GORDA: North Sound, *Fishlock 11* (GH, NY, US). ANGUILLA: *Goodwin & Goodwin 9* (NY). ST. MARTIN: *Boldingh 2785B* (NY), *Rijgersmaa* (S). BARBUDA: Codrington, *Beard 373* (A). ANTIGUA: Pelican Bay, *Box 552* (US); *Wullschlaegel 498* (GOET). GUADELOUPE: *Beaupertuis* (P), *Duchassaing* (GOET, P), *L'Herminier* (G), *Perrottet* (G), *Segretain* (P); Vieux-Fort, Gosier, *Duss 2444* (NY, US); Gosier, *Quentin 555* (P). ILE DESIRADE: *Duss 210* (P), *Stehle 215* (NY). MARIE-GALANTE: Guadeloupe et Marie-Galante, *Richard* (P). MARTINIQUE: *Belanger* (P), *Hahn 323* (G, P); Jardin botanique, *Duss 2044* (NY, US), *Plee* (P). BARBADOS: *Curran 59* (GH), *Waby 34* (US); Chancery Lane, *Dash 554* (NY, US); Forster Hall Wood, *Eggers 7234* (GOET, P, US); Bathsheba, *Miller 94* (US). TRINIDAD: *Sieber Flor. Trinitat. 337* (G, MO; cultivated?).

Subspecies *epiphyllanthus* is one of the most familiar of the West Indian representatives of *Phyllanthus* due to its abundance on limestone shores throughout much of the Greater and Lesser Antilles. It has received many common names, including "seaside laurel" and "sword bush" (Fawcett and

Rendle), "mutton parish" (in Barbuda, ex Beard), "duppy bush" (in Cayman Islands), "farine à zombi," "farine chaude," "langue à chat" (in Guadeloupe), and "panetela" (in Cuba). Roig (Dict. Bot. Nombres Vulg. Cub. ed. 2. 2: 743. 1953) considers that the Cuban name alludes to the pleasant nocturnal aroma of the flowers, which resembles a certain kind of pastry; the epithet "farine chaude" from Guadeloupe would appear to be derived in the same way. This distinctive nocturnal fragrance is interesting, since it has not been observed in any other species of the genus.

The report of Stehlé and Quentin (Fl. Guad. 2(1): 51. 1937) from St. Barthélemy is doubtless correct and refers to this subspecies, but most other reports of *P. epiphyllanthus* from localities other than cited herein are to be regarded with suspicion. The record of *P. epiphyllanthus* from Jamaica on the basis of a Purdie specimen at Kew (Fawc. & Rend. Fl. Jam. 4: 261. 1920) can presumably be discounted, since numerous subsequent collectors have encountered only *P. angustifolius* along the shores of that island. Since Purdie is known to have collected on Puerto Rico and Guadeloupe (Urban, Symb. Ant. 3: 107. 1902), his specimen may have been taken on either of those islands. The report of *Xylophylla epiphyllanthus* from the Florida Keys by Small (Flora Florida Keys 76. 1913) is based on a misidentification of a doubtfully indigenous specimen of *P. angustifolius*. Lemée (Fl. Guyane Fr. 2: 263. 1952) has recorded *P. epiphyllanthus* from French Guiana on the basis of an ambiguous citation by Aublet (Hist. Pl. Guy. Fr. 2: 853. 1775), but if Aublet encountered the plant there it must have been cultivated. The only disjunct record which cannot be positively rejected is that from Trinidad by Sieber, but the failure of recent collectors to confirm it strongly suggests that Sieber's plant too may have been taken from cultivation.

Subspecies *epiphyllanthus* consists of many isolated populations which may be grouped into three races. The plants of the Bahamas and eastern Cuba have relatively short phylloclades with fewer nodes and a distinctly tuberculate fruit. The plants from Matanzas and Las Villas are vegetatively similar to the Bahaman ones but have peculiarly dilated more or less calyptriform styles. The populations of Puerto Rico and the Lesser Antilles tend to have longer phylloclades (up to 20 cm. long) with more nodes, and nearly smooth capsules. However, the Barbados population is vegetatively so like the Bahaman that it breaks down the distinction between that race and the Lesser Antillean one; and, since it is not certain that the distinctive styles of the central Cuban race are a consistent character, it does not seem necessary to define formal varieties within the subspecies.

The peculiar distributional relationships of ssp. *epiphyllanthus* demand further investigation. Typically the subspecies is (like *P. angustifolius*) a littoral plant of coral benches, but in central Cuba and Puerto Rico it occurs in upland rain-forest. In both eastern Cuba and Hispaniola, on the other hand, it does not appear to go inland, but is instead replaced by ssp. *dilatatus* and ssp. *domingensis* respectively. In areas where mountainous regions approach near the coastline, it might be expected that ssp.

epiphyllanthus would come in contact with the other two subspecies; but thus far they have not been observed to grow sympatrically at any point and no specimens intermediate between any of the subspecies have been collected.

83b. **Phyllanthus epiphyllanthus** ssp. **domingensis,** ssp. nov.[23]

Phyllanthus epiphyllanthus β genuinus Muell. Arg. in DC. Prodr. **15**(2): 428. 1866 (ex p., excl. typ.).

Shrub or small tree, 1–2 m. high or more (up to 10 m., ex Jiménez); cataphylls of branches massive, 3–6 mm. long, blade and stipules fused at base (c. lower 1 mm.) but distally free. Phylloclades more or less rigid, narrowly linear to broadly oblanceolate, straight to distinctly falcate, 10–31 cm. long, (0.4–) 0.7–1.3 (–2.5) cm. broad, usually long-attenuate at the tip, with (15–) 20–40 nodes.

Male flower: pedicel distally thickened, 1–2.5 mm. long. Calyx-lobes subequal, basally connate above the receptacle into a cup c. 0.2–0.3 mm. high; free ends of lobes erect, obovate, 0.8–1.3 mm. long and broad. Disk-segments mostly 0.2–0.3 mm. across. Filaments almost completely united into a column 0.5–0.8 mm. high. Female flower: pedicel becoming 1.3–2 mm. long. Calyx-lobes erect, basally connate into a cup c. 0.4–0.5 mm. high; free ends of lobes broadly obovate, 0.8–1.2 mm. long and broad, becoming up to 1.5 mm. long in fruit. Disk cupuliform, c. 0.3–0.5 mm. high, usually enclosing the ovary for about ⅓ to ½ its height, crenulate-rimmed. Ovary smooth; styles free or united below the middle, dilated and channelled distally, c. (0.3–) 0.5–0.7 mm. high, the deflexed limb lobed but lobes often inturned and thus margin appearing entire. Entire capsules not seen; valves 2.8–3.2 mm. long; seeds 1.7–1.9 mm. long, 1.2–1.4 mm. broad.

TYPE: Dominican Republic, *Ekman H12642*.

DISTRIBUTION: wooded hillsides, sandy or calcareous soil, northern Hispaniola (MAP XXXIV).

HISPANIOLA: "St. Domingue," *Poiteau* (G), *Richard* (P).

HAITI. NORD: Cap Haitien, slopes of Morne Haut du Cap, alt. 500 m., *Ekman H2727* (S, US).

DOMINICAN REPUBLIC. MONTE CRISTI: Monción, banks of Río Mao, alt. 200 m., *Valeur 164* ex p. (A, US). SANTIAGO: Monción, at Río Magua, alt. 200 m., *Ekman H12642* (S, HOLOTYPE; US, ISOTYPE); Arroyo Vallecito, Jicomé, *Valeur 164* ex p. (G, MO, NY). SAMANÁ: Samaná Peninsula, Laguna, Pilón de Azucar, alt. 100–500 m., *Abbott 2360* (US).

Vegetatively, ssp. *domingensis* closely agrees with ssp. *dilatatus* in its unfused cataphylls and usually elongated or broadened phylloclades. It

---

[23] **Phyllanthus epiphyllanthus** ssp. **domingensis**, ssp. nov.
Cataphyllis trifidis; laciniis calycis ad basin connatis; filamentis omnino coalitis; disco femineo cupuliforme 0.3–0.5 mm. alte; ovario laeve; stylis liberis vel infere connatis.

is transitional between ssp. *dilatatus* and ssp. *epiphyllanthus* in its floral characters, having the smooth ovary of the former but a shallow female disk tending toward that of the latter; however, its basally cupulate calyx is different from either of the other two subspecies. On the whole, ssp. *domingensis* is much more closely related to ssp. *dilatatus* than to ssp. *epiphyllanthus*.

83c. **Phyllanthus epiphyllanthus** ssp. **dilatatus** (Muell. Arg.), stat. nov. (PLATE XXXI, *fig. Z*).

Phyllanthus epiphyllanthus α dilatatus Muell. Arg. in DC. Prodr. **15**(2): 428. 1866.
Phyllanthus epiphyllanthus β genuinus Muell. Arg., ibid., ex p.

Shrub or small tree up to c. 3 m. high; cataphylls of branches massive, 2–4 mm. long, the linear-lanceolate stipules and blade fused in the lower 1 mm. but distally free. Phylloclades more or less rigid, linear to oblanceolate, straight or somewhat curved (5–) 10–20 cm. long, (0.3–) 0.7–2.5 (–2.8) cm. broad, with c. 20–30 nodes.

Male flower: pedicel 1–3 mm. long. Calyx-lobes subequal, erect (tips sometimes flaring), barely if at all connate below, obovate, 0.8–1.2 mm. long, 0.6–1.5 mm. broad. Filaments completely united into a rather slender column 0.5–0.8 mm. high. Female flower: pedicel 1–2 mm. long; calyx-lobes subequal or somewhat unequal, oblong to broadly obovate, 0.9–1.3 mm. long, 0.5–1.3 mm. broad; disk urceolate, longitudinally ribbed, entirely enclosing the ovary, 0.8–1.3 mm. high; ovary smooth; styles 0.5–0.8 mm. high, free or more commonly united into a column 0.3–0.6 mm. high, style-tips spreading or reflexed, adaxially channelled, with 3 or 4 lobes. Capsule 3.5–4 mm. broad, smooth; valves 2.8–3.3 mm. long; seeds 1.8–2.1 mm. long, 1.4–1.5 mm. broad.

TYPE: Cuba, *Wright 1951*.

DISTRIBUTION: calcareous uplands, eastern Cuba (MAP XXXIV).

CUBA. ORIENTE: valley of Río Cauto, *Linden 2140* (G, P); Sierra de Nipe, Río Piloto, *Ekman 3391* (S); Monte Picote, *Ekman 7408, 9130* (S); Caridad de los Indios, *Jervis 1369* (GH, MICH); Monte Libano, San Fernandez, *Ekman 10271* (S); El Palenquitò, alt. 600 m., *Eggers 4844* (GOET, P); cliffs (paredones), Monteverde, *Wright 1951* (G, HOLOTYPE; GOET, MO, NY, P, US, ISOTYPES; data ex NY); Baracoa, pinelands on road to Florida, *Ekman 3989a* (S); top of El Yunque, 1955 *Harvard Trop. Bot. Course 469* (GH).

The epithet *dilatatus* assigned to this taxon by Mueller is not wholly appropriate, for some forms such as that represented by *Linden 2140* have long narrow phylloclades as in ssp. *epiphyllanthus*. On the basis of the much more extensive material which has become available since Mueller's treatment, it is now apparent that ssp. *dilatatus* cannot be distinguished vegetatively from ssp. *epiphyllanthus* except by its cataphylls. Even the "typical" broad-bladed form of ssp. *dilatatus* (as *Wright 1951*) can be matched by phylloclades from Bahaman populations of ssp. *epiphyllanthus* (e.g., *Coker 524* and *Britton & Millspaugh 6294* from Long Island). The diagnostic characters of ssp. *dilatatus* reside not in the vegetative parts but rather in the distinctive female flowers. No form of ssp. *epiphyllanthus* has such a highly developed female disk and, if it were not for the transitional character of the plants placed in ssp. *domingensis*, the population in the inland parts of Oriente province would have all the attributes of a distinct species.

ACKNOWLEDGMENTS

The basic framework of this study was constructed during the writing of a doctoral dissertation which was submitted at the University of Michigan in 1953. The inspiration for the investigation was given by Dr. Rogers McVaugh, who suggested the need for detailed study of *Phyllanthus* and who directed the research program with sympathy and understanding. Professor H. H. Bartlett generously supported field work in the southern United States, Cuba, and Jamaica, criticised the manuscript with thoroughness, and revised (and in many instances entirely recast) the author's attempts at scientific Latin. Dr. W. H. Wagner, Jr. gave valuable advice and encouragement on morphological techniques and suggested some important improvements in terminology. Financial assistance from the Research Club of the University of Michigan and from a Rackham Fellowship greatly expedited completion of the dissertation.

Investigations on the West Indian species of *Phyllanthus* were continued at Harvard University under a National Science Foundation fellowship kindly sponsored by Dr. Reed C. Rollins and Dr. I. W. Bailey, who made available various needed facilities. Dr. Richard A. Howard assisted in many ways, including supporting field work in Jamaica, furnishing many interesting specimens, and imparting freely of his extensive knowledge of Caribbean plant life.

Dr. Roy N. Jervis, of East Texas State College (Commerce), made possible field work in Cuba in 1951, collected extensive series of specimens, and generously supplied a valuable series of outline maps drafted by himself. Mr. Bernard Lewis and other staff members of the Institute of Jamaica materially assisted in the success of field work on that island in 1954. Mr. George Proctor, of the Institute, aided in many ways in these explorations, and has since forwarded both living and dried collections of unusual interest. Dr. Kenneth A. Wilson collaborated helpfully on the Jamaican field work throughout the summer of 1954. Special collections or materials of West Indian species of *Phyllanthus* were also furnished by Hermano Alain (Colegio de la Salle, Havana), Ing. Julian Acuña (Santiago de las Vegas), Dr. E. P. Killip, and Dr. Fred A. Barkley.

Several persons have lent assistance in the preparation of illustrations. Dr. Ding Hou kindly furnished the drawings for PLATES XIII and XIV; Mrs. Martha Szerlip Wittels applied her talented pen to the execution of *Text-fig. 4* and PLATES V, VIII, and IX; and Dr. Richard A. Scott took most of the photographs used for PLATES VI, VII, XI, and XII. Photo-

graphs of type specimens were taken at the University of Michigan through the courtesy of Dr. McVaugh. The other drawings were skillfully reconstructed from the author's sketches by his wife, Dr. Barbara D. Webster. In addition to the outline maps of Cuba and Jamaica furnished by Dr. Jervis, outline maps of Caribbean America and the Western Hemisphere from Goode's series of base maps (University of Chicago) were utilized in preparing distribution maps. For the publication of all of these illustrations in their present form and for the execution of those not specifically mentioned, the author is alone responsible.

Particular gratitude is expressed to Dr. C. E. Kobuski and to Dr. Carroll E. Wood for their forbearance and patience in editing what must have appeared to be a never-ending manuscript.

Finally, the author wishes to record his particular indebtedness to his wife, Barbara, for her untiring and indispensable assistance. Not only has she contributed by typing manuscript, inking in most of the line drawings, and preparing mounts for microscopic study, but she has with great understanding provided encouragement throughout the extended period in which this manuscript has taken its final form.

BIOLOGICAL LABORATORIES
HARVARD UNIVERSITY

CORRECTIONS

37: 92. Changes in concept during the course of this work have resulted in a total of 83 West Indian species (instead of "90-odd") of *Phyllanthus*, of which about 75 are indigenous.

37: 99. Read 1,000 pages for 1,000 species.

37: 120. Read 1450 μ instead of 4150 μ for *P. pachystylus*.

37: 219. *Phyllanthus elegans* has not been introduced into the West Indies; it has been confused here with *P. pulcher*.

37: 256. Read *Phyllanthus hyssopifolioides* HBK. for *Phyllanthus hyssopifolius* HBK.

37: 340. Read Isla de Providencia instead of Providenciales.

37: 344. Delete footnote 3.

37: 345. Sect. *Apolepis* (Subg. *Conami*) will not run down properly in the key to subgenera unless the expression "entirely woody" under lead 2 is ignored.

38: 177. Read **Cyclanthera** for **Cyllanthera.**

38: 298. Plate XXII, A is more applicable here than XXII, B.

38: 323. Read *fig. B* for *fig. A* under *P. fadyenii.*

39: 58. Read *P. anderssonii* for *P. barbadensis.*

APPENDIX I*

ARTIFICIAL KEY TO THE WEST INDIAN TAXA OF PHYLLANTHUS

1. Branching not phyllanthoid (i.e., ultimate axes persistent, their subtending leaves not reduced to scales).
    2. Herbs; stamens free; pedicel of female flower and seeds less than 2 mm. long. . . . . Sect. LOXOPODIUM (**37**: 346)
    2. Shrubs or trees; stamens connate; pedicel of female flower and seeds more than 2 mm. long. . . . . Sect. ELUTANTHOS (**39**: 51)
1. Branching phyllanthoid (i.e., ultimate axes deciduous, their subtending leaves usually reduced to scales).
    2. Branchlets with normal leaves, not greatly dilated.
        3. Branchlets pinnatiform (with a single lateral axis in spp. of Sect. *Cyclanthera*).
            4. Specimens with flowers.
                5. Stamens (including anthers) wholly confluent into a circumcissile synandrium.
                    6. Dioecious; stipules blackened and indurate; column of synandrium 1 mm. or more high. . . . . *P. dimorphus* (Sect. PHYLLANTHUS) (**38**: 341)
                    6. Monoecious; stipules paler and thinner; column of synandrium less than 1 mm. high. . Sect. CYCLANTHERA (**38**: 177)
                5. Stamens not wholly confluent.
                    6. Dioecious.
                        7. Herbs; flowers in axillary cymules. . . . . Sect. PHYLLANTHUS, Subsect. PENTAPHYLLI (**38**: 298)
                        7. Trees; flowers in cauliflorous thyrses. . . . . Sect. APOROSELLA (**38**: 72)
                    6. Monoecious (male flowers sometimes soon deciduous and specimens then appearing female).
                        7. Annual herb; stamens 5, entirely free. . . . . Sect. FLORIBUNDI (**38**: 51)
                        7. Habit various; stamens, if 5, at least partially connate.
                            8. Flowers, at least in part, in naked thyrses.
                                9. Stamens free; styles bifid, slender . . . . Subg. CICCA (**38**: 60)
                                9. Stamens united; styles thickened or 3–4 lobed.
                                    10. Anthers dehiscing vertically; disk of female flower urceolate, enclosing the ovary. . . . . Sect. EMBLICA (**38**: 75)
                                    10. Anthers dehiscing horizontally; disk of female flower much shorter, not enclosing the ovary. . . . . Sect. EPISTYLIUM (**39**: 153)
                            8. Flowers in cymules axillary to normal leaves.
                                9. Ovary with c. 9 or 10 carpels, styles minute and aggregated into an irregular mass; androecium of

---

* Numbers in parentheses refer to volume and page number of the taxon under which the unknown plant may be traced to species.

5 stamens united in two sets. . . . . Sect. ANISONEMA (38: 56)

9. Ovary with only 3 carpels, styles otherwise.
   10. Annual or perennial herbs; stamens 2 or 3; styles bifid, free except at the base, never greatly dilated or united into an erect column.
      11. Leaves as broad as or broader than long (c. 5–10 mm.); stamens 3, free; female disk dissected into 6 segments. . . . . Sect. APOLEPIS (38: 371)
      11. Not with this combination of characters. . . . . . . Subg. PHYLLANTHUS (38: 170)
   10. Shrubs or trees; stamens 2–15; styles various, often united into a column.
      11. Calyx-lobes dark red with lacerate margins; stamens 2, filaments united; axes reddish-hirsutulous. . . . . Sect. ERIOCOCCUS (38: 360)
      11. Calyx-lobes at most minutely denticulate, never lacerate. . . . . . Subg. XYLOPHYLLA . . . . (39: 68)

4. Specimens with fruits only.
   5. Fruits woody or fleshy, indehiscent or tardily dehiscent.
      6. Fruits baccate. . . . . Sect. ANISONEMA (38: 56)
      6. Fruits drupaceous or woody.
         7. Cocci firmly united, not separating. Subg. CICCA (38: 60)
         7. Cocci at length separating.
            8. Leaves linear-oblong, 2–5 mm. broad. . . . . Sect. EMBLICA (38: 75)
            8. Leaves much broader. Sect. OMPHACODES (39: 142)
   5. Fruits dry, dehiscent.
      6. Herbs; seeds less than 2 mm. long.
         7. Leaves orbicular or broader than long. . . . . Sect. APOLEPIS (38: 371)
         7. Leaves otherwise. . . . . Subg. PHYLLANTHUS (38: 170)
      6. Shrubs or trees; seeds often 2 mm. long or more. . . . . Subg. XYLOPHYLLA (39: 68)

3. Branchlets bipinnatiform (primary axis bearing several to many lateral axes).
   4. Calyx-lobes 6; pubescence not reddish; leaves (at least the petioles) and female pedicels scabridulous or hirsutulous. . . . . Sect. NOTHOCLEMA (38: 363)
   4. Calyx-lobes 5; pubescence more or less reddish; leaves and female pedicels smooth and glabrous. Sect. HEMIPHYLLANTHUS (39: 163)

2. Branchlets with at least the lateral axes modified to phylloclades, leaf-blades usually greatly reduced or absent. . . Sect. XYLOPHYLLA (39: 179)

APPENDIX II

WEST INDIAN SPECIES EXCLUDED FROM PHYLLANTHUS

PHYLLANTHUS ANTILLANUS (A. Juss.) Muell. Arg. Linnaea **32**: 51. 1863. (*Cicca antillana* A. Juss. Tent. Euphorb. *pl. 4, fig. 13B.* 1824.) = **Margaritaria nobilis** L. f. Suppl. Pl. 428. 1781.

PHYLLANTHUS BAHAMENSIS Urb. Symb. Ant. **3**: 289. 1902. (*Margaritaria bahamensis* (Urb.) Br. & Millsp. Bahama Fl. 220. 1920.) = **Margaritaria tetracocca** (Baill.) Webster, Jour. Arnold Arb. **38**: 66. 1957.

PHYLLANTHUS CUNEIFOLIUS (Britton) Croizat, Jour. Wash. Acad. Sci. **33**: 12. 1943. (*Andrachne ? cuneifolia* Britton, Mem. Torr. Bot. Club **16**: 72. 1920.) Not *Phyllanthus*; the disposition of this species is still uncertain.

PHYLLANTHUS GLABELLUS (L.) Fawc. & Rend. Jour. Bot. **57**: 68. 1919. (*Croton glabellum* L. Syst. ed. 10, 1275. 1759.) = *Croton lucidus* L. (as to type, not as to Fawcett and Rendle's application). Fawcett and Rendle cited as basionym *Croton glabellum* L. Amoen. **5**: 409. 1760 (non Syst., 1759), which supposedly is the plant accepted below as an *Astrocasia*; but this procedure is, of course, inadmissible under present rules of nomenclature.

PHYLLANTHUS HOTTEANUS Urb. & Ekm. Ark. Bot. **22A**(8): 60. 1928. = **Margaritaria hotteana** (Urb. & Ekm.) Webster, Jour. Arnold. Arb. **38**: 66. 1957.

PHYLLANTHUS LAURIFOLIUS A. Rich. in Sagra, Hist. Nat. Cuba **11**: 216. 1850. = **Savia sessiliflora** (Sw.) Willd. Sp. Pl. **4**: 771. 1806.

PHYLLANTHUS NEOPELTANDRUS Griseb. Goett. Nachr. **1865**: 167. 1865. (*Chaenotheca neopeltandra* (Griseb.) Urb. Symb. Ant. **3**: 285. 1902; *Securinega neopeltandra* (Griseb.) Urb. ex Pax & Hoffm. Natürl. Pflanzenf. **19c**: 60. 1931.) = **Chascotheca neopeltandra** (Griseb.) Urb. Symb. Ant. **5**: 14. 1904.

PHYLLANTHUS NOBILIS (L. f.) Muell. Arg. in DC. Prodr. **15**(2): 414. 1866. = **Margaritaria nobilis** L. f. Suppl. Pl. 428. 1781.

PHYLLANTHUS PORTORICENSIS (O. Ktze.) Urb. Symb. Ant. **4**: 338. 1905. (*Diasperus portoricensis* O. Ktze. Rev. Gen. **2**: 602. 1891; *Conami portoricensis* (O. Ktze.) Britton, Sci. Surv. Puerto Rico **5**(4): 475. 1924.) = **Flueggea virosa** (Willd.) Baill. Etud. Gen. Euphorb. 593. 1858.

PHYLLANTHUS PUBIGERUS A. Rich. in Sagra, Hist. Nat. Cuba **11**: 216. 1850. = **Savia sessiliflora** (Sw.) Willd. Sp. Pl. **4**: 771. 1806.

PHYLLANTHUS SCANDENS (Griseb.) Muell. Arg. in DC. Prodr. **15**(2): 415. 1866. (*Cicca scandens* Wr. ex Griseb. Goett. Nachr. **1865**: 165. 1865.) = **Margaritaria scandens** (Wr. ex Griseb.) Webster, Jour. Arnold Arb. **38**: 66. 1957.

PHYLLANTHUS TREMULUS Griseb. Fl. Br. W. Ind. 34. 1859. (*Phyllanthus glabellus* sensu Fawc. & Rend., non *Croton glabellum* L.; *Astrocasia phyllanthoides* Robins. & Millsp. Bot. Jahrb. Beibl. **80**: 20. 1905.) = **Astrocasia tremula** (Griseb.) Webster, comb. nov. The details of typification will be taken up in a forthcoming study on the genus *Astrocasia*.

PHYLLANTHUS VIRENS (Griseb.) Muell. Arg. in DC. Prodr. **15**(2): 415. 1866. (*Cicca antillana* var. *β virens* Griseb. Mem. Amer. Acad. Sci. **8**: 158. 1860; *Cicca virens* (Griseb.) Wr. ex Griseb. Goett. Nachr. **1865**: 166. 1865) = **Margaritaria tetracocca** (Baill.) Webster, Jour. Arnold Arb. **38**: 66. 1957.

INDEX

Synonyms are printed in *italics*; new names in **bold-face** type.

JOURNAL
OF THE
ARNOLD ARBORETUM

VOL. XXXIX JULY 1958 NUMBER 3

THE CITATION OF SOME GENERA OF THE LAURACEAE[1]

CARROLL E. WOOD, JR.

IN THE COURSE of a review of the genera of Lauraceae occurring in the southeastern United States it has been necessary to verify the citations of the native and naturalized genera and their typification. Hardly any uniformity in these matters exists in the literature of this difficult family, especially in connection with groups published prior to C. G. Nees' basic monographic treatment in 1836. *Cinnamomum,* for example, is still being cited variously as of Linnaeus, Blume, Trew or Nees & Ebermaier. Still another author has been proposed for this genus and for *Persea* and *Sassafras* in recent papers by Kostermans (1952, 1957).

It is hoped that the notes which follow will help to clarify the bibliographic citation of these and other genera grouped by Linnaeus under his all-inclusive *Laurus* (Gen. Pl. ed. 5. 173. 1754). Supposing that the glands of the third series of stamens were a constant generic characteristic (rather than one of very nearly the entire family), Linnaeus lumped under his "452. LAURUS.* *Tournef.* 367." plants formerly treated as separate genera (and later restored to generic rank by one or more authors in spite of the Linnaean influence which lasted almost fifty years). Included by Linnaeus were "Cinnamomum *Herm.* H. L. B. 656. *Burm. zeyl.* 28: 1. Camphora *Gronov. Diss.* Persea *Plum.* 20. Borbonia *Plum.* 2. Benzoë *Boerh.* Sassafras *Off.*" In the Linnaean interpretation, each of these generic names was used for that of a species under *Laurus*.

Recently, in an historical review of the Lauraceae (1952) and in his synopsis of the family (1957), both works representing an enormous amount of time and effort and of great value toward an understanding of the group, Kostermans has accepted G. R. Boehmer's 1760 edition of C. G. Ludwig's *Definitiones Generum Plantarum* as the place of valid publication of *Cinnamomum, Camphora, Borbonia, Persea, Benzoin,* and *Sassafras.* While it is most certainly desirable to establish the earliest possible date for these names, in this instance the publication appears to be invalid

---

[1] Continuing a series of miscellaneous notes and papers on the flora of the southeastern United States made possible through the interest and support of George R. Cooley and a grant from the National Science Foundation.

under the International Code of Botanical Nomenclature. On page 63 of this edition, under "188. LAURUS. *Linn.* Ed. V. n. 452," following a generic description identical with that in the edition of 1747, come the pertinent lines: "*Sexus et numerus partium variat, staminum tubercula pro constanti generico charactere assumit Linnaeus*; *et ab eodem huc refertur*." There follow the names and good short descriptions (here omitted) of:

LAURUS *Tourn.* 597.
CINNAMOMUM *Burm. Zeyl.* 28. CARVA *H. Mal. T. I. p.* 107.
CAMPHORA *Boerh. II.* 261.
BORBONIA *Plum. G.* 3.
PERSEA *Plum. G.* 44.
BENZOIN *Boerh. II.* 259.
SASSAFRAS *C. B. Pin.* 431.
LAURUS INDICA *Aldini licet monente Hallero Goett. p.* 15.

These are unnumbered, placed beneath *Laurus* in the fashion of similar notes and clearly intended synonyms throughout the book, and are in italics in the index (the usual practice for synonyms). The descriptions are also in italics, in contrast to the roman type of accepted genera in this work.

The earlier edition of Ludwig (1747) includes on p. 35 under "133. LAURUS. *Linn.*" the same generic description followed by the note "*Huc igitur a Linnaeo referuntur:*" and the same generic names of the later edition, with the exception of *Laurus indica* which was added by Boehmer along with more complete citations.

Clearly the names appended to *Laurus* were not accepted by either Ludwig or Boehmer, both of whom followed Linnaeus in construing that genus in its very broadest sense. They cannot be attributed properly to Boehmer for, being placed by him in the synonomy of *Laurus*, they must be regarded as invalid. (*Cf.* Art. 33, Internat. Code Bot. Nomencl. 1956.)

Although Boehmer's names are not acceptable, it would seem necessary to follow Rehder (1949) and Little (1953) in adopting those of Lauraceae from Trew in Blackwell's Herbal (1757, 1760). This work is a nomenclatural hodge-podge following no particular system, but *Sassafras*, *Cinnamomum*, and *Camphora* are adequately described and illustrated with clear and unmistakable references linking them to the corresponding Linnaean species. If the generic names now generally cited as dating from Miller, Gard. Dict. Abr. ed. 4. 1754, are legitimate under the Code, those of Trew must be equally acceptable. *Cinnamomum*, *Camphora*, and *Sassafras* of Trew antedate by a number of years the other possible authors of those names.

The citations which follow are not complete but include the earliest place of publication, the second earliest in most instances, and other data.

BENZOIN Fabr. Enum. Meth. Pl. Horti Medici Helmstad. ed. 2. 401. 1761. nom. rejic. (Type: *Laurus Benzoin* L. [= *Lindera Benzoin* (L.) Blume]). =

Lindera Thunb. Nova Gen. Pl. 2: 44. 1783 (Type: *L. umbellata* Thunb.); Blume, Mus. Bot. Lugd.-Bat. 1: 323. 1851, nom. cons. Non *Lindera* Adanson, Fam. Pl. 2: 425. 1763.

BORBONIA Miller, Gard. Dict. Abr. ed. 4. 1754 (based on a mixture including at least *Persea* Miller and *Nectandra* Rol. ex Rottb.; *cf.* Kostermans, 1952); Adanson, Fam. Pl. 2: 341. 1763 (a mixture, including *Persea, Nectandra, Ocotea* Aubl.). Non **Borbonia** L. 1753 (Leguminosae).

CAMPHORA Trew, Herb. Blackwell. Cent. 4, signature L. *t. 347.* 1760 (Type: *Laurus Camphora* L. [= *Cinnamomum Camphora* (L.) T. F. L. Nees & Ebermaier]); C. G. Nees in Wallich, Pl. As. Rar. 2: 61, 72. 1831 (Type: *Camphora officinarum* C. G. Nees [= *Cinnamomum Camphora*]). = **Cinnamomum** Trew, sect. **Camphora** (Trew) Meissn. [attributed by Meissner to C. G. Nees].

Cinnamomum Trew, Herb. Blackwell. Cent. 4, signature M. *t. 354.* 1760 (Type: *Laurus Cinnamomum* L. [= *C. zeylanicum* Blume]); Blume, Bijdr. Fl. Nederl. Indië 568. 1826 (Type: *C. zeylanicum* [Garc.] Blume).

Persea Miller, Gard. Dict. Abr. ed. 4. 1754, nom. cons.[2] (Type: *Laurus Persea* L. [= *P. americana* Miller, 1768]); Miller, Gard. Dict. ed. 8. 1768 (Type: *P. americana* Miller); Gaertn. f. Fruct. 3: *222. t. 221.* 1805 (Type: *P. gratissima* Gaertn. f. [= *P. americana* Miller]).

Sassafras Trew, Herb. Blackwell. Cent. 3, signature P. *t. 267.* 1757 (Type: *Laurus Sassafras* L. [= *S. albidum* (Nutt.) C. G. Nees]); T. F. L. Nees & Ebermaier, Handb. Med.-Pharm. Bot. 2: 418. 1831 (Type: *S. officinale* T. F. L. Nees & Ebermaier, "*officinalis.*" [= *S. albidum*]).

REFERENCES

KOSTERMANS, A. J. G. H. A historical survey of the Lauraceae. Jour. Sci. & Indus. Res. Indonesia 1: 83–95, 113–127, 141–159. 1952.

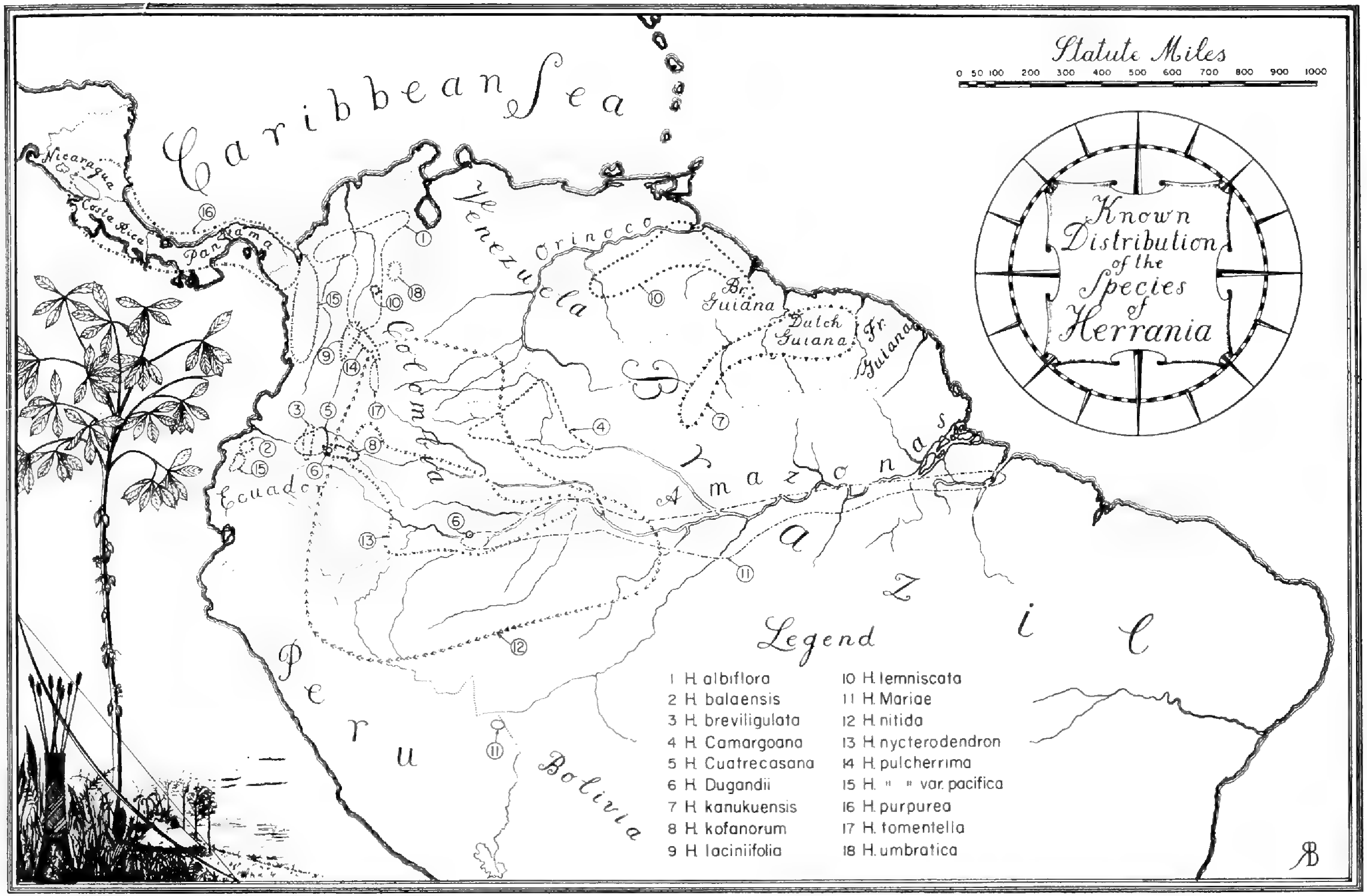
————. Lauraceae. Reinwardtia 4: 193–256. 1957. (First publ. as Comm. Forest Res. Inst. Indonesia 57. 1957.)

LITTLE, E. L., JR. Check list of native and naturalized trees of the United States (including Alaska). U. S. Forest Serv. Agr. Handbook 41. 1953.

REHDER, A. Bibliography of cultivated trees and shrubs. Arnold Arb., Jamaica Plain, Mass. 1949.

---

[2] Conservation unnecessary.


Known Distribution of the Species of Herrania
Statute Miles
0 50 100 200 300 400 500 600 700 800 900 1000
Caribbean Sea
Nicaragua
Costa Rica
Panama
Venezuela
Orinoco
Br. Guiana
Dutch Guiana
Fr. Guiana
Colombia
Ecuador
Peru
Bolivia
Amazonas
Brazil
Legend
1 H. albiflora
2 H. balaensis
3 H. breviligulata
4 H. Camargoana
5 H. Cuatrecasana
6 H. Dugandii
7 H. kanukuensis
8 H. kofanorum
9 H. laciniifolia
10 H. lemniscata
11 H. Mariae
12 H. nitida
13 H. nycterodendron
14 H. pulcherrima
15 H. " " var. pacifica
16 H. purpurea
17 H. tomentella
18 H. umbratica
AB

A SYNOPSIS OF THE GENUS HERRANIA

Richard Evans Schultes

With seventeen plates

> La flor se podrá mirar como la mayor maravilla del reino vegetal, y apenas se pudiera creer que la económica y sencillísima naturaleza hubiese gastado tantas cintas y atavíos para engalanarla casi con la ostentación de las modas.
>
> — *Eloy Valenzuela* (1784)

More than an academic interest moves me to present this study of the sterculiaceous genus *Herrania*, a close relative of *Theobroma*, the genus of the cultivated cacaos. In recent years, the chocolate industry of the world has become increasingly alarmed over the ravages of certain fungal and virus diseases of the cultivated forms of *Theobroma*. These are so serious that the industry has waned almost to extinction in several parts of the world, and our sources of certain grades of chocolate are seriously threatened. Extensive investigations toward a control of the disease have been carried out in a number of scientific institutions; much has been done in plantations toward selection of resistant strains, and several attempts to do this from wild material have been made; furthermore, attention has been devoted toward the possibility of overcoming the difficulties through hybridization and other techniques.

It is my belief, however, that sooner or later an extensive program for selection of new germ plasm from the jungle must be initiated, if the chocolate industry is to be saved. Naturally, such a project would include all near allies of *Theobroma* (Schultes, R. E. "El género *Herrania*, pariente silvestre del cacao cultivado." Agric. Trop. **7**: 43–48. 1951; "Le genre *Herrania*, parent sylvestre du cacaoyer cultivé." L'Agron. Trop. **6**: 661–663. 1951). In 1952–53, the Imperial College of Tropical Agriculture in Trinidad and the Colombian Ministerio de Agricultura carried out jointly a very thorough study of *Theobroma* and *Herrania* in the Amazonian sector of Colombia. This study, which was headed by the late Prof. Richard E. D. Baker and Dr. Francis W. Cope, of the Imperial College, and which included half a dozen additional British and Colombian scientists, explored many of the major rivers of the region and made selections of interesting or outstanding material for the cacao-improvement scheme in Trinidad.

Herrania first attracted my attention in 1941, when I collected a then undescribed species in southern Colombia. The process of determining and describing this collection brought out the great need for a revisionary treatment of the genus. Nevertheless, in view of the sparse and fragmentary collections then in our herbaria, as well as the unavailability during the war of material from European institutions, it seemed advisable to await a more favorable time before undertaking such a revision.

From 1941 to 1953, I was engaged in almost uninterrupted field studies (chiefly of the genus *Hevea*) in the Amazon Valley. In connection with this work, it was often possible for me to give special attention to *Herrania* in its native habitat and to make collections over a wide area. This intimate association with the living plants enabled me to study a number of morphological and ecological characters which are lost in the preparation of herbarium material. It has also been possible, in some cases, to study and collect fruits which, although often wanting in our herbaria, can be highly significant from the taxonomic point of view.

In addition to field studies, I have consulted all available specimens from the principal herbaria in the United States and South America in the preparation of the following synopsis. Furthermore, in 1947 and again in 1950, I was able to study the collections preserved in England and on the continent of Europe.

Although it would seem that sufficient material upon which to base an admittedly preliminary treatment of *Herrania* has now been consulted, we must realize that certain concepts are still rather poorly understood. Further field studies will almost certainly lead to alterations in our present treatment and will undoubtedly enhance our knowledge of the composition and geographic distribution of the genus.

ACKNOWLEDGEMENTS

So many friends have aided me in so many ways in both the herbarium and the field that I find it difficult to thank them all individually. The late Professor Oakes Ames, of Harvard University, followed my field and herbarium investigations of *Herrania* from their beginning and, by letter and conference, stimulated me with his many suggestions and with his deep interest in economic botany. It is with warm appreciation that I thank Professor Paul C. Mangelsdorf, director of the Botanical Museum of Harvard University, for his constant encouragement in the work of preparing this study of *Herrania*. My colleagues at the Botanical Museum, especially Dr. Albert F. Hill and Mr. Charles Schweinfurth, have likewise given generously of their time, advice and encouragement throughout the years of preparation of this study. My deep gratitude must go to Dr. E. W. Brandes and Dr. Robert D. Rands, who directed my work on *Hevea* rubber for the United States Department of Agriculture, for their encouragement and understanding of my botanical activities which, like the *Herrania* investigation, were not directly concerned with my regular studies in latex-bearing plants. Dr. N. Y. Sandwith of the Royal Botanic Gardens, Kew, has been most generous with his help during the last few years of this study. To Dr. Armando Dugand, former director of the Instituto de Ciéncias Naturales in Bogotá, and Dr. Felisberto Camargo, former director of the Instituto Agronômico do Norte in Belém do Pará, Brazil, I am especially indebted for their interest and for many kindnesses during my years of field work. Mr. Gordon W. Dillon, the late Señorita Inés de Zulueta and Miss Helen Schieffer deserve my warmest thanks for their drawings which were published in some of my earlier taxonomic papers on *Herrania*.

It is difficult for me to express adequately my gratitude to Mr. Elmer W. Smith for the highly accurate and artistic drawings which illustrate this synopsis. Sincere thanks go also to the American Cocoa Research Institute and the National Science Foundation for generous grants of money towards the illustrating of my taxonomic studies in this genus of close relatives of the chocolate plant.

My deepest appreciation is due to the numerous members of the Anglo-Colombian Cacao Collecting Expedition, especially to the late Prof. Richard E. D. Baker and to Dr. Francis W. Cope, together with which Expedition I was able to spend many months in the field and to test the workability and completeness of this synopsis of *Herrania.*

To the directors and staffs of the following American botanical institutions I send my thanks for the loan of specimens or for their kind permission to consult material in their care; the Gray Herbarium, the Arnold Arboretum, and the Economic Herbarium of Oakes Ames (Harvard University); the Bailey Hortorium (Cornell University); the New York Botanical Garden; the Missouri Botanical Garden (St. Louis, Mo.); the Chicago Natural History Museum; the United States National Herbarium (Washington, D. C.); the United States National Arboretum [Herbarium] (Beltsville, Md.); the Philadelphia Academy of Natural Sciences; and the Yale School of Forestry (New Haven, Conn.). I am deeply grateful also to the officers of the following European and South American botanical centers for their many courtesies during my periods of study in their herbaria; the Royal Botanic Gardens (Kew) and the British Museum (Natural History) (London); the Botanisch Museum en Herbarium (Utrecht); the Rijksherbarium (Leiden); the Universitats Botaniska Museum (Copenhagen); the Museum National d'Histoire Naturelle (Paris); the Jardín Botánico (Madrid); the Conservatoire Botanique (Geneva); the Herbier Boissier (Geneva); Jardin de l'État (Brussels); the Botanische Staatssammlung (Munich); the Naturhistoriska Riksmuseum (Stockholm); the Instituto de Ciéncias Naturales (Bogotá); the Facultad Nacional de Agronomía (Medellín); the Instituto Agronômico do Norte (Belém); the Museu Goeldi (Belém); the Jardim Botânico (Rio de Janeiro); the Instituto Miguel Lillo (Tucumán); and the Instituto Interamericano de Ciéncias Agrícolas (Turrialba, Costa Rica).

HISTORICAL NOTES

Herrania was described by Justin Goudot in 1844 and was named in honor of General Pedro Alcántara Herrán (1800–1872), president of New Granada (Colombia) from 1841 to 1845. In spite of civil unrest in the country, Herrán showed much interest in the botanical investigations of Colombia during this period. It is therefore quite appropriate that this genus, which has its center of diversification in Colombia, should bear his name.[1]

---

[1] It is equally appropriate for me to express, in this paper, summarizing our present knowledge of *Herrania*, my gratitude to Dr. Alvaro Herrán Medina, his great grand-

The specimens upon which this genus and its first two species, *Herrania albiflora* and *H. pulcherrima*, were based had been brought to the attention of the scientific world long before the actual publication of the genus in 1844. At the meeting of the Linnean Society of London on January 15, 1828, Goudot referred to "a plant of the genus nearly akin to *Theobroma* from which it differs chiefly in habit, in the form of the calyx, and the structure of the stamens . . . 'Arbuscula foliis digitatis, quinatis' " (Philosoph. Mag. 3: 132. 1828). Before presenting his diagnosis of *Herrania*, Goudot devoted much careful study to the new genus, for he wrote "[since 1828] . . . I have had frequent occasions to study these plants and to assure myself that they ought to constitute a distinct genus" (Ann. Sci. Nat. Paris III. 2: 229. 1844). Goudot's original diagnosis of *Herrania*, reproduced below, is so detailed and so carefully prepared, with such a clearly outlined concept as to relationship, that now there is no need to alter either the description or the concept, and this in spite of the fact that the number of species known has been measurably increased.

Long before *Herrania* was actually described, however, several species were recognized as distinct from *Theobroma*. The Botanical Expedition of Mutis in New Granada (Exped. Bot. Mutisii Novae-Granat.), which was carried out in Colombia by a capable and devoted group of scientists under the leadership of Padre José Celestino Mutis from 1783 to 1808, collected some 4055 specimens, including several species of *Herrania*. The greatest heritage of the expedition is the collection of water-color paintings of Colombian plants, numbering 6900 plates and representing 2800 species. The plates, in perfect condition, are preserved in the Jardín Botánico in Madrid and their publication has only recently been initiated. I was fortunate in 1950 to have an opportunity to study many of these plates, but permission to publish any of them could not be granted.

Amongst the 6900 plates, there are several extraordinarily artistic and accurate illustrations representing three species of *Herrania*. These plates, labelled simply "*Theobroma*" by the artists, are all included in Volume No. 28 under number 5333. They were first determined as representing several concepts of *Herrania* by Triana, who annotated each plate in pencil and signed his annotations. These plates were made about half a century before the genus *Herrania* and the three species so beautifully represented by the Mutis plates were described by Goudot.

Recently, a most significant discovery related to the work of the Mutis Expedition was made. The Colombian historian, Dr. Guillermo Hernández de Alba uncovered, in 1950, a beautifully preserved manuscript prepared by Padre Eloy Valenzuela, one of the most active members of the Expedition. The manuscript is without title, but Dr. Enrique Pérez-Arbeláez entitled it "Diario de la Expedición Botánica del Nuevo Reino de Granada

---

nephew, and my good friend. Dr. Herrán Medina, who served for a number of years as Colombian Consul General in Manáos, Brazil, followed the progress of my work in the Amazonian area of both Colombia and Brazil with enthusiastic interest and performed innumerable services and favors without which that work would have been much more difficult.

dirigida por Don José Celestino Mutis y llevado por Eloy Valenzuela desde el día 29 de abril de 1783 al día 8 de mayo de 1784" (Pérez-Arbeláez, E., Un hallazgo histórico y científico: el diario de D. Eloy Valenzuela. El Tiempo (Bogotá), February 11, 1951). Thanks to Dr. Pérez-Arbeláez, I may quote in full this extraordinarily detailed description of a species of *Herrania* which Valenzuela wrote in his diary and publish a photograph of one of the pages in Valenzuela's own hand.

This description, referring without doubt to *Herrania pulcherrima*, is the earliest reference to *Herrania* of which we have any knowledge. In it, Valenzuela clearly sets forth his recognition of the plant as different from the *cacao común* (*Theobroma Cacao*). Goudot's validly published diagnosis and description of *Herrania* is, for all practical taxonomic purposes, the earliest; but, for historical reasons, I am publishing herewith a transcript of Valenzuela's diary-notes on his *cacao esquinado*. There is every reason to believe that the plant to which these notes refer grew in the vicinity of Mariquita, where the Expedition carried out a great part of its labor.

Día 13 de marzo de 1784. Sin concluir el Guácimo real, se trabaja hoy en el cogollo de la theobroma de cintillas o Cacao esquinado. El otro día repetí mi visita a la mata y el dueño me dijo que los cuatro tallos que tiene aproximados corresponden a una raíz sola. Los tallos serán hacia el pie tan gruesos como el dedo pulgar sin ramo alguno tupidísimos juntamente con las hojas de pelo chico, apelmazado y amonado; por dentro blanco, fibroso, ligeros; la parte leñosa es radiada con líneas que tiran para el centro; el meollo gruesesito, blanquísimo, esponjoso, regado de puntos lucientes y cercado con algunas fibras huecas. Una de estas partes despide algo de un licor diáfano y viscido. Hojas son alternas bastante inmediatas, patentes, decusadas. — Estípulas dos laterifolias algo retiradas opuestas adpressas, subuladas pollicares y de la misma pubescencia que el tallo y hojas. — Flor: agregadas axilares y supraaxilares, peculiares de la parte inferior; pedícelos sencillos, recurvos o levantados para arriba.

Día 14. Domingo.

Día 15. Se trabaja en dibujar el tallo del cacao esquinado o theobroma de cintillas en la parte que carga las flores y como vinieron muchas de éstas, he tenido lugar de hacer el apunte casi por entero.

Cacao Esquinado. Raíz. Tallo: De la altura humana, derecho, rollizo, sencillísimo, tupidísimo de pelo chico, grueso al tanto del dedo pulgar: y parece que acompañado de 3 a 4 sobre una raíz; su color parduzco sucio, hacia el pie es algo desnudo y color de café y aquí mismo tiene la epidermis menudamente hendido-reticulada y algo levantada. — La corteza es gruesesita, verdosa debajo de la epidermis y flexibilísima, el interior blanco, fibroso, ligero y en el corte transversal se ve radiado con rayas que tiran al meollo desde la misma corteza: este es blanquísimo bofo y cercado de orifícios capilares por donde mana un jugo muy cristalino y gelatinoso.

Hojas: Grandes, alternas, túpidas, de pelo chico, 1-partidas hasta el mismo pezón común. — Pezón: común: patentes, pedales, multisulcados a lo largo y geniculados en los extremos. — Hojuelas: cuneiformes en la mitad inferior, escabradas por encima, membranáceas, y de bordes enteros, regados de puntas rigidiúsculas; la mayor excede al pezón común: las anteriores chicas obovato-oblongas, obtusas con punta: las exteriores se ensanchan desde la mitad y abren en lacinias pinnadas, anchas, acuminadas, de las que son más grandes las dos primeras, más anchas las 3 terminales. En algunas hojas se suele añadir una chica y roma antes de las primeras. — Venas: paralelas, rectas, distantes. — Estípulas: 2 laterifolias, algo distantes de la axila, subuladas adpressas, pollicares y conformes a la extensión del tallo.

Flor: amontonadas, túpidas, axilares y supraaxilares en la parte inferior del tallo y casi siempre en las axilas desnudas, pollicares ligeramente olorosas y de color purpúreo, o bien de carmín profundo. — Pedúnculos: ningúnos. — Pedícelos: sencillos, levantados, delgadisimos por el pie y con dos o tres subulas cortas. — Cáliz: periantio monófilo, coriáceo, colorido, paludo exteriormente; antes de abrir es cerrado, ovado, obtuso; no se divide hasta cerca de la base en 3 partes cóncavas, enteramente reflexas, semipollicares; la una aguda; las dos anchas y agudamente semibífidas; parece que por su naturaleza es semiquinquéfido agudo y que al reflectar se hiende algo más, y no se apartan algunas veces los tres segmentos.

Nectarios: de 5 piezas, subrotundas, chicas, convexas exteriormente, embroscadas hacia adentro, plegadas y venulosas longitudinalmente y puestas alrededor del receptáculo: sus apéndices: son otras tantas cintillas angostas lineares, con 6 pollicares corridas a lo largo de dos o más venitas de color más subido. Antes de abrir están envueltas en piezas paradas sobre los pétalos y el color tira al amarillo.

Corola: de 5 piezas alternas con las del nectario y más interiores, lanceoladas, derechas, patentes de una longitud con el periantio, surcadas por encima a lo largo y cuadunadas ligeramente en la base.

Estambres: de 10 filamentos nacidos del lado de los pétalos, cortados, gruesos, recurvados para afuera, apareados y aproximados por los apices; anteras lineares, univalves, rayadas a lo largo, convexas, adnatas, a otras tantas lacinúlas de los filamentos, blancas y escondidas en el seno de los nectarios; 4 están en un filamento y 2 en el lateral. Estas forman como un ángulo y las primeras forman dos, metido el uno en el otro.

Gérmen: superior, pentágono, pyramidal, hirsuto, chico, de color herbáceo. — Estilo único linear, subduplo de la altura de los pétalos. — Estigma un poco obtuso y parece sencillo.

Fruto: bayas sentadas sobre la flor marchita, o bien mazorca ovada acuminada, tripolicar, 5 angular verde lustrosa y regada de tomento caedizo; el acumen es entero algo oblícuo; los ángulos levantadísimos, anchos, enteros, sólidos, venulosos lateralmente y alternan con 5 venas gruesas, algo anguladas, extendidas longitudinalmente por la depresión de ellos; la corteza blanda quebradiza, subglutinosa en la partidura, blanca y destituída de ángulos por dentro. Meollo ovado, 5 surcado, libre de la corteza y prendido por la base. — Granos: 70 convexo-angulados, rugoso-reticulados, coloridos de rosado blanquísimo, arilados con un saco fibroso empapado en jugo agridulce, y aproximados como en 5 hileras con alguna pulpa intermedia. — Receptáculo común, leñoso y central; parciales filiformes.

El interior . . .

El córculus asoma la cabecilla en la superficie interior . . . Cotiledones sin las complicaciones del cacao común.

Hojas seminales:

Tengo puestos algunos granos de tierra húmeda para ver si nacen y con esto determinar el modo con que se explica su interior y el tiempo que se necesita.

Nace con mucha frecuencia en el monte y rozas de esta inmediación: el grano amargo y sumamente mantecoso, dicen ser apetecido y consumido por los micos.

La flor se podrá mirar como la mayor maravilla del reino vegetal y apenas se pudiera creer que la económica y sencillísima naturaleza hubiese gastado tantas cintas y atavíos para engalanarla casi con la ostentación de las modas.

El periantio por fuera es de color acanelado, sucio salpicado de carmín, casi borrado. Por dentro es lustroso y de carmín hermoso.

Nectario: en el fondo es blanquecino o descolorido; las venitas y pliegues son de púrpura oscura. Las cintillas son carmesíes con venas oscuras.

Pétalos de púrpura afinadísima sub-oscura.

Estambres: en los filamentos son carmesíes y en las ánteras blancos.

Gérmen: pálido verdoso. Estilo purpúrea; estigma blanco.

Mazorca verde: por dentro sub-rósea.

Día 16. Se trabaja hoy en la hoja del cacao esquinado.

ECOLOGICAL PREFERENCES OF SPECIES OF HERRANIA

Herrania is distributed from sea level to about four thousand feet, but the altitudinal range of each species is often strictly limited. *Herrania purpurea* has been collected at sea level, and most of the specimens of this species are from localities below two hundred feet. *Herrania Mariae* occurs on the great flat Amazon planada from sea level at the mouth of the Amazon River to approximately three hundred and fifty feet in the western parts of the Amazon Valley. *Herrania nitida* and *H. tomentella* can be found in the western Amazon and Orinoco drainage-areas, from about two hundred and fifty feet above sea level up to the base of the Andes at about nineteen hundred feet. *Herrania albiflora* inhabits the slopes of the Andes between about three hundred and three thousand feet, thus exhibiting a more surprising altitudinal tolerance. The only known collection of *H. umbratica* was taken at about twenty-one hundred feet. Although the type collection of *H. pulcherrima* was made on the eastern slope of the Colombian Andes at about fifteen hundred feet altitude, most of the other collections are from the central Andean regions at about three thousand feet, with a distinct variety near sea level in western Colombia. Apparently rather intolerant of altitudinal variation is *Herrania laciniifolia*, which is known only from regions between three and four thousand feet. One of the species which seems to be confined to a narrow altitudinal range is *H. breviligulata* known from two collections from the eastern slopes of the Andes between eighteen and twenty-five hundred feet. The occurrence of *H. Camargoana* merits special mention, for it is unknown except in the upper Rio Negro basin of Brazil and Colombia, where it is found near or on the summits of barren granitic mountains rising to an altitude of about five hundred feet above the level of the river (or approximately twelve to seventeen hundred feet above sea level) and, rarely, in sandy riverside savannahs. *Herrania Cuatrecasana*, *H. Dugandii*, *H. kofanorum* and *H. nycterodendron* appear to be confined to the dense forests of the westernmost parts of the Amazon Valley at an altitude of from three hundred to one thousand feet. *Herrania lemniscata* is found between four hundred and three thousand feet and *H. kanukuensis* between four hundred and one thousand two hundred feet.

The species of *Herrania* do not seem to be exacting in their soil requirements, with the single exception of *H. Camargoana* which prefers and, actually, is found exclusively on sterile white sand and on the most inhospitable of rocky slopes strewn with granite blocks and often nearly devoid of soil. Most species thrive on well-drained slopes, but I have seen *Herrania purpurea* in the northwestern part of Colombia along the banks of rivers where, in the rainy season, the plants stand in from four to six feet of water. Similarly, *Herrania Mariae* often grows in Amazon forest which is subject to deep flooding half the year. *Herrania lemniscata* is also reported to grow in "mixed forest in swamp and on rather swampy soil" or "en selva anegada en la estacion lluviosa." The widely distributed *Herrania nitida,* in the Amazon Valley, is found usually just above the reach of the deep annual inundation, although occasionally it occurs where a few feet of water may stand for several weeks; it cannot, however, be classified as a flood-tolerant species.

There is one point which stands out in relief concerning the ecology of the various species of *Herrania*: both in altitudinal tolerance and in topographical preference there is a tremendously wide range within the genus. Some species seem to be extremely exacting, whereas others show an unbelievable tolerance in both altitudinal and topographical distribution.

Although all species of *Herrania* are primarily forest trees, a number act like weeds and propagate rapidly in agricultural clearings. The heliophilic tendency is especially marked in *Herrania nitida.* In the Amazon area, especially in Indian settlements, trees of *Herrania* are never sacrificed in the clearing of a field for planting or in the weeding of a cultivated patch. Since most cultivation is attempted on land above the reach of the annual flood, the species most commonly met with under conditions of partial human care is *Herrania nitida.* The only reason for not cutting down *Herrania* trees is, apparently, the esteem in which the natives hold the acidulous pulp surrounding the seed. Under conditions of ample room and sunlight, many more fruits mature than in the forest, and man is thereby repaid for his little consideration in sparing the tree. This toleration of the tree in planted fields is undoubtedly the basis of occasional reports that *Herrania* is sometimes cultivated. I have never seen *Herrania* under conditions of cultivation, nor have I been able to find reliable reports in the literature or on herbarium specimens to this effect.

USES OF SPECIES OF HERRANIA

As has been pointed out above, the principal importance of *Herrania* lies in its potentialities as a source of new germ-plasm in a possible hybridization program with the cultivated species of *Theobroma.*

In addition to this potential use, a few species find employment among native peoples. Everywhere *Herrania* trees are left standing in cultivated ground, because the white, acidulous pulp in which the seeds are embedded is eaten. Apparently this pulp is most delicious just before complete ripening of the fruit, and for this reason, it is often difficult to find a mature capsule. It is said that monkeys also search for the fruit as a food. Among the Ingano Indians of Mocoa, in the Putumayo of Colombia, the ashes of the bark of *Herrania breviligulata* are employed to dry up and "cure" infected wounds and ulcers (*Schultes & Smith 2050*). In British Guiana, according to notes accompanying *Archer 2514, Herrania lemniscata* is utilized in the preparation of a "beverage like chocolate." Similarly, Pittier reports (Plantas Usuales de Costa Rica. 72. 1908) that the Bribrí Indians of Costa Rica employ the seeds of *Herrania purpurea* to make a bitter drink. It has been reported (Van Hall, Cacao. ed. 2. 74. 1932) that formerly, in northern Colombia, the seeds of *Herrania albiflora* were purposely mixed with those of commercial cacao to improve the flavor of the chocolate and that these same seeds were often used to prepare a bitter febrifuge. *Herrania Mariae* seeds were formerly found as an adulterant in "Pará cacao" (Van Hall, loc. cit.).

RELATIONSHIPS AND TAXONOMY

Herrania appears taxonomically to be intermediate between *Guazuma* and *Theobroma*. It approaches *Guazuma* in the placement of its anthers but has an entirely different habit and fruit. It can be separated from *Theobroma* immediately by its habit (having compound-digitate leaves and, in general, comprising small, delicate and slender treelets). It further differs from *Theobroma* in the placement of its stamens, in the number of divisions of the calyx, in the length and form of its ligules, in its wood anatomy and in the structure of the pollen grains. The fruit of *Herrania* resembles, in outward form, that of *Theobroma*, but the seeds of *Herrania* have thick cotyledons which are almost entire and which are apparently not folded. The field botanist has perhaps a better opportunity of noting the differences between *Theobroma* and *Herrania*, for, in addition to the technical characters listed above, he is able to appreciate the great difference in habit and to observe that the jorquetting habit of branching, so characteristic of *Theobroma*, is not found in *Herrania*.

Although it would appear, on the basis of a taxonomic and morphologic examination of recent collections and field studies, as well as on experimental evidence, that *Herrania* may very justifiably be considered as a genus distinct from *Theobroma*, it has, in the past, usually been relegated to the position of section or subgenus under *Theobroma*. Schumann (in Martius, Fl. Brasil. 12(3): 70–72. 1886), for example, considered Goudot's *Herrania* to constitute merely a section of *Theobroma*, which genus he divided into the two sections: *Herrania* and *Eutheobroma*. Bernoulli (Uebersicht der bis jetzt bekannten Arten von *Theobroma*. 4. 1871), on the contrary, had divided *Theobroma* into four sections but kept *Herrania* as a distinct genus, stating, ". . . *Theobroma* ab *Herrania* Goudot genere proxime affini differt praecipue habitu, foliisque integris nec digitatim quinque- sexfoliolatis."

The general tendency in recent years has been to keep *Herrania* and *Theobroma* as distinct genera. Cook (Contr. U.S. Nat. Herb. 17: 616. 1916), for example, followed this course. Cheesman (The economic botany of cacao. Suppl. Trop. Agric. 1. 1932) pointed to *Herrania* and *Guazuma* as the nearest relatives of *Theobroma*. Chevalier (Révision du genre *Theobroma* d'après l'Herbier du Museum National d'Histoire Naturelle de Paris. Rev. Bot. Appl. Agric. Trop. **26**: 265. 1946) excluded *Herrania* from his treatment of *Theobroma*. A recent morphological and taxonomic study of *Guazuma* (Freytag, G. F., A revision of the genus *Guazuma*. Ceiba **1**: 193 ff. 1951) offers data which very convincingly support the separation of *Herrania* from *Theobroma*.

A comparative study of the pollen of *Herrania*, *Guazuma*, *Theobroma* and other allied genera, outlined in detail below, has indicated that there are appreciable differences between the pollen of *Herrania* and *Theobroma*.

There is still not complete agreement, however, in the generic interpretation of *Herrania*. In 1940, Ducke (Rodriguesia **4**: 273. 1940) treated *Herrania* as a "subgenus (or section)" of *Theobroma*. A chromosome study of several species of *Theobroma* and *Herrania* carried out by Muñoz (Estudios cromosómicos en el género *Theobroma* L. Unpubl. Thesis. Fac. Inst. Interam. Ciénc. Agríc. Turrialba 30–35. 1948), indicates that the number in both concepts is $2n = 20$. The chromosomes are very similar, but they are generally more slender and more definitely contrasted in *Herrania albiflora*, *H. purpurea* and *H. pulcherrima* (the only three species studied) than in those species of *Theobroma* which were examined. Muñoz feels, but is not entirely certain, that *Herrania* should be treated as a section of *Theobroma*.

Most recently, Ducke (As espécies brasileiras do gênero *Theobroma* L. Bol. Técn. Instit. Agron. Norte **28**: 3–20. 1953) has reiterated his belief that *Herrania* and *Theobroma* should be treated as a single genus.

It is pertinent to this discussion that recently *Theobroma* and *Herrania* have been shown experimentally to be very closely allied. Ing. Agron. Addison, geneticist at the Instituto Agronômico do Norte in Belém do Pará, Brazil, successfully pollinated *Theobroma Cacao* with *Herrania Mariae*, but the embryos failed to develop (Addison, G. O'N., & R. M. Tavares, Observações sobre as espécies do gênero *Theobroma* que ocorrem na Amazônia. Bol. Técn. Instit. Agron. Norte **25**: 1951).

Van Hall (Cacao. ed. 1. 1914; and ed. 2. 1932) treated *Herrania* as a section of *Theobroma*. On the other hand, Pound (Cacao and witchbroom disease (*Marasmius perniciosus*) of South America. 47 ff. 1938), while not definitely committing himself, outlined in very great detail the characteristics of *Herrania* and pointed out the important differences between *Herrania* and *Theobroma*.

The following key (adapted primarily from Schumann's key to his sections *Herrania* and *Eutheobroma* of the genus *Theobroma*) sets forth the gross characters by which *Herrania* may be separated from *Theobroma*.

A. Arbores parvae et graciles. Folia quinque- ad novem-digitata. Petalorum ligulae lineares vel filiformes, comparate longissimae, cucullum multo superantes, in alabastro circinnato-involutae. Calyx usualiter 3-fidus. Fructus saepissimae conspicue costatus, pericarpio vulgo aliquid crassulento. .... **Herrania.**

AA. Arbores. Folia integra. Petalorum ligulae, duplo vel triplo cucullum superantes, vel breviores, in alabrastro reflexa vel erecta. Calyx usualiter 5-fidus. Fructus saepe obscure costatus vel sublaevis, pericarpio ut videtur saepius sicco et duro. .... **Theobroma.**

Herrania Goudot, Ann. Sci. Nat. III. **2**: 230. *t. 5.* 1844; Walpers, Rep. **5**: 111. 1845–46; Endl. Gen. Pl. Suppl. **4**: 62. 1850; Karst. Linnaea **28**: 446. 1856; Tr. et Planch. Prodr. Fl. Novo-Granat. 209. 1862; Benth. et Hook. Gen. Pl. **1**: 225. 1862; Walpers, Ann. Bot. Syst. **7**: 225. 1862, **7**: 430. 1868; Baill. Hist. Pl. **4**: 131. 1873, Dict. Bot. **3**: 49. 1891.

Lightia Schomb. Rep. Brit. Assoc. Adv. Sci. **2**: 71. 1844. Non *Lightia* Schomb. Linnaea **20**: 757. 1847.

Brotobroma Karst. et Tr. ex Tr. Nuev. jén. y esp. plant. fl. Neo-Granad. 11. 1854.

TYPE SPECIES: *Herrania albiflora* Goudot.

GENERAL DISTRIBUTION: From Costa Rica down the Andes to Peru, along the Pacific coast of Colombia and Ecuador, across Venezuela and the Guianas and in the Amazonian basin of Brazil, Colombia, Peru and, probably, Bolivia.

ORIGINAL DESCRIPTION: Calyx 3-partitus, coloratus, deciduus, laciniis aequalibus concavis; aestivatio valvata. Corolla 5-petala, hypogyna, cucullato-concava, apice inflexo in ligulam linearem, ante anthesin concolutam, producta. Androphorum 5-fidum, carnosum, glabrum; laciniis sterilibus cum petalis alternantibus suprene in appendicem erectam vel reflexam dilatatis; laciniis fertilibus longitrorsum adnatis, petalis oppositis, brevioribus, singulis, 3-andris. antheris ovatis didymis. Stylus cylindraceus. Stigmata 5, teretiuscula, obtusa. Ovarium 5-gonum, 5-loculare sessile, disco hypogyno destitutum. Ovula anatropa in singulo loculo anguloque centrali 1-seriata, horizontalia. Fructus ovato-oblongus, costatus, basi et apice subacuminatus, coriaceo-lignosus, indehiscens. Semina in pulpa nidulantia, ovata, angulata, testa pergamacea venosa. Embryo cotyledonibus crassis, hinc convexis, inde planis, radicula brevissima.

Small trees. Leaves unusually large, digitate, 4–9-foliolate. Flowers cauline, fasciculate. Calyx 3–5-fid; sepals more or less divided, valvate in the bud. Corolla 5-parted; petals hypogynous, cucullate-concave, apically inflexed, with a linear or filiform ligule which, before anthesis, is circinnate-involute. Androphore 5-fid, fleshy, glabrous; sterile segments alternate with the petals, enlarged above into erect or reflexed, ovate-lanceolate or linear, petaloid staminodes; fertile segments 1–4(mostly 3)-antheriferous, anthers short-stipitate, with diverging, didymous locules. Ovary sessile, 5-locular, the lower with many anatropous ovules. Style filiform, cylindrical. Stigmas 5, rather terete, obtuse. Fruit ovate-oblong, costate, apically usually subacuminate or acuminate, toughly coriaceous, indehiscent. Seeds enclosed in a pulp, flattened-ovate, angulate, with a papery testa, exalbuminous; cotyledons thick, sometimes flat, with a very short radicle. Chromosomes: $2n = 20$ (in three species studied).

In his "Woods of northeastern Peru" (Field Mus. Nat. Hist. Bot. Ser. **15**: 323–324. 1936), Llewelyn Williams has published what appears to be the only detailed description of the wood of *Herrania.* Williams cited five collections which were used as a basis for this description and referred all of the collections to "*Theobroma Mariae.*" I have found that they represent *Herrania nitida.* Until wood samples are collected in exact correlation with herbarium specimens from many areas and for numerous species, an understanding of specific differences in the wood of *Herrania* cannot be appreciated. For this reason, Williams' description of *Herrania nitida* must serve as a guide to the wood structure of the whole genus.

Sapwood pale pink; heartwood pinkish brown. Wood has no distinctive odor or taste; straight- or wavy-grained, coarse-textured; light in weight and soft; requires a sharp knife to cut smoothly across grain; perishable. Growth rings absent or present. Parenchyma indistinct. Pores fairly small or very small; not numerous and well-scattered; solitary or in radial multiples of 2–3. Vessel lines fairly long, not prominent, but discernible to unaided eye. Rays coarse, lighter-colored than background, sometimes wavy, and conspicuous on cross section; darker than background and fairly distinct on tangential; of darker color than adjacent elements and conspicuous on radial surface. Pith light or dark greyish brown.

The examination of the pollen grains of *Herrania,* to the best of my knowledge the first which has been made, was carried out by Dr. Theodor van der Hammen of the Colombian Servicio Geológico Nacional. Pollen of *Herrania tomentella* was analyzed. All terms are used in accordance with Iverson and Troels-Smith's nomenclature proposed in 1950.

Herrania tomentella R. E. Schult. Pollen collection Serv. Geol. Nac. #IV 86. Collection Col. 34377.

Pollen grains: tricolporate, reticulate, subsphaeroidal; granulae of the muri visible but not separated. Lumina of reticulum irregular of size, rather large, polygonal, smaller near the colpae. In the lumina, rather faint granulae are visible. Colpae clear, edges separated; pores clear, without ectexine elements; sometimes indications of small transversal furrows. Magnitudo pollinis: media (28–33 μ). Magnitudo luminum: meso-macro (2–4.7 μ) and smaller. Index pollinis: subsphaeroidea (1–1.12); ('*prolate sphaeroidal*' of Erdtman). Index areae poli: middle (0.30–0.35). Index exinae: middle (0.05–0.08).

Van der Hammen reports further that *Theobroma, Guazuma, Sterculia* and *Herrania* have tricolporate and reticulate pollen grains but that the grains of *Waltheria* and *Helicteres* are of different types. A comparison of the four genera with tricolporate and reticulate grains leads to the really unexpected conclusion that, insofar as pollen morphology is concerned, there is no evidence that *Herrania* and *Theobroma* are very closely allied. On the contrary, the pollen grains of *Theobroma* resemble those of *Guazuma* even more than they do those of *Herrania*. Van der Hammen compares the grains of *Theobroma Cacao* and of *Herrania tomentella* as follows: "The grains of *Theobroma Cacao* are subsphaeroidal ('*oblate sphaeroidal*' of Erdtman); index pollinis ± 0.8–0.9; magnitudo pollinis ± 22 μ. The polar area is relatively much larger than that of *Herrania*, the colpae are very narrow, unclear and short. Pores are small and not very clear; lumina of ret much smaller than those of *Herrania* (greatest size measured 1–1.75 μ), and more regular. Exine (including sculpture) relatively thicker than those of *Herrania*."

A most careful and detailed chemical analysis of the seeds of *Herrania* has been made by MacLean (MacLean, J. A. R., Oil-bearing seeds of possible economic importance to West Africa. Nature **169**: 589. April 5, 1952). The material studied was reported to be referable to *Herrania balaënsis* and *H. Mariae*, but unfortunately no voucher specimens were cited for checking, and the specific identifications are open to doubt. The plants were introduced from Trinidad to West Africa in 1944. The photographs published on pages 589 and 590 would suggest that one of the species analyzed (probably the one called *Herrania Mariae*) was *H. nitida*.

MacLean reported a very high oil content (up to 66.1%) of the seeds, and it is suggested that optimum cultural conditions might improve this figure. He found that the "percentage of total alkaloids is approximately one-third that of Amelonado beans, and the theobromine-caffeine ratio is reversed." The caffeine values were found to be comparable with the lower limit of range for coffee beans and kola nuts, with values greater than 1% being obtained on two occasions. Freshly extracted fat from *Herrania* seeds is liquid at 25–29°C with an odor resembling that of linseed oil; its specific gravity is 0.93–0.94; and its unsaponifiable matter is less than 1%. The figure for reducing sugars (0.4%) is four times that of Amelonado beans. The iodine values varied from 39 to 47, and the saponification value ran from 203 to 206. The percentage of free fatty acids in the oil ranged from 2.3 to 2.8 The composition of the oil was found to be 18–26% linoleic, 2–7% oleic and 74–76% of saturated acids.

Herrania comprises two groups of species which are sufficiently well marked one from the other to permit their segregation into sections. These two sections are not only distinct in the morphology of the flower; they also fall naturally into two distinct, though overlapping, geographical areas.

Sect. **Herrania**

Calyx patelliformis, sepalis media pro parte connatis. Subgeneris typus: *Herrania albiflora* Goudot.

Sect. **Subcymbicalyx** R. E. Schultes, sect. nov.

Calyx subcymbiformis, sepalis plerumque fere usque ad basim liberis. Subgeneris typus: *Herrania nitida* (Poepp.) R. E. Schultes.

The characters upon which these concepts are founded serve for the first dichotomy in the following key to the species. *Herrania albiflora*, *H. purpurea* and *H. umbratica* are the only species with the curious patelliform calyx. Their flowers, because of this condition, have a completely different appearance from those of all other species: the patelliform calyx lends a "closed" or compact appearance to the flower, whereas the subcymbiform condition allows for a greater expansion of the petals and their ligules and the staminodes. Furthermore, the ligules of *Herrania albiflora, H. purpurea* and *H. umbratica* are extremely short, whilst those of all other species are longer — with the single exception of *H. breviligulata*, very much longer.

The species of the section *Herrania* are confined to Middle America and the northernmost regions of Colombia in South America. Those of *Subcymbicalyx* extend over the whole northern half of South America, in northern Colombia overlapping the area occupied by the three species of Sect. *Herrania*.

Although, at the present state of our understanding of the genus, it is rather difficult to form any well founded phylogenetic picture, the patelliform calyx would appear to me to represent a derived condition and the subcymbiform calyx, conversely, a primitive condition in *Herrania*.

CLAVIS SPECIERUM HERRANIAE

A. Calyx patelliformis. Sepala medio pro parte connata. Ligulae usque ad 20 mm. longae. Sect. HERRANIA.
  B. Petala, ligulae et staminodia alba. Sepala usque ad 7 mm. longa. .... 1. *H. albiflora.*
  BB. Petala, ligulae et staminodia purpurea vel sanguinea. Sepala 12 mm. longa vel longiora.
    C. Ligulae usque ad 15 mm. longae. Capsulae costae valde inaequales, aliquid tenues, distantes. Fructus usque ad 9 cm. longus. .... 15. *H. purpurea.*
    CC. Ligulae 19 mm. longae vel longiores. Capsulae costae quasi aequales, crassissimae, non distantes. Fructus 11 cm. longus vel longior. .... 17. *H. umbratica.*

AA. Calyx subcymbiformis. Sepala plerumque fere usque ad basim libera. Ligulae 25 mm. longae vel longiores. Sect. SUBCYMBICALYX.
  D. Foliola profunde incisa vel lobata.
    E. Foliola grosse et regulariter pinnatisecta; lobulis anguste triangulari-lanceolatis, acutissimis; lamina subtus densissime et molliter stellato-tomentosa, usque ad 60 cm. longa. Ligulae 180 mm. longae. Capsula maturitate fusco-rubescens; costis longitudinalibus bene conspicui et sine costis transversalibus prominentibus. .... 9. *H. laciniifolia.*
    EE. Foliola maxime grossissime sed irregulariter pinnatilobata; lobis late triangularibus, acutis lamina subtus aspera, stellatis cum pilis, usque ad 80 cm. longa. Ligulae 85 mm. longae. Capsula maturitate ochracea (?); costis transversalibus bene prominentibus. .... 10. *H. lemniscata.*
  DD. Foliola integra vel leviter dentato-sinuata vel undulata.
    F. Ligulae 25–35 mm. longae. Foliola subtus cum indumento subcinereo-velutino. .... 3. *H. breviligulata.*

FF. Ligulae 60 mm. longae vel longiores. Foliola subtus glabra vel cum indumento aspero vel molle, sed numquam velutino.

G. Foliola glabra vel subtus sparsissime aspero-tomentulosa. .... 12. *H. nitida.*

GG. Foliola variabiliter sed molliter pilosa vel tomentosa.

H. Foliola valde et regulariter sinuata.

I. Capsula costis quinque longitudinalibus rectis armata et laevis vel transverse striatofibrosa; maturitate flava. Staminodia quam 17 mm. longiora, apice acuta vel conspicue trifida.

J. Foliola maxima, 45–60 cm. longa vel saepissime longior × 19–35 cm. lata, latissime lanceolato-ovata, ½ lata duplo longior quam latior, apicem versus grossiuscule sinuata, dentibus 5–9 cm. distantibus. Petala et ligulae rufo-purpurea. Ligulae 2–3 mm. latae. Staminodia apice trifida. .... 14. *H. pulcherrima.*

JJ. Foliola minor, usque ad 60 cm. longa sed saepissime brevior × 10–15 cm. lata, anguste lanceolato-elliptica, quadruplo longior quam latior, dentibus 2–4 (rarenter 5) cm. distantibus. Petala et ligulae albicantes, ligulae minores quam 2 mm. latae. Staminodia apice acuta.

K. Foliola usque ad 30 cm. longa × 11 cm. lata. Sepala inaequalia; majora 15–16 mm. × 15 mm.; minora 10 mm. × 6 mm. Petala 9 mm. × 7 mm. Staminodia lanceolato-elliptica, 22 mm. × 6 mm. .... 8. *H. kofanorum.*

KK. Foliola usque ad. 60 cm. longa sed vulgo brevior × 15 cm. lata. Sepala subaequalia, 14 mm. Petala 8 mm. × 5 mm. Staminodia elliptica, 18 mm. × 8 mm. .... 2. *H. balaënsis.*

II. Capsula costis quinque longitudinalibus rectis armata sed etiam transverse bene costata, in junctionibus costarum longitudinalium et transversalium projectionibus spiniformibus longis, mollibus et crassis productis; maturitate sanguinea vel rarenter flava. Staminodia usque ad 14 mm. longa, apice valde obtusa. .... 4. *H. Camargoana.*

HH. Foliola normaliter integra, subintegra vel apicem versus plus minusve sinuosa.

L. Foliola lanceolato-oblonga, usque ad 60 cm. longa × 22 cm. lata, basi longe et sensim attenuato-decurrentia. Petioli 45–60 cm. longi.

M. Capsulae costae tenues, late cultriformes, principaliter costa versus pilis urticantibus armatae, tactu asperae; capsula alibi glabra vel glabrescens. .... 5. *H. Cuatrecasana.*

MM. Capsulae costae crassae, hebetato-rotundatae, sine pilis urticantibus; capsula omnino molliter indumento stellato-velutino armata.

N. Capsula ovoidea, apice breviter cuspidata vel subrotundata, costis minoribus, primariis usque ad 2 mm. altis, secundariis haud prominentibus. .... 7. *H. kanukuensis.*

NN. Capsula ellipsoidea, apice obtusa vel attenuata, costis majoribus, primariis usque ad 8 mm. altis, secundariis usque ad 3–5 mm. altis.
  O. Capsula 10–12 cm. longa, 4–5 cm. in diametro, apice longe et sensim attenuata, cum costis hebetatis crassissimis, non bene distantibus, inter costas prominenter fibroso-rugosa. Ligulae usque ad 90–100 mm. longae. Staminodia apice leviter trifida. . . . . 13. *H. nycterodendron.*
  OO. Capsula 9 cm. longa, 4 cm. in diametro, apice vulgo obtusa, cum costis hebetatis crassis, bene distantibus, inter costas paullo et leviter fibroso-rugosa. Ligulae usque ad 70 mm. longae. Staminodia apice acuta. . . . . 16. *H. tomentella.*
LL. Foliola obovato-oblonga vel subrhomboidea, usque ad 31 cm. longa × 12 cm. lata, basi aliquid attenuata vel quasi cuneata. Petioli plus minusve 30 cm. longi.
  P. Foliola obovato-oblonga, vulgo 35 cm. longa vel minora. Sepala aequalia vel subaequalia, 21 mm. longa × 12 mm. lata, intus subdense ferrugineo-pilosa. Petala 11–12 mm. × 5–6 mm. Ligulae atrosanguineae vel atropurpureae, 100 mm. longae, 2 mm. latae. Staminodia lanceolata, apice acutissima, integra 12–15 mm. × 5 mm. . . . . 6. *H. Dugandii.*
  PP. Foliola rhomboideo-obovata, vulgo 30–35 cm. longa. Sepala valde inaequalia; majora 12–15 mm. longa × 6–10 mm. lata; minora 11–13 mm. × 11–12 mm., intus glabra vel minutissime pilosa. Petala 7–9 mm. × 6–8 mm. Ligulae albicantes, 75–100 mm. longae, usque ad 1 mm. latae. Staminodia lanceolato-elliptica, apice obtusa et saepe indentato-mucronata vel serrata, aliquid sinuato-undulata, 20 mm. × 6–7 mm. . . . . 11. *H. Mariae.*

1. **Herrania albiflora** Goudot, Ann. Sci. Nat. Paris III. 2: 230. *t. 5, fig. 1–10.* 1844; Tr. et Planch. Prodr. Fl. Novo-Granat. 1: 209. 1862; Schultes, Caldasia 2: 325. 1944.

Theobroma albiflorum (Goudot) De Wildeman, Pl. Trop. Grande Cult. 90. 1902.

DISTRIBUTION: Northern sector of the Magdalena basin in Colombia and in westernmost Venezuela.

Small tree up to 16 feet tall consisting of several round, simple or (rarely) branching trunks, 11–14 cm. in diameter, with a greyish bark. Leaves grouped at the apex of the trunk, digitate, stipulate, 5–6-foliolate. Branches densely and minutely ferruginous-tomentulous, probably becoming almost glabrous. Petioles terete, densely and minutely ferruginous-villose, somewhat dilated at the base, as long as the leaves, conspicuously striate-sulcate, up to 45 cm. long, 4–6 mm. in diameter. Stipules conspicu-

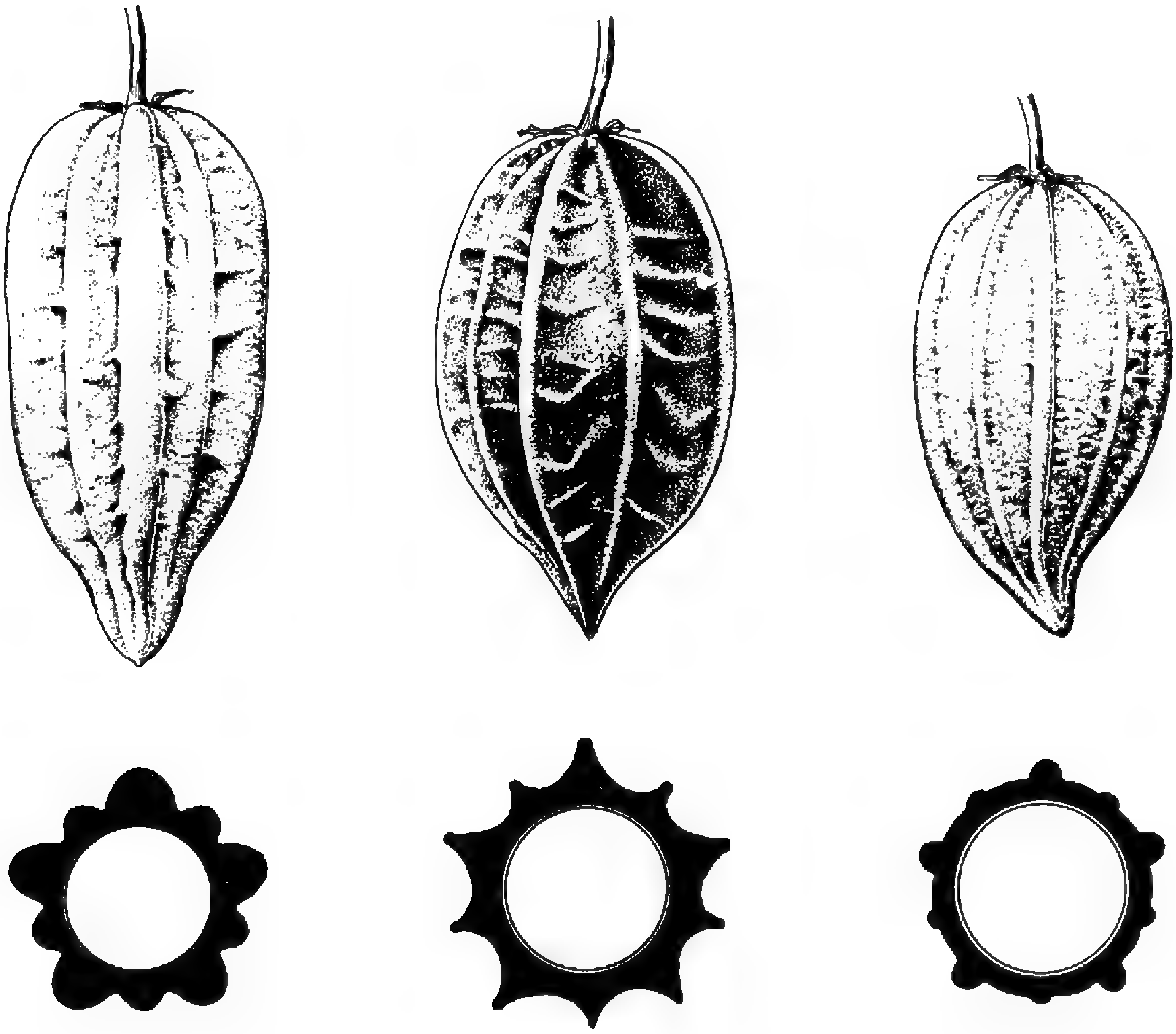


Fig. 1. Fruits of *Herrania nycterodendron*, *H. Mariae*, and *H. kanukuensis* (left to right) with schematic cross sections.

ous, linear, entire, acute, caducous, ferruginous, 50 mm. long, 3–4 mm. wide. Leaflets lanceolate-obovate, acuminate, basally long-attenuate-decurrent, very shortly petiolulate (petiolule strong, 3–4 mm. long), marginally entire, thin-chartaceous, 20–60 cm. (usually 50 cm.) long, 9–15 cm. wide, dark green and glabrous above, pale green and almost glabrous, or with extremely remote and microscopic stellate hairs, beneath; the veins of both surfaces prominent, clothed with ferruginous, minute and weak puberulence. Inflorescence fasciculate, few-flowered (5 or 6 flowers). Flowers subglobose, 15 mm. in diameter, borne in contracted racemes on the lower and middle part of the trunk, white, pedicellate. Pedicels very short, cylindric, fulvous-tomentulose, subtended at the base by a minute, very densely fulvous-tomentulose, linear bract. Flower buds small, globose, tomentose. Calyx patelliform. Sepals 3, subequal, connate half their length, rotund-ovate, rounded, marginally entire, yellowish white, externally densely stellate-villose, internally glabrous, about 7 mm. long, 6 mm. wide. Petals 5, very broadly rotund-ovate, cucullate, glabrous near the apex, thick-membranaceous, somewhat muricate-granulose on both surfaces, 5 mm. long, 4 mm. wide, longitudinally striate-veined, internally with conspicuous veins, ligulate, white. Ligules linear, reflexed, white, glabrous, membranaceous, with 6 or 7 brownish nerves, up to 2 cm. (usually shorter) long, less than 1 mm. wide at the base. Stamen tube 5-fid, alternately 2- and 3-antheriferous with short, simple, free filaments and 2-locular, divergent, longitudinally dehiscent anthers. Staminodes petaloid, very broadly ovate, acute, reflexed, 6 mm. long, 5 mm. wide, densely muricate-granulose on both sides, marginally entire. Pistil short, more or less 1.5 mm. long. Style linear, erect, glabrous with a 5-parted stigma. Ovary sessile, subglobose, pilose, 1.3 × 1 mm. Fruits capsular, oblong, apically short-acuminate, the tip somewhat rounded, hispid, 10-costate, yellow when ripe, 11–14 cm. long. Seeds 30–40, irregular, compressed, enveloped in a white, mucilaginous pulp, slightly acid, covered with an internal membranous tegument and an internal pellicle, coriaceous and exteriorly rugose. Embryo brown, with 2 thick, unequal, rarely folded cotyledons and a very short radicle.

Colombia. [No definite locality, probably near Mariquita], *Exped. Bot. Mutisii Novae-Granat. 3759.* ANTIOQUIA: Vuelta de Acuña, Río Magdalena [leaves only referable to *H. albiflora*], *Pennell 3799*; opposite Boca Carare, alt. 125 m., *Pennell 3832.* BOLIVAR: Bojorque [Bohórquez], Río Magdalena, *Bonpland 1580*; Norosi-Tiquisio Trail, Lands of Loba, alt. 150–600 m., *Curran 135*; Boca Verde, Río Sinú, alt. 100–300 m., *Pennell 4208.* CUNDINAMARCA: Muzo, *Goudot s.n.* (Type); Río Guaco, near Muzo, *Purdie s.n.* SUR DE SANTANDER: vicinity of Puerto Berrio, between Carare and Magdalena Rivers, alt. 100–700 m., *Haught 1598.* **Venezuela.** ZULIA: vicinity of Perija, *Tejera 268.* **Trinidad.** Royal Botanic Gardens, Port-of-Spain, *No Collector Cited*; *Bailey s.n.*; Imperial College of Tropical Agriculture, Diego Martin Estate, *Schultes 18639.*

Herrania albiflora is very closely allied to *H. purpurea* from which it can be distinguished by its white or cream-colored flowers. There are also other differences: the sepals of *Herrania albiflora* are usually much smaller than those of *H. purpurea*; the stipules of the former are longer than those of the latter species; the leaflets of *H. albiflora* are lanceolate-obovate, whereas those of *H. purpurea* tend to be obovate-oblong; and the petals of the former species are very broadly rotund-ovate, 5 mm. × 4 mm., whilst those of the latter are obovate, 8 mm. × 8 mm.

The habit and general floral structure of *Herrania albiflora*, *H. purpurea* and *H. umbratica* are strikingly similar. These species alone in the genus have a patelliform calyx, which gives the flower a completely different appearance from the usual cymbiform calyx. The ligules in these three species are likewise similar in structure and are under 20 mm. in length.

Purdie s. n., one of the earliest collections of the species, was identified as *Herrania albiflora* at Kew by Planchon, who annotated the sheet, a topotype. The report of the collector of this specimen relative to his having seen "several hundreds of fruits" on a cultivated tree of *Herrania albiflora* must be recognized as an exaggeration. Although fruits are often very numerous in most of the species of *Herrania*, I have never met any condition which would indicate "hundreds of fruits".

It has always been presumed that the type of *Herrania albiflora*, the type-species of the genus, was preserved in the herbarium at Paris, but in June, 1950, I found Goudot material at Geneva which may very well be the type of *Herrania albiflora*. In Geneva, there are three sheets representing the Goudot collection of this species, all labelled, in his handwriting: "C. N. 1 *Herrania albiflora* mihi. Annales Sc. Nat. 1844. Muzo." One sheet has several very young and membranaceous leaves and an envelope in which there are fragments of a fruit belonging possibly to an annonaceous plant and which, by some error, have been associated with the *Herrania* collection. Another sheet has a complete and mature leaf. The third sheet has three envelopes: one contains several seeds of *Herrania albiflora*; another has a few flowers and a very young capsule; the third has a flower completely dissected, with the parts glued flat to the envelope. An examination of these floral parts and of Goudot's description and drawing of *Herrania albiflora* leads me to the conclusion that, at least for the flowers and fruits, the Geneva material is the type of the species and genus. As to how has it been possible for Goudot type material to find its way to Geneva one cannot be certain. There are, of course, many Goudot collections in the Delessert Herbarium (cf. A. Lasègue, Musée Botanique de M. Benjamin Delessert. 471. 1845).

It may be of interest to note that a comparison of the Goudot floral dissection with the description of *Herrania albiflora* has uncovered several minor discrepancies or omissions. The sepals, described as glabrous within, have a very minute and sparse puberulence on the lower portion of the inner surface; and the petals are extremely muricate-granulose externally, as are also the very short ligules in the basal portion near their junction with the petal.

One of the Mutis plates in Madrid, executed by the Colombian botanical artist Francisco Javier Matíz, represents a fruiting and flowering branch of *Herrania albiflora*. Not only are ripe and unripe fruits shown in excellent detail, but a large number of flowers are depicted so painstakingly that it is clear that Mutis and his colleagues could, so long ago, differentiate between the patelliform calyx of *Herrania albiflora* and the subcymbiform calyx of the other species illustrated. No foliage is drawn on the plate of *Herrania albiflora*. Triana correctly annotated this plate as "*Herrania albiflora* Goudot."

In the Mutis collection of plants in Madrid, there is a sterile collection of leaves, misidentified as "*Theobroma Mariae*," which represent *Herrania albiflora*. They undoubtedly belong to the plant the flowers and fruits of which are portrayed on the Mutis plate of *Herrania albiflora*.

Van Hall (Cacao. ed. 2. 74. 1932) claims that "according to Goudot, who collected this species near Muzo (Colombia), the seeds are mixed with those of the commercial cacao for home use; they are said to improve the taste of the chocolate." He credits Goudot with the report that "the seeds are also used, unmixed, for the preparation of a very bitter product which is used by the population as a febrifuge".

Herrania albiflora is generally recognized as a cacao-relative. Hart (Cacao. 13. 1911) reports that "*Herrania albiflora* and *Pachira insignis* have both been sent to the author as 'wild' cacao, but neither of these trees has anything in common with *Theobroma Cacao* and neither of them produces saleable samples".

1a. **Herrania albiflora** Goudot f. **titanica** R. E. Schultes, Caldasia 3(15): 442. *t. pag. 443.* 1945.

DISTRIBUTION: Western or Magdalena slope of the eastern Cordillera in the Departamento del Sur de Santander, Colombia.

Usually a robust tree up to 30 feet in height, differing from *Herrania albiflora* principally in having much larger leaves and flowers.

Colombia. SUR DE SANTANDER: Carare, Landazuri alt. 1000 m., *Richter s.n.* (Type); vicinity of Barranca Bermeja, Magdalena Valley, between Sogamosa and Colorado Rivers, alt. 100–150 m., *Haught 1490.*

The collection *L. Richter s. n.* seems to present clear evidence that there exists a very large variant of *Herrania albiflora*, which may probably best be treated as a distinct *forma*. The leaves are not only very large for the species, but, in *Richter s. n.*, the entire plant is exceptionally robust for the genus, measuring up to 10 meters in height. The height of the plant from which *Haught 1490* came is not given, but the collector notes that it was "a small tree;" this would seem to indicate, in the case of such a meticulous collector as Haught, that it was *not*, as in nearly all the species known, a "treelet." The leaves of *Haught 1490* are much larger than in the Richter collection.

I have found that within a species of *Herrania* the size of the leaves is more or less standard, regardless of whether it grows in shaded forest or open pasture. This causes me to feel that the unusual size of the leaves of *Herrania albiflora* f. *titanica* does not represent a mere ecological variant.

Vegatatively, the new form is almost indistinguishable from *Herrania umbratica* of the same general region, but there are important differences in the fruits (Caldasia 2: 261–264. *tt. 2, b, c, d.* 1943). It is unfortunate that, except for the drawing which accompanies the original description, we know very little of the fruit of *Herrania albiflora*. The capsule of *Herrania albiflora* f. *titanica* is similar to that of *H. purpurea*, being somewhat intermediate between *H. purpurea* and *H. umbratica*. It measures 12.5–14 cm. in length and 5–5.5 cm. in diameter and has low, rounded unequal ribs; the apex is acuminate.

Richter informed me that he collected a few dried flowers from the base of the type of *Herrania albiflora* f. *titanica* and that they showed evidence of having been white or yellowish in life. Unfortunately, these were lost in shipment. The color of the flower in *Haught 1490* is uncertain, for the label bears no note in this respect. But with *Haught 1598* (a collection representing *Herrania albiflora*) is a note stating: "a small cauliflorous tree, cf. *1490*, from which this differs in having white flowers."

2. **Herrania balaënsis** Preuss, Exped. Centr.- und Süd-Amerika (1899–

1901). 253. *t. 7.* 1901; Bull. Soc. Études Col. Ann. 9(4): 220. *t. pag. 221. 256, fig. 1–8.* 1902 (non accurate titulata).

Theobroma balaënsis (Preuss) De Wildeman,[2] Pl. Trop. Grande Cult. 89. 1902.

Small tree up to 25 feet in height, with a slender, simple, very straight cylindrical trunk about 15 cm. in diameter at the base. Leaves arranged at the apex of the trunk, digitate, usually 7-foliolate, petiolate. Petioles terete, sulcate, very densely ferruginous-tomentose, up to 30 cm. long, about 5 mm. in diameter. Leaflets unequal, lanceolate-elliptic, marginally conspicuously sinuate, apically strongly acuminate, basally long attenuate-decurrent, sessile, firmly chartaceous, up to 60 cm. long, 15 cm. wide; leaf blade dark green and glabrous or subglabrous (microscopically scabridulous with minute stellate puberulence) above, brownish green and very densely and softly ferruginous-stellate-pilose beneath; the veins prominent and brown-tomentose on both sides, especially beneath. Inflorescence fasciculate, many-flowered (12–15 flowers), on the lower and middle portions of the trunk. Pedicels robust, densely greyish stellate-pilose, 8–9 mm. long, 1–1.5 mm. in diameter, subtended at the base by a minute, very densely stellate-pilose, linear bract. Calyx subcymbiform. Sepals 3, subequal, externally reddish brown, internally deep purple, lanceolate-elliptic, apically subacute, marginally entire, very densely muricate-papillose or granulose, 14 mm. long, 6 mm. wide. Petals 5, very broadly ovate, strongly cucullate, 8 mm. long, 5 mm. wide, whitish with 8–10 purplish veins, densely muricate-papillose, sparsely stellate-pilosiusculous externally, papillose, glabrous internally, ligulate. Ligules of the petals white and rose-colored, filiform, glabrous, very minutely granulose, membranaceous, 100 mm. long, less than 2 mm. wide. Staminal tube 5-parted; stamens alternately 2- and 3-antheriferous with relatively long, simple, glabrous filaments and 2-locular, divergent, longitudinally dehiscent anthers. Staminodes 5, petaloid, reflexed, membranaceous, elliptic, apically acute, marginally entire, glabrous, minutely and densely muricate-granulose on both sides, probably purplish red, 17–18 mm. long, 7–8 mm. wide. Pistil about 5 mm. long. Style linear, erect, glabrous with a 5-parted stigma. Ovary sessile, subglobose, 5-ribbed, densely white-pilose, 1.8–2 mm. in diameter, 3 mm. long. Fruit elongate-ovoid, the apex long-acuminate, 10-costate with 5 primary and 5 secondary ribs, olive-green when young, yellow-green and hispid when ripe, about 14 cm. long.

Ecuador. Río de Peripa, *Andre K26*; El Recreo, *Eggers 14362*; Balao, *Eggers 14362*. **Trinidad.** CULTIVATED: Imperial College of Tropical Agriculture, Diego Martin Estate, *Schultes 18638*.

Herrania balaënsis appears to be most closely allied to *H. kofanorum*. This relationship will be discussed under *Herrania kofanorum*. This species also resembles *H. Dugandii*, from which it differs in being very

---

[2] This combination, as "Theobroma balonsis," has recently been made by Llano Gómez (p. 18, Cultivo del cacao. Publ. Min. Econ. Nac. Bogotá. 1947), who apparently was unaware of the earlier publication.

much larger in its vegetative parts; in having conspicuously sinuate (instead of nearly entire) leaflets; in having much smaller sepals which are externally granulose (instead of stellate-pilose) and smaller petals which are whitish (instead of red-purple) and sparsely covered with a stellate puberulence; in having much larger staminodes; and in several other minor respects.

Herrania balaënsis has a type of fruit which immediately sets it apart from most other species. The structure of the fruit, according to the drawing of the capsule which was published with the original description, is similar to that of an unrelated species, *Herrania kanukuensis*.

The specific epithet *balaënsis* refers to the locality from which the type was taken.

Llano Gómez (loc. cit. 18) reported that this species is cultivated to some extent in Ecuador, but whether this refers to the toleration of the plant as a wild intruder in plantings or to actual cultivation is not clear. It seems probable that *Herrania balaënsis* is actively cultivated.

3. **Herrania breviligulata** R. E. Schultes, Caldasia **1**: 19–24. *t. pag. 21, figs. 1–4, t. pag. 24, fig. 5.* 1942.

DISTRIBUTION: Upper reaches of the Putumayo River, Colombia, and adjacent Ecuador.

Small, slender, graceful tree up to about 15 feet in height. Trunk erect, branching near the apex, terete, 6–7 cm. in diameter, with ashy-brown rimose-scrobiculate bark. Branches apparently tomentose, becoming glabrous. Branchlets densely villose, with rust-colored hairs, becoming almost glabrous. Leaves large, 4- or 5-digitate, very long-petiolate. Petioles terete, basally slightly swollen, subferruginous, tomentulose, up to 46 cm. long, about 0.5 cm. in diameter. Leaflets sessile, unequal, lanceolate-oblong, the margin entire, firmly chartaceous or papyraceous, mostly 20–40 cm. long, 6–30 cm. wide, very cuspidate-acute, up to 3 cm. long-decurrent-attenuate, puberulent on both surfaces but especially so beneath; above light green, very sparsely and minutely stellate-pubescent with white hairs, beneath pale green, densely and velvety stellate-villose-sericeous; the veins prominently elevated and brown-tomentose on both surfaces but especially so beneath. Inflorescence fasciculate, 5–8-flowered. Flowers cauline, in contracted racemes from the upper portion of the trunk, dark crimson-purple, pedicellate. Pedicels about 5–7 cm. long, very densely brown-tomentose, articulate, basally subtended by a short, linear, very densely brown-tomentose bract 1–1.5 mm. long. Bud globose, 4–9 mm. in diameter, very densely rusty-villose. Calyx 3-parted, divided almost to the base, subcymbiform. Sepals 3, broadly elliptic-oblong, obtuse, marginally slightly revolute, crimson-purple, 13–14 mm. long, 7–9 mm. wide, internally very sparsely puberulent or glabrescent, externally beset rather densely with long, white, stellate hairs, valvate in the bud. Petals 4, basally sessile, obovate, 6–7 mm. long, 5–6 mm. wide, concave, strongly cucullate, muricate-papillose or granulose on both surfaces but especially so externally, 5-nerved, longitudinally striate-veined, internally with prominent veins, dark crimson-purple, ligulate. Ligules linear, 25–35 mm. long, 1.5–2 mm. wide, hanging, basally slightly and abruptly contracted, apically slightly inrolled in a spiral position, 3-nerved, yellowish-red, with purple nerves, very minutely muricate-papillose or granulose. Staminal tube 5-parted, with stamens alternately 2- and 3-antheriferous and simple, short, free filaments. Staminodes petaloid, dark scarlet, lanceolate-elliptic, acute, margin entire, muricate-granulose on both surfaces, 15 mm. long, 4 mm. wide, crimson-purple. Pistil 2.8 mm. long. Style terete, simple, purplish, with a deeply 5-parted stigma. Ovary sessile, very densely pilose, pale yellow, subglobose, 3 mm. long, 2 mm. wide. Fruit unknown, but said to be pale yellow when ripe.

Colombia. PUTUMAYO: Mocoa, alt. 850 m., *Schultes & Smith 2050* (Type), *Schultes & Cabrera 19082*, *Anglo-Colombian Cacao Collecting Expedition (Cope & Holliday) 78*; Río Caquetá, Puerto Limón, *Schultes & Cabrera 18720*. **Ecuador.** NAPO-PASTAZA: near Archidona, alt. 650 m., *Mexia 7320*.

Herrania breviligulata seems to be closely allied to no other known species of the genus. In some respects it resembles *H. Cuatrecasana* but can be separated from this species readily by having seven (instead of four or five) smaller leaflets with an entire (instead of crenate-denticulate) margin, a more cuneate base and a much softer and denser indumentum on the lower surface; an inflorescence with only six or eight (instead of eighty or ninety) flowers; much smaller buds; pedicels which are 5–7 mm. (instead of 20–30 mm.) long; somewhat smaller sepals and petals; ligules 25–30 mm. (instead of 130 mm.) long; and much smaller staminodes (14 mm. × 4 mm. instead of 25 mm. × 8 mm.) which are apically acute. Both species are known only from the upper reaches of the Putumayo River and adjacent regions, an area which would appear to be one focus of speciation in the genus.

Herrania breviligulata has the shortest ligules known for any of the species with a subcymbiform calyx, a characteristic which is suggested by the specific epithet. It is likewise distinguished from all other known species by the very soft and dense, greyish indumentum which is velvety on the under surface of the leaflets.

The Ecuadorean collection *Mexía 7328* bears the data: "Fruit green, deeply ribbed." I have been able to find only one specimen of this collection (that in the Riksmuseum in Stockholm) and this is without a capsule. The fruit of *Herrania breviligulata*, therefore, remains unknown, Mexía's field notes notwithstanding.

4. **Herrania Camargoana** R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. **14**: 120. *tt. 29, 32.* 1950.

Theobroma Camargoana (R. E. Schultes) Ducke, Bol. Técn. Inst. Agron. Norte **28**: 15. 1953.

DISTRIBUTION: Upper Rio Negro basin in Brazil and Colombia.

Small, slender and graceful tree, usually up to 10 (but sometimes up to 27) feet tall. Trunk erect, sparsely branched or else unbranched near the top, about 4–5 inches in diameter, covered with a black bark. Branches tomentose, but soon glabrous. Branchlets densely villose, ferruginous, subglabrescent. Leaves very large, digitate, 7- to 9-foliolate, very long-petiolate. Petioles terete, strongly constricted at the base, softly golden-ferruginous-tomentellous, up to 60 cm. long, 10 mm. in diameter. Stipules persistent, subulate, very densely tomentellous, up to 3 cm. long. Leaflets sessile, oblanceolate or broadly lanceolate-ovate, slightly erect, unequal, membranaceous-papyraceous, acuminate, basally attenuate, marginally regularly and conspicuously sinuate in the upper half and everywhere armed with cilia-like stellate hairs (up to 1.5 mm. long), 60–75 cm. long, 16–26 cm. wide, asperous above, sparsely pilose with long and single hairs, beneath rather softly tomentellose with long stellate hairs. Inflorescence fasciculate, many-flowered, growing from all parts of the trunk but principally from the lower portions. Pedicels articulate, up to 28 mm. long, 0.8 mm. in diameter. Buds globose, up to 10 mm. in diameter, stellate-pilose. Calyx 3-parted, divided nearly to the base, subcymbiform. Sepals widely elliptic-oblong, subacute, marginally entire, externally dark purple, internally blood-red, mostly 12 mm. long, 8–9 mm. wide, glabrous within, stellate-pilose with rust-colored hairs (up to 1 mm. long) and very minute white hairs without. Petals 5, sessile, obovate-rotund, very strongly concave-cucullate, about 8 mm. long, 6 mm. wide, with 5 dark purple longitudinal nerves as well as finely reticulate nerves, elsewhere yellow, externally conspicuously muricate-verrucose, apically extended into a ligule. Ligules linear, mostly 90 mm. long, at the base 1.7 mm. wide, apically filiform, at the very base blood-red but for the greater part of their length whitish yellow. Staminal tube 5-parted with 2-antheriferous stamens and short free and simple filaments. Ovary ellipsoid, 3.5 mm. long, 2–2.5 mm. in diameter, very densely and coarsely white-pilose. Style terete, simple, yellow, with the stigma apically inconspicuously 5-parted, 3 mm. long. Staminodes conspicuous, rhomboid-elliptic, obtuse, marginally entire, verrucose on both surfaces, ashy purple, 14 mm. long, 5 mm. wide. Fruits numerous, almost globose, or slightly ellipsoid, apically very abruptly long-apiculate (apicule 2–2.5 cm. long), mostly 8–8.5 cm. long, 3.5–4.5 cm. in diameter, basally attenuate, with persistent sepals, longitudinally 10-costate with the primary and secondary ribs almost equal, thin, knife-shaped, irregular in height but for the most part (in life) 5–6 mm. high, transversely irregularly but conspicuously costate with knife-shaped ribs, which are slightly lower or often somewhat higher than the longitudinal ribs, the junction of the longitudinal and transverse ribs prolonged into a softly carnose, mammose or spine-like projection (which is somewhat blunt at the tip) with stinging, stellate hairs in all parts but especially along the ribs; the pericarp thick, usually dark red or blood-red (but sometimes yellow) when ripe; seeds 25, obtusely round-pyramidal, about 9 mm. long × 11 mm. wide × 7 mm. thick, imbedded in a white pulp.

Brazil. AMAZONAS: Rio Negro, Serra de São Gabriel, *Schultes & López 9722* (Type); Rio Negro, *Fróes 21468*; Rio Negro, Uaupés (São Gabriel), *Fróes 21540*; summit of Serra de São Gabriel, alt. 100 m., *Schultes & López 8758, 8759, 8762, 8763, 9162, 9619*; Tapurucuara (Santa Isabel), *Schultes & López 8956*; Serra de Uanarí, *Murça Pires 775; Schultes & Murça Pires 8978*; mouth of Rio Xié, *Schultes & López 9205*; Nazaré, *Schultes & López 9240*; Serra Jacamín, *Schultes 9747*; between São Felipe and Karapaná, *Schultes & López 9869*; Rio Padauiary, *Fróes 22673*; Rio Uaupés, between Ipanoré and confluence with Rio Negro, Serra Wabeesee, on left bank below Bela Vista, *Schultes & López 9144* (Type of flowers); *Schultes & Murça Pires 9130*; *Murça Pires 1159.*

Colombia. VAUPES: Caño near north end of Inambú, *Anglo-Colomb. Cacao Coll. Exped.* (*Bartley & Holliday*) *56*; Río Negro, San Felipe and vicinity (below confluence of Río Guainía with Casiquiare), alt. about 600 ft., Caño Marijabo, *Schultes, Baker & Cabrera 18050*; *Anglo-Colomb. Cacao Coll. Exped.* (*Bartley & Holliday*) *45.*

Restricted apparently to the uppermost Río Negro basin of Brazil and Colombia, *Herrania Camargoana* seems to have as its closest ally the Guianan and Venezuelan *H. lemniscata.* This relationship is strikingly evident when one compares the fruits of the two concepts. Both species have relatively small capsules in which there are transverse ribs nearly as large as the cultriform longitudinal ribs, and soft, pointed mammoid projections at each junction of the longitudinal and transverse ribs. The former species, however, has much longer and more upturned projections than the latter, and would seem, in this as in some other characters, to represent an extreme in the evolution of the genus. There would appear to be a rather easily traceable trend from *Herrania Mariae* through *H. lemniscata* to *H. Camargoana,* on the one hand, and to *H. laciniifolia* on the other.

The coloration of the flowers of *Herrania Camargoana* and *H. lemniscata* is similarly complex and may also indicate a relationship. No other known species of *Herrania* can match these two for complexity of floral coloration. *Herrania Camargoana* has sepals which are dark blood-red externally but scarlet internally; petals which are ashy red or purple with yellowish stripes; staminodes which are ashy purple-maroon with white-yellow patches internally but entirely dark red externally; and ligules, red without and white-yellow within, which are folded or inrolled, so that the red is enclosed and is not seen directly. *Herrania lemniscata* has, according to field notes (*Steyermark 60558*), sepals which are white in the uppermost two-thirds and rose-salmon below, with rose stripes; and staminodes (called "petals" on the label) which are dull yellow with dull rose specks in the lower half.

The shape and size of the leaflets, however, differ strikingly in the two concepts. *Herrania Camargoana* has oblanceolate or broadly lanceolate-ovate leaflets which measure 60–75 cm. in length and 16–26 cm. in width with the upper half regularly and conspicuously sinuate. *Herrania lemniscata* has leaflets which are at least 80 cm. long and 40 cm. wide with the margin very deeply pinnatilobate with usually four irregular and, for

FIG. 2. Crown of *Herrania Camargoana.*

the most part, widely triangular or widely lanceolate-acuminate segments, each up to 18 cm. long and 9–10 cm. wide.

Herrania Camargoana is unusually abundant near the summits of the isolated granitic mountains of the upper Río Negro valley. It has also been found in sandy patches along the banks of the rivers themselves. A search through the Spruce collections and notes from this area has failed to turn up any evidence of *Herrania Camargoana* in the extensive material which this early explorer gathered in the long period (1851–1856) which he spent in diligent study of the area to which the species is confined.

There has been no collection of *Herrania Camargoana* made as yet from Venezuela, but it is undoubtedly represented in the upper Río Negro drainage area of that country.

Herrania Camargoana was named in honor of Dr. Felisberto Camargo, founder and first director of the Instituto Agronômico do Norte in Belém do Pará, Brazil.

5. **Herrania Cuatrecasana** García-Barriga, Caldasia 2: 57. *t. 2.* 1941.

DISTRIBUTION: Upper reaches of the Putumayo River in Colombia.

Small tree 9 feet tall with whitish, maculate bark. Petioles terete, densely brown-stellate-tomentose. Leaves digitate, large, long-petiolate, 7-foliolate. Leaflets sessile, spreading, oblanceolate-oblong, the margins very remotely and obscurely crenate-denticulate, acuminate, basally long and gradually attenuate-decurrent, the lower leaflets about 33 cm. long, 9 cm. wide, the middle 50 cm. long, 17 cm. wide; the leaf surface papyraceous, above sparsely and minutely stellate-pubescent, the veins brown-tomentose, beneath softly stellate-pilose, the veins more prominent and hirsute above than beneath. Inflorescence fasciculate, 80–90-flowered. Flowers cauline, growing from the upper portions of the trunk, pedicellate. Pedicels slender, articulate, stellate-tomentulose, 2–3 cm. long, basally subtended by a linear or filiform, pilose, caducous bract. Buds ellipsoid or globose, 8–9 mm. in diameter. Sepals 3, equal, oblong, obtuse, dark purplish red, outwardly stellate-pilose with long hairs, inwardly with very short, reddish hairs, 15–18 mm. long, 7–11 mm. wide. Petals concave, rotund-ovate, strongly cucullate, glabrous, muricate-papillose, longitudinally striate-nerved, 10–11 mm. long, 7–8 mm. wide, with a long, filiform ligule, 130 mm. long, 1.5 mm. wide. Staminal tube 5-parted, with the stamens all bearing 4 anthers. Staminodes petaloid, purple, rhomboid-lanceolate, attenuate towards the apex, rather obtuse or acute, 25 mm. long, 8 mm. wide. Ovary shortly depressed, ovoid, densely pilose with whitish yellow hairs, 2 mm. long. Stigmas 3. Fruit ellipsoid, about 11–12 cm. long and 7–8 cm. in diameter, apically attenuate-acuminate, 10-costate, with 5 primary and 5 secondary ribs, cultriform, covered, especially along the ribs, with very minute stinging, stellate hairs, rind very thin and brittle, yellow when ripe. Seeds about 60, regular, compressed, triangular in outline, 14 mm. long, 12 mm. wide, 5 mm. thick, enveloped in a white, mucilaginous pulp, covered with a coriaceous tegument, exteriorly rugose.

Colombia. PUTUMAYO: Río Guamués, San Antonio de Guamués, alt. about 310 m., *Cuatrecasas 11168* (Type); Río Uchupayaco, alt. 300 m., *Schultes 3342*; Mocoa and vicinity, alt. 1800–2400 ft., *Schultes & Cabrera 19100*; *Anglo-Colomb. Cacao Coll. Exped.* (*Cope & Holliday*) *80*; Río Caquetá, Puerto Limón, *Schultes & Cabrera 18712, 18715*; Río Putumayo, Puerto Ospina and vicinity, *Schultes & Cabrera 18976*; Montclar, *Anglo-Colomb. Cacao Coll. Exped.* (*Cope & Holliday*) *86*.

Ecuador. Río Sucumbios, 17 hrs. by motor upstream from Puerto Ospina. *Anglo-Colomb. Cacao Coll. Exped.* (*Cope & Holliday*) *84*.

Apparently the closest ally of *Herrania Cuatrecasana* is *H. tomentella.* This relationship is discussed under *Herrania tomentella.*

Herrania Cuatrecasana has been considered to be related to *H. Mariae* through the concept *H. Mariae* var. *putumayonis.* It differs from *H. Mariae* chiefly in having leaflets which are very much more long-attenuate-decurrent at the base, in the indument and size of the leaflets, in the length of the pedicels, in having obtuse instead of acute sepals, and in having very characteristic and conspicuous rhomboid-lanceolate staminodes, and in the length of the petals. It is much more softly and densely pubescent than *Herrania Mariae.* It is also apparently a very much smaller and weaker plant than *H. Mariae.*

Herrania Cuatrescasana likewise resembles *H. Dugandii* in some respects. The former differs from the latter principally in having denticulate, instead of almost entire, leaf margins and in being puberulent on both surfaces of the leaflets instead of being glabrous above. Furthermore, *Herrania Cuatrecasana* has many-flowered (80–90) inflorescences, whereas *H. Dugandii* has an inflorescence composed of but twenty flowers or fewer. The pedicels of the flowers of the former species are twice as long as those of the latter, and there are important differences in the shapes and sizes of the floral parts and leaflets.

Vegetatively, *Herrania Cuatrecasana* bears some resemblance to *H. nycterodendron*; this will be discussed under that species.

The description of the fruit of *Herrania Cuatrecasana* is based upon *Schultes 3342* from the Putumayo. The leaves and dried remains of floral parts adhering to the ripening fruits as well as floral parts which were collected on the ground at the base of the tree have enabled me to determine the specimens as representing the species in question.

The specific epithet *Cuatrecasana* honors the botanist Dr. José Cuatrecasas, formerly of the Instituto de Ciéncias Naturales in Bogotá, and the Chicago Natural History Museum, now at the Smithsonian Institution.

6. **Herrania Dugandii** García-Barriga, Caldasia **2**: 59, 61. *t. 3.* 1941.

DISTRIBUTION: Westernmost Amazonia, especially in the Putumayo basin of Colombia.

Small tree, 9 feet tall, sparsely branched at the apex of the trunk. Petioles terete, densely hirsute with reddish stellate hairs, 30 cm. long. Leaves digitate, long-petiolate, 7-foliolate. Leaflets sessile and spreading, the margins almost entire or near the apex slightly sinuate, obovate-oblong, acute or obtusely subacuminate, basally gradually attenuate, the lower 18 cm. long, 6 cm. wide, the middle 31 cm. long, 12 cm. wide; leaf surface firmly papyraceous or thinly coriaceous, above glabrous or very remotely strigillose, the nerves subimpressed and pubescent, beneath stellate-hirsute, roughish, the nerves reddish hirsute. Inflorescence axillary, 15–20-flowered. Flowers cauline in contracted, subumbelliform racemes, on the upper portions of the trunk, dark purple, pedicellate. Pedicels very densely brown-tomentose, articulate, 1 cm. long or shorter, basally subtended by a short linear, villous, caducous bract. Bud ovoid-oblong, 11 mm. in diameter, 18 mm. long. Calyx subcymbiform. Sepals 3, oblong, obtuse, dark purple, externally subdensely armed with stellate hairs, internally with very short rust-red hairs, up to 21 mm. long and 12 mm. wide. Petals concave, obovate, basally slightly attenuate, striate-nerved, glabrous, 11–12 mm. long, 5–6 mm. wide, apically strongly cucullate, with a long ligule. Ligule filiform, dark purple, 100 mm. long, 2 mm. wide. Staminal tube

5-parted. Staminodes narrowly lanceolate, basally and apically attenuate, apically very acute, squamulate-rugulose on both surfaces, 12–15 mm. long, 5 mm. wide. Ovary 4 mm. long, 3 mm. in diameter, densely covered with yellow hairs. Stigmas 5. Fruit unknown.

Colombia. PUTUMAYO: Río Putumayo, Puerto Porvenir, above Puerto Ospina near La Loma, alt. 230–250 m., *Cuatrecasas 10742* (Type). AMAZONAS: Trapecio Amazónico, Río Loretoyacu, alt. about 100 m., *Schultes 6038.*

Herrania Dugandii seems to be most closely allied to *H. kofanorum*, a species from the same general region. Both are rather similar in their vegetative parts, although the leaflets and certain floral parts of the latter are very much larger than those of the former. *Herrania kofanorum* further differs from *H. Dugandii* in having much more coriaceous leaflets which are more deeply and regularly undulate-sinuate; in having very strongly unequal sepals, the outer one of which is apically slit (the sepals of *Herrania Dugandii* appear at once to be much longer than *H. kofanorum* because they are much narrower in relation to their length; but, in reality, they are smaller); in having round-ovate petals which measure 9 mm. × 7 mm. (instead of obovate, basally attenuate petals measuring 11–12 mm. × 5–6 mm.); in having a more filiform ligule which measures 80–100 mm. in length × 1 mm. (instead of 100 mm. × 2 mm.); and in having much larger staminodes, which measure 22 mm. × 6 mm. (instead of about 12–15 mm. × 5 mm.). These size differences combine with slight differences in shape of floral parts to give the flowers of the two species rather dissimilar aspects. It is obvious, however, that the two are closely related. Further collections and studies, especially when the fruit of both are known, may indicate that *Herrania kofanorum* should be treated as a variety of *H. Dugandii.*

The specific epithet *Dugandii* honors Dr. Armando Dugand, outstanding botanist, and director from 1940 to 1952 of the Instituto de Ciéncias Naturales of the Universidad Nacional, Bogotá, Colombia.

7. **Herrania kanukuensis** R. E. Schultes, Caldasia 2: 11. 1943; Bot. Mus. Leafl. Harvard Univ. 13: 277. 1949; ibid. 14: *t. 33.* 1950.

Theobroma Mariae (Mart.) Decaisne ex Goudot var. *lobata* Pulle, Rec. Trav. Bot. Néerl. 9: 151. 1912.

DISTRIBUTION: Southern Venezuela, adjacent Brazil and British and Dutch Guiana.

Small tree, slender and graceful, up to 16 feet in height. Trunk with a somewhat striate, brownish-black bark. Branchlets very densely brown-tomentose. Leaves large, 5- or 6- digitate, stipulate, very long-petiolate. Stipules caducous, linear, acute, somewhat rigid and dry, very densely brown-tomentose, 15 mm. long, basally about 1.5 mm. wide. Petiole strong, up to about 53 cm. long, 6–7 mm. in diameter, very densely and softly brown-tomentose, basally rather swollen, then abruptly constricted. Leaflets sessile, unequal, strongly obovate, abruptly acuminate, basally abruptly cuneate, almost entire, often near the apex subundulate-sinuate and often very conspicuously, though minutely, mucronate (with the prolongations of the lateral veins up to 1 mm. long), firmly papyraceous, the central leaflets 30–44 cm. long, 13–16 cm. wide, above dark green or exceedingly sparsely hirsute, aspero-strigose with long white hairs noticeable along the veins, the veins very densely and softly stellate-pilose and rust-colored, the nerves on both surfaces, but especially beneath, prominently raised. Inflorescence fasciculate. Flowers not completely known (remains of the persistent calyx showing 3 densely brown-stellate-tomentose, elliptic-lanceolate, acute sepals, 14 mm. long, 6 mm. wide; the 5 petals, concave, strongly cucullate, elongate-obovate, about 8 mm. long, 4–5 mm. wide, ligulate). Fruit long-pedunculate (peduncle rather robust, densely stellate-puberulent, up to 3 cm. long, about 2–3 mm. in diameter), ovoid, 7–8 cm. long, about 4 cm. in diameter, apically very shortly cuspidate or subrotundate, basally rounded, extremely velutinous with dense and minute stellate-puberulence, lacking stinging hairs, 10-costate, with 5 narrow and low (1 mm. wide and rarely up to 2 mm. high) blunt primary ribs and 5 secondary ribs which are similar but smaller and barely noticeable; pericarp extremely thin and apparently somewhat fragile, yellow when ripe. Seeds probably more than 60, triangular or angulate-ovate in outline, complanate, 12 × 10 × 10 mm., 4 mm. thick, in a white pulp.

Brazil. Rio Branco: lower Rio Branco, Tapanaruca, *Fróes 23003.* **British Guiana.** Northwestern slopes of Kanuku Mountains, drainage-area of Mokumoku Creek, tributary of Takutu River, alt. 150–400 m., *A. C. Smith 3541* (Type). **Dutch Guiana.** Upper River Corantijne, *Hulk 26*; River Corantijne, Kaurikreek, *Gonggrijp 2111*; *Stahel & Gonggrijp 3015*; River Coppename, *Gonggrijp 2565*; Placer L'Aiva, *Gonggrijp 4126*; River Marowijne, *Gonggrijp 4101*; near Amerikan Kondre, *Lanjouw & Lindeman 2304*; River Tapanahonie, Jaikreek, *Gonggrijp 4117.*

Herrania kanukuensis stands rather apart from the other known species of the genus. Its fruit differs strikingly from that of all other species, with the single exception of the unrelated *H. balaënsis* of Ecuador. The capsule is relatively small (measuring 9 cm. × 5 cm.) with a rounded or very shortly tipped apex (not elongate ovoid or ellipsoid with an acuminate tip, as in most species); the rind is very thin and brittle when dry (in contrast to the usual thick, leathery and fibrous condition), and the ribs are not prominent.

The few fragmentary floral parts which remained adhering to the fruit of *Smith 3541* indicate that there are also floral differences between *Herrania kanukuensis* and other species.

A duplicate type of *Herrania kanukuensis* at Kew has several leaflets which tend to be slightly irregularly dissected, suggesting a condition which approaches that of some specimens of *H. lemniscata* with abnormally developed leaflets. *Herrania kanukuensis* would appear vegetatively to be somewhat intermediate between *H. Mariae* and *H. lemniscata*, but the indumentum on the under surface is more softly tomentose with brownish stellate hairs than in either *H. Mariae* or *H. lemniscata.*

In 1932, Uittien (in Pulle, Fl. Surin. 3: 44. 1932) reduced *Theobroma Mariae* var. *lobata* to synonymy under *T. Mariae,* identifying all of the then available material from Dutch Guiana as representing this Amazonian concept. In 1943, it appeared to me that the Surinam concept described as *Theobroma Mariae* var. *lobata* represented the plant which Schomburgk described from nearby British Guiana as *Lightia lemniscata,* and I placed it in synonymy under *Herrania lemniscata* (Schultes, Caldasia 2: 13. 1943), a species with remarkably lobate leaflets. During the war, the Utrecht material was unavailable for study. Recently, I have had an opportunity of consulting all of the Surinam specimens and am convinced that *Theobroma Mariae* var. *lobata* and *Herrania kanukuensis* represent the same concept.

From the numerous collections, for the most part from Surinam, it is now obvious that *Herrania kanukuensis* is both a widespread and, at least locally, an abundant element of the flora of Surinam, eastern British Guiana and the adjacent rim of northern Brazil.

The specific epithet *kanukuensis* is derived from the name of the Kanuku Mountains in British Guiana, where the type specimen was collected.

8. **Herrania kofanorum** R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. 14: 126. *t. 28, upper fig. t. 34.* 1950.

DISTRIBUTION: Upper Putumayo valley of Ecuador and Colombia.

Small tree, slender and graceful, up to 15 feet tall, usually with one trunk from each root, columnar, apically branched or unbranched, covered with an ashy black scrobiculate and scabrid bark, up to 7 cm. in diameter. Branches ferrugineous-tomentose, becoming almost glabrous, subterete and sulcate. Branchlets similar but more densely tomentose. Leaves at apex of trunk, large, digitate, very long-petiolate, 7-foliolate, stipulate. Stipules caducous, linear, acute, 2.5–3 cm. long, about 3 mm. wide, dry, outside hispidulous or strigillose, inside usually subglabrous. Petioles robust, terete but very obscurely sulcate, basally slightly dilated, subferruginous, very densely and softly tomentose, up to 30 cm. long, 6 mm. in diameter. Leaflets sessile, unequal, lanceolate-oblong, apex with a cusp about 2 cm. long, basally attenuate-decurrent, margin conspicuously and regularly undulate-sinuate; blades firmly coriaceous, mostly 17–30 cm. long, 6–11 cm. wide, above dark green, glabrous or exceedingly sparsely and very minutely strigillose-pilose with caducous white hairs, brownish-hirsute along the principal veins, beneath brownish green, very densely and softly stellate-pilose, ferruginous-tomentose along the principal veins; veins on both surfaces but especially beneath rather prominently raised. Inflorescences fasciculate, up to 20-flowered. Flowers cauline, long-pedicellate, on the lower parts of the trunk, in contracted racemes. Buds large, elongate-globose, 1.8 cm. in diameter, stellate-pilose, rather brownish red. Pedicels strong, terete, articulate, very densely and minutely stellate-pilose, with ashy-colored hairs, mostly 9–10 mm. long, 1–1.5 mm. in diameter, at the base with small linear, acute and densely tomentose bracts, 2–4 mm. long. Calyx subcymbiform, divided almost to the base. Sepals 3, very strongly unequal, subchartaceous, entire, within minutely papillose, subglabrous and probably eventually glabrous, without sparsely stellate-strigillose, with hairs up to 1 mm. long and also with extremely minute stellate hairs, valvate in bud; the inner 2 sepals elliptic, acute, 10 mm. long, 6 mm. wide; the outer round-ovate, 15–18 mm. long, 15 mm. wide, apically rounded and often deeply (up to 2 mm.) cut, the slit extended interiorly as a furrow nearly to the base. Petals 4 or 5, round-obovate, sessile, concave, strongly cucullate, glabrous, on both surfaces (but especially on the outside) muricate-papillose or granulose, dark red, 5-nerved, striate-nerved with longitudinal purplish veins, ligulate, 9 mm. long, 7 mm. wide. Ligules filiform, pendulous, membranaceous, entirely glabrous but basally minutely granulose, about 1 mm. wide, 80–100 mm. long, at the base strongly dilated. Staminal tube 5-parted, the stamens with alternately 2 and 4 anthers and strongly flattened, short, free filaments. Staminodes conspicuously petaloid, lanceolate-elliptic, acute, basally attenuate, coarsely muricate-papillose on both surfaces, entire, 22 mm. long, 6 mm. wide. Ovary sessile, elongate-ovoid, distinctly 10-ribbed and 5-locular, yellow, very densely stellate-pilose, 2.5–3 mm. in diameter. Pistil flattened, 3 mm. long, glabrous, simple. Fruit unknown, but said to ripen yellow.

Colombia. PUTUMAYO: path between Puerto Ospina and Concepción, alt. 250 m., *Schultes 3670*. CAQUETÁ: upper Putumayo River, Caucaya, *Anglo-Colomb. Cacao Coll. Exped.* (*Cope & Holliday*) *89*. **Ecuador.** Río San Miguel or Sucumbíos, between Río Putumayo and Quebrada Teteyé, alt. 260 m., *Schultes 3478* (Type).

Herrania kofanorum differs from its close ally *H. balaënsis* in being smaller, in having leaflets only half as large, and in having the sepals very conspicuously unequal instead of nearly alike. *Herrania kofanorum* has two inner sepals which are elliptic, 20 × 6 mm. and an outer one which is rotund-ovate, 15–16 × 16 mm., whereas *H. balaënsis* has three lanceolate-elliptic sepals which measure 14 × 6 mm. Furthermore, the outer sepal of *Herrania kofanorum* is so constructed that it is often conspicuously slit to a depth of 2 mm., and this slit is prolonged as a furrow to the base of the interior of the sepal. (When the split is not present, there is a markedly thin furrow.) Nothing similar is seen in *H. balaënsis*. Both of these species are closely related to *Herrania Dugandii*.

The specific epithet refers to the Kofán Indians who inhabit the area where the species is known to occur.

9. **Herrania laciniifolia** Goudot ex Tr. et Planch. Prodr. Fl. Novo-Granat. 209. 1862, nomen subnudum; García-Barriga, Caldasia **1**: 55. *tt. 1, 4*. 1941.

Theobroma laciniifolium (Goudot ex Tr. et Planch.) De Wildeman, Pl. Trop. Grande Cult. 90. 1903.[3]

DISTRIBUTION: Middle Magdalena Valley, Colombia.

Small tree 12 to 18 feet tall with a simple, erect trunk, about 5 cm. in diameter. Leaves very large, 7-digitate, round in outline, long-petiolate, grouped towards the top of the trunk. Leaflets sessile, strongly patent, the margins deeply pinnatisect with irregular segments (similar to leaves of *Carica Papaya*), for the most triangular or lanceolate-acuminate, up to 22 cm. long and 3 cm. wide (but usually smaller), papyraceous or membranaceous, basally long-decurrent-attenuate, laciniate towards the apex, the apex itself acuminate, 38–58 cm. long, above sparsely stellate-pilose with suberect hairs along the nerves, the central and lateral veins densely red-tomentulose, beneath rather pale and rather densely and softly stellate-pubescent, with the veins as above. Petiole 25–31 cm. long, terete, striate, densely red-tomentulose, basally swollen. Flowers cauline, fasciculate, borne on upper portion of trunk, pedicellate, with the pedicel about 2 cm. long and stellate-pubescent. Sepals 4, lanceolate, rather concave, apically very acute, 17 mm. long, about 7 mm. wide, pubescent on both surfaces, externally with fewer and larger reddish stellate hairs, internally near the apex incanous, with smaller and denser hairs. Petals 5, glabrous, broadly elliptic, very concave, purplish (with yellowish veins) or "greenish white" (*Kalbreyer 2047*), apically strongly cucullate, ligulate, marginally revolute, 12 mm. long, 8 mm. wide. Ligule filiform, glabrous, red or whitish, 180 mm. long, 1 mm. wide. Staminal tube 5-parted, the stamens all 4-antheriferous. Staminodes petaloid, widely lanceolate, purple, 17 mm. long, 5 mm. wide, the margin slightly sinuous, acute or 3-dentate. Ovary globose or ovoid, 3 mm. long, densely covered with pale yellow hairs. Fruit coriaceous, oblong-ovoid, basally rounded, apically long attenuate-acuminate, the tip itself rather obtuse, 10-costate, the 5 primary ribs conspicuously raised, the 5 secondary ribs much less raised, transversely rugose, brownish red when ripe, 10.5 cm. × 5 cm. in diameter; peduncle 4 cm. long.

Colombia. [No precise locality], *Exped. Bot. Mutisii Novae-Granat. 937*; "New Granada, 4,000 ft.", *Kalbreyer 2047*. CUNDINAMARCA: Peño de Conejo, basin of Río Magdalena, *Goudot s. n.* TOLIMA: Falán, region of Calamonte, alt. 1120 m., *García-Barriga 8375*; Mariquita, alt. 547 m., Pérez-Arbeláez *10303*.

Herrania laciniifolia is apparently not an abundant element of the flora of Colombia, for it has been collected but thrice in a century, although it grows in one of the most populous parts of the nation. It is most closely allied to *Herrania lemniscata* from which it may be distinguished chiefly by having leaflets which are deeply and regularly pinnatisect (instead of very deeply and irregularly pinnatilobed). The under surface of the

---

[3] This combination has recently been made independently as "*Theobroma laciniifolia*" (Goud. ex Tr. et Planch.) Llano Gómez in "Cultivo del cacao" (Publ. Min. Econ. Nac., Bogota) 19. 1947.

leaflets of *Herrania laciniifolia* is very much more densely and softly stellate-pilose than in *H. lemniscata*; the leaflets are, in general, smaller; and the ligules measure 180 mm. (instead of 85 mm.) in length. The fruit of *Herrania laciniifolia* ripens red, whereas that of *H. lemniscata*, in common with all other species but one, ripens bright yellow. This other exception is *Herrania Camargoana* of the upper Río Negro basin. The fruit of *Herrania Camargoana* ripens scarlet, but this species does not appear to be closely allied to *H. laciniifolia*, and the similarity of fruit color is probably coincidental.

In the collection of Mutis plates preserved at Madrid, there are several illustrations representing *Herrania laciniifolia*. Drawn by Matíz, these are all in black and white, not in color. One plate has a leaf with a complete leaflet and a length of stem with several flowers and buds; another plate has analytical drawings of the flowers and fruits; a third has analyses only of the floral parts.

The Mutis specimen in Madrid (cited above) is sterile, but it was undoubtedly taken from the tree from which the plate was made. In view of the scarcity of collections of *Herrania laciniifolia*, it is unfortunate that a definite locality for the Mutis collection is not available. Both the specimen and the plates agree perfectly with the type and the later material of this remarkably distinct species.

10. **Herrania lemniscata** (Schomb.) R. E. Schultes, Caldasia **2**: 13. 1943; Pittier et al. Cat. Fl. Venez. **2**: 134, 139. 1947; R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. **13**: 281. *t. 30.* 1949.

Lightia lemniscata Schomb. Rep. Assoc. Advancem. Sci. **13**: 71. 1844. Nomen subnudum.

DISTRIBUTION: British and Dutch Guiana and the Orinoco basin of eastern Venezuela, extending into northeastern Colombia.

Small tree, with a simple, round, slender trunk up to 30 feet tall, with leaves grouped at the tip of the trunk. Branches apparently tomentose, becoming subglabrous. Leaves very large, 7-digitate, very long-petiolate, stipulate. Stipules caducous, minutely subulate, extremely densely and softly ferruginous-tomentose, about 2 cm. long, basally 2 mm. wide. Petioles robust, terete, sulcate, apically widely complanate-flabelliform, very densely and softly rusty tomentose, slightly swollen then immediately strongly constricted, up to 45 cm. long, 8–10 mm. in diameter. Leaflets sessile, unequal, the central one up to 80 cm. long, 40 cm. wide, acuminate, basally long-decurrent-attenuate, the margin very profoundly pinnatilobate with (usually) 4 irregular, usually triangular or broadly lanceolate-acuminate segments, in the longest part of leaflet up to 18 cm. long, 9–10 cm. wide, papyraceous or membranaceous, above dark green, subglabrous or beset with very remote stellate hairs, densely ferruginous-strigillose along the nerves, beneath pale green, densely and softly stellate-pilose, the nerves densely ferruginous-tomentose, the veins prominent on both surfaces. Inflorescence fasciculate, bearing probably up to 30 or 40 (but usually about 20) flowers. Flowers borne in contracted racemes on the lower portion of the trunk, dark crimson-purple, pedicellate. Pedicels strong, terete, minutely and densely stellate-tomentellose, articulate, 7–8 mm. long, basally subtended by a short, linear, tomentose bract, 1 mm. long. Buds globose, 9–10 mm. in diameter, very densely and minutely stellate-tomentellose and stellate-pilose. Calyx divided almost to the base, subcymbiform. Sepals 3, reflexed, almost equal, thick, internally very densely puberulent, externally very densely stellate-tomentose and stellate-pilose (2 distinct types of hairs), with an entire and strongly inflexed margin, brownish red; the two larger sepals ovate, subobtuse, 12–13 mm. long, 7 mm. wide; the smaller one lanceolate-elliptic, apically subobtuse, 13–15 mm. long, 5–8 mm. wide. Petals 5, sessile, elongate-obovate, concave, strongly cucullate, entire, dark blood-red (sometimes possibly yellowish) with 5 prominent black or purplish nerves, 6–7 mm. long, 4 mm. wide, glabrous, on both surfaces but densely muricate-papillose externally, thick, ligulate. Ligules hanging, membranaceous, filiform, glabrous, without nerves, basally 1–1.5 mm. wide, about 85 mm. long, blood-red, sometimes becoming yellowish. Staminal tube 5-parted with stamens alternately 2- and 4-antheriferous, filaments short, free and simple. Staminodes conspicuous, petaloid, dark blood-red, sometimes apically yellowish, elliptic, slightly and obscurely undulate, acuminate, 10–12 mm. long, 4–5 mm. wide, glabrous, densely muricate-granulose on both surfaces. Ovary sessile, ovoid-globose, 4.5–5 mm. long, 2.5 mm. in diameter, distantly 10-costate with 5 primary and 5 secondary ribs, yellow, very densely hispid-pilose. Style terete, glabrous, simple, with an obscurely 5-parted stigma. Fruit long pedunculate (with a strong, glabrous or glabrescent peduncle up to 4.5 cm. long and 3 mm. in diameter) perfectly ovoid, 7 cm. long, 4 cm. in diameter, apically very shortly and abruptly cuspidate, basally almost rounded, densely and minutely stellate-puberulent, apparently lacking stinging hairs, 10-costate with 5 narrow, comparatively low, subcultriform primary ribs which are 2 to 4 mm. high and 1–2 mm. thick (in the dried specimen) and 5 similar but smaller ribs, the very thin pericarp strongly reticulate-costate between the longitudinal ribs, probably yellow when ripe. Seeds apparently more than 60, triangular or angular-ovate in outline, flattened, 12 × 11 × 11 mm., above 4 mm. thick, buried in a white pulp.

British Guiana. Banks of Barima River. *Schomburgk s. n.* (Type); [no precise locality], *im Thurn s. n.* (Type of fruit); Essequibo River, White Creek, Groete Ck., *Forest Dept. Brit. Guian. Field No. F1763, Research No. 4500.* **Colombia.** SANTANDER: 15 km. east of Puerto Berrio, alt. about 250 m., *Scolnick, Araque & Barkley 195001.* **Venezuela.** Near mouth of Orinoco River, *Rusby & Squires 252*; Pakaraima Mountains, *Myers 3371.* BOLÍVAR: Salto de Pará, Medio Caura, alt. 120 m., *L. Williams 11339*; lower part of Quebrada O-paru-mo, tributary of Río Pacairao, below Santa Teresita de Kavanayen, alt. 915–1065 m., *Steyermark 60558.*

Herrania lemniscata is undoubtedly one of the most strikingly distinct species of the genus. It can be distinguished at once by its very large and broad leaves with pinnatilobed leaflets. It is, apparently, most closely related to *H. laciniifolia* of central Colombia, but its leaflets are much more coarsely incised, with fewer and wider lobes. Florally, *H. lemniscata* does not seem to be very distantly allied to *H. Mariae* and *H. kanukuensis*.

It would appear that the Guianan *Herrania lemniscata* occupies a somewhat intermediate position between the Colombian *H. laciniifolia* on the one hand and the Amazonian *H. Camargoana* on the other. This relationship has been discussed under the latter species.

The name *Lightia lemniscata* was published by Schomburgk in 1844 without an adequate description and without the citation of specimens. It must be considered a *nomen subnudum*. Several years later, Schomburgk (Linnaea 20: 756. 1847) reduced the name to synonymy under *Herrania Mariae*, and, wishing to perpetuate a generic name honoring Governor Light of British Guiana, he transferred the name *Lightia* to a new genus in another family.

In 1848, he (Schomburgk, Fauna und Flora von British-Guiana. 993. 1848) listed under *Herrania Mariae* specimen(s) which he had collected in British Guiana along the River Barima and its affluents. It is probable, then, that this represents the area from which the type material of *Lightia lemniscata* came.

Fortunately, I have had an opportunity to study a beautiful collection (*Archer 2514*) from this same region. I have considered it as a topotype, although it must be remembered that Schomburgk's mention of the "River Barima and its affluents" circumscribed a rather extensive area.

All of the material of *Herrania* from British Guiana and northeastern Venezuela which I have seen is (with exception of collections from near the Brazilian border) referable to one species. This species is distinct from others of Middle and South America. I am inclined to believe that these specimens are referable to the concept which Schomburgk called *Lightia lemniscata*.

In the New York Botanical Garden there is a specimen collected in the easternmost part of Venezuela near the mouth of the Río Orinoco in 1896 (*Rusby & Squires 252*). On the label of this specimen, a handwritten notation states: " = *coll. by Schomburgk in Brit. Gui.*" On the basis of this annotation and the near homogeneity of the Guianan collections, I validated Schomburgk's *nomen subnudum* and transferred it to the genus *Herrania* in 1943.

When I validated the Schomburgk concept, making the new combination *Herrania lemniscata*, European collections were unavailable for study. Recently, additional and extensive material which I have seen in England indicates that *Herrania lemniscata* is indeed a very distinct species. Schomburgk's original water-colors, made in the field, are preserved at the British Museum (Natural History). Included in the collection is an excellent painting of this concept (as *Lightia lemniscata*) which depicts with unusual accuracy the habit of the small tree. There is, likewise, what appears to be a Schomburgk water-color attached to one of the herbarium sheets at Kew.

The collection *Myers 3371* consists only of flowers. It is referred with some reservation to *Herrania lemniscata*. The collection *L. Williams 11339* has been reported in the literature (L. Williams, Exploraciones botánicas en la Guayana venezolana. 309. 1942) as *Herrania Mariae*.

By using the specific epithet *lemniscata*, Schomburgk intended to call attention to the very long ribbon-like ligules which adorn the flower.

11. **Herrania Mariae** (Mart.) Decaisne ex Goudot, Ann. Sci. Nat. III. **2**: 233. 1844.

Abroma Mariae Mart. Denkschr. Regensb. Bot. Gesell. **3**: 297. *tt. 6, 9.* 1841. *Theobroma Mariae* (Mart.) Schum. ex Mart. Fl. Brasil. **12**(3): 71. *t. 15.* 1886; Ducke, Rodriguesia **4**: 273. *t. 5, fig. 2. tt. 6, 7.* 1940.

DISTRIBUTION: General in the Amazon basin, with the exception of the northern and northwestern sectors.

Small or large tree, up to 30 (doubtfully up to 60) feet tall; trunks (often 5 or 6 from a root) erect, columnar, 7–30 cm. in diameter, with brownish-black or black, rimose or scrobiculate bark. Branches sometimes closely crowded, forming a subglobose crown, in which the lower branches are subhorizontally spreading, rather flexuous, sometimes few and wide-patent; ferruginous-tomentose but becoming subglabrous, subterete, sulcate. Branchlets similar, spreading. Leaves large, digitate, long-petiolate, 6–9 (usually 7-) -foliolate, stipulate. Stipules caducous, linear, acute, 2.5–4 cm. long, about 3 mm. wide, dry, tomentose. Petioles strong, terete, subsulcate, basally somewhat swollen, 30–50 cm. long, 7 mm. in diameter, subferruginous, very densely and softly tomentose with erect, brown, stellate hairs. Leaflets thin-membranaceous to thin-papyraceous, sessile, unequal, usually strongly rhomboid-ovate, apically acuminate (acumen about 2 cm. long), basally attenuate-decurrent, entire or very slightly subundulate towards the apex and conspicuously armed with small, spine-like, hirsute, mucronulate prolongations of the veins up to 1 mm. long; the leaf surfaces usually 27–54 cm. long; 7–19 cm. wide, above dark green, very sparsely and minutely hirsute (or, in rare specimens, subglabrous) with white hairs (very rarely with brownish stellate hairs), more densely hirsute along the principal veins and along the margin, beneath pale green, subasperous or soft with minute stellate-sericeous hairs, ferruginous-tomentose along the principal veins; the veins prominent on both surfaces, but conspicuously elevated beneath. Inflorescences fasciculate, usually few-flowered (with about 10–15 flowers) but frequently many-flowered (80–90). Flower buds subglobose, large, 17 mm. in diameter, densely stellate-hispid. Flowers cauline, long-pedicelled, growing from the middle and lower portions of the trunk in contracted racemes. Pedicels densely fulvo-tomentose, hispidulous with minute, appressed strigillose hairs and also sparsely setose, articulate, 1.5–5 cm (mostly 3.5–5) long, basally subtended with a short linear, acute, densely tomentose bract 3 mm. long. Calyx subcymbiform, divided nearly to the base. Sepals 3–5, strongly unequal, entire, externally densely stellate-strigose, internally glabrous, or very minutely pilose, thick-membranaceous, brown, valvate in bud later reflexed, longitudinally striate; the interior broadly elliptic-oblong, apically subacute, with coarse hairs frequently up to 1 mm. long, 12–15 mm. long, 6–10 mm. wide; the exterior very broadly rotund or broadly ovate, apically abruptly and obscurely acuminate, with coarse hairs 1 mm. long, 11–13 mm. long, 11–12 mm. wide. Petals 4 or 5, basally sessile, concave, rotund-obovate, apically very strongly cucullate, 7–9 mm. long, 6–8 mm. wide, glabrous, muricate-papillose on both sides, 5-nerved, pale purplish red with black or purple veins, apically ligulate. Ligules filiform, pendulous, membranaceous, pale yellow or white, with purple venation, minutely granulose in all parts but especially so at the base, basally up to 4 mm. and apically hardly 1 mm. wide, 75–100 mm. long (very rarely less), apically slightly coiled. Staminal tube 5-parted, stamens alternately 2- and 4-antheriferous, filaments short and free, anthers yellow. Staminodia conspicuous, petaloid, reflexed, red, lanceolate or lanceolate-elliptic, apically obtuse and usually indentate mucronate or serrate, somewhat sinuate-undulate, glabrous, muricate-granulose on both sides, up to 20 mm. long, 6–7 mm. wide. Ovary sessile, elongate-subglobose, pentagonal (distinctly 10-costate and 5-locular), densely stellate-pilose, rose-colored or yellow-white. Style short, subcylindric-pentagonal, reddish. Stigmas 5, filiform, rose-colored. Fruit baccate, elliptic-ovoid, apically acuminate, long-peduncled (peduncle up to 2.5 cm. long), conspicuously 10-costate; the 5 primary ribs large, protruding, acute-scutelliform, about 8 mm. tall, 5 secondary ribs similar but smaller, about 4 mm. tall, conspicuously fibrous-striate transversely between the ribs, very densely stellate-hispid with stinging hairs along the ribs, up to 10–12 cm. long, 6–7 cm. in diameter, pericarp thick, subsucculent (not conspicuously fibrous), yellow when ripe. Seeds 30–40 (possibly –60), obtusely rhomboid, flattened, with a subcoriaceous testa, about 10 cm. long, 9 mm. wide and 4 mm. thick, in a white, acidulous pulp.

Brazil. AMAZONAS: Rio Solimões, *von Martius s. n.* (Type); Paleta, Teffé, *Krukoff's 4th Exped. Brazilian Amazon 4523*; Fonte Bôa, *Fróes 20630*; Rio Jurua, Marary, *Ule 5031*; Rio Amazonas, Taperinha, near Santarém, *Ginzberger 804*; Rio Madeira, Humayta, near Tres Casas, *Krukoff's 5th Exped. Brazilian Amazon 6085*; Riosinho, Juruema, *Fróes 21041*. PARÁ: Belém, *Ducke 595*; Museu Goeldi, *Murça Pires & Black 740*; Utinga, *Schultes 8072*; Belterra, *Black 47–1916*. **Colombia.** AMAZONAS: Trapécio Amazónico, interior regions of trapecio between Amazon and Putumayo watersheds, alt. about 100 m., *Schultes 6759*; mouth of Río Atacuari, *Black & Schultes 46–223*. **Peru.** MADRE DE DIOS: near Iberia, *Schultes 6461*.

Due primarily to the detailed drawing of *Herrania Mariae* which was published in *Flora Brasiliensis* and to the general availability and reliability of this work, botanists have had a tendency to consider as representing this species collections from a wide area but which actually belong to very diverse concepts. Almost all collections in our herbaria have been referred to *Herrania Mariae*. Indeed, very recently, Ducke has stated that *Theo-*

broma Mariae is "the only species in the Brazilian Amazonia representing the subgenus (or section) *Herrania* . . . ," that this "species is found throughout the hylea (including the Guianas) . . . ," and that "it is probable that, in addition to *atrorubra,* still other species of the subgenus *Herrania,* described from northern and northwestern South America, will in the future be reduced to synonymy under *Theobroma Mariae*" (Rodriguesia **4**: 273. 1940).

Herrania Mariae is probably the tallest species in the genus and, unlike almost all other species (except *H. pulcherrima*), it often has many trunks growing from one root. Martius described the plant as being 20–30 feet in height, and the drawing which was published with the original description shows an extremely robust and corpulent tree with a basal diameter of some 15–30 cm. and with a very heavy, round and full crown. My field work with *Herrania* leads me to believe that this drawing, herein reproduced for historical reasons, is erroneous and greatly exaggerates the size of the trunk and crown. Ducke commented similarly on this illustration when he wrote (loc. cit.), "In Martius' drawing, reproduced in 'Flora Brasiliensis,' *Th. Mariae* appears as a much-branched tree which does not in any way correspond with the real habit of our plant . . . ." The few collections of this widespread species which are at hand at the present time exhibit some variation, but an abundance of comparative material is lacking for determining with precision the character and extent of the variation. I am certain that when more abundant collections and field observations have been made, it will be necessary to recognize several definite geographical variants. An example of our inability to treat with complete certainty some collections is seen in *Krukoff 6085* which may possibly be an hybrid between *Herrania Mariae* and *H. nitida. Schultes 6238* and *6461,* unfortunately sterile, represent perhaps one of the extremes exhibited by the available material of *Herrania Mariae.* They are the southernmost collections of the genus, occurring on high land which never floods (in contrast to the flood-land habitat of the banks of the Amazon), and appear to have on the under surface of the leaflets a much denser and softer indumentum which tends to be rather greyish in life.

In the herbarium at Munich, there are seven very ample specimens of Martius' type collection. A study of this material has enabled me to evaluate the concept more critically. The type material has extremely membranaceous to very thinly papyraceous leaflets which have a rather softly asperous indumentum on the lower surface and a sparse asperous pilosity on the upper. The leaflets are strongly rhomboid-obovate, a shape which is peculiar to *Herrania Mariae.* The petiole, shorter and less robust than in most species, is densely tomentose, and the inflorescence is many-flowered.

Herrania Mariae is related to *H. Cuatrecasana, H. nitida* and *H. pulcherrima.* All four species have a similar type of fruit with very large and protruding cultriform ribs which are unequal and with strong transverse wrinkles between the ribs and more or less at right angles to them.

Herrania Mariae resembles *H. Cuatrecasana* very closely in some characters, and I once suspected that the latter might well be considered a variety of the former. Further field work and additional collections of *Herrania Cuatrecasana,* however, and the discovery of *H. Mariae* var. *putumayonis* give us reason to maintain the two concepts as completely distinct. The most obvious difference between the two species is the shape of the leaflets: very long oblanceolate-oblong and very long and gradually attenuate towards the base in *Herrania Cuatrecasana* and rhomboid-obovate and more abruptly attenuate towards the base in *H. Mariae*; the leaflets of the former are also usually very much longer than those of the latter species, and the petiole is much longer, stouter and more softly ferruginous-tomentose. *Herrania Mariae* has lanceolate or lanceolate-elliptic, somewhat sinuate-undulate and apically often serrate or indentate-mucronulate staminodes which are, for the most part, 20 mm. long and 6–7 mm. wide, whereas *H. Cuatrecasana* has definitely rhomboid-lanceolate, entire and apically non-serrate staminodes which measure 25 mm. long and 8 mm. wide. The ligule of the former species usually measures from 75 to 100 mm. in length, of the latter, 130 mm.

The differences which set *Herrania Mariae* apart from *H. nitida* are very evident. The latter is separated at once from the former by its complete lack of indumentum on the leaflets (or, when slightly tomentulose underneath, by the sparsity and asperous nature of the hairs); by its leaflets which are usually lanceolate-elliptic, more firmly chartaceous and most often entire; and by a number of floral characters.

Herrania pulcherrima is most easily separated from *H. Mariae* by the enormous size of its leaflets (up to 60 cm. long) which are oblong, for the most part about half as wide or wider, with the secondary and tertiary veins extraordinarily conspicuous and raised beneath, giving the upper surface, in most specimens, a verrucose appearance; by the unusually long and strong petioles; and by the larger flowers which are dark red in all parts, excepting the ligules which in some specimens are cross-banded scarlet and whitish. Both of these species have a characteristically trifid staminode.

With the specific epithet of *Herrania Mariae* Martius honored Maria, Queen of Saxony, whose father, King Maximilian Joseph of Bavaria, patronized Martius' extensive botanical explorations in South America.

Van Hall (Cacao. ed. 2. 74. 1932) states that seeds of this species are occasionally found as an adulterant in "Pará cacao", but it is not certain that his identification can be taken as reliable: his confusion of *Herrania Mariae* with another species is obvious from the statement that "it is very common in the forests of Surinam near Paramaribo and also deep into the interior" (loc. cit.).

11a. **Herrania Mariae** (Mart.) Decaisne ex Goudot var. **putumayonis** R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. **14**: 129. *t. 30, upper fig.* 1950.

DISTRIBUTION: Western part of the Amazon Valley, especially in the Putumayo River basin.

Small tree up to 12 or 14 feet tall, differing from *Herrania Mariae* chiefly in having much larger (up to 52 cm. long, 18 cm. wide), lanceolate-elliptic (not conspicuously rhomboid) leaflets; stronger and longer petioles; larger flowers up to 17 mm. in diameter, with the buds globose, and shorter ligules up to 70 mm. long, but usually somewhat less.

Brazil. AMAZONAS: Rio Jurua, Lago Cerrado, *Traill 65*. **Peru.** LORETO: Río Putumayo, between Río Igaraparana and Río Yaguas, alt. 100–150 m., *Schultes 4010* (Type).

Additional material may indicate that this concept is deserving of specific rank. At the present time, however, it would seem advisable to treat it as representing a variety of *Herrania Mariae*. The fruit of *Schultes 4010* is hardly distinguishable from that of typical *Herrania Mariae*. The flowers have several differentiating characters, the most conspicuous of which is the shorter ligule. Vegetatively, the collection is extremely similar to *Herrania nycterodendron* (with the type plant of which it was growing) and differs markedly from *H. Mariae* chiefly in the departure from the typical rhomboid form of the leaflets and in their unusually large size. The type plant of *Herrania Mariae* var. *putumayonis* consisted of four or five trunks in a clump, whereas *H. Mariae* is a treelet with a single trunk, although the condition of several trunks from one root is not uncommon in *H. Mariae*.

In the Paris herbarium there is a specimen, the collector and date of which we are ignorant, referable with reservation to *Herrania Mariae* var. *putumayonis*. It was collected at the upper Amazon town which is now called Teffé: "fluv. Amaz. Ega. *2660*. *Abroma* n. sp. Arbor debilis." The specimen is sterile, but it was thus early recognized as a distinct concept.

Herrania Mariae var. *putumayonis* may represent a western variant of the species which is most abundant in the eastern half of the Amazon basin. The varietal epithet refers to the Putumayo River.

12. **Herrania nitida** (Poepp.) R. E. Schultes, Caldasia **2**: 16. *t. pag. 17.* 1943.

Abroma nitida Poepp. in Poepp. & Endl. Nov. Gen. ac Sp. Pl. **3**: 73. 1845.
Brotobroma aspera Karst. & Tr. ex Tr. Nuev. jén. y esp. pl. fl. Neo-Granat. 12. 1854.
Herrania aspera (Karst. & Tr. ex Tr.) Karst. Linnaea **28**: 447. 1857.
Theobroma nitidum (Poepp.) Schum. ex Mart. Fl. Brasil. **12**(3): 72. 1886. Non *T. nitida* Bernoulli, Neue Denkschr. all. Schweiz. Gesell. gesam. Naturw. **24**(3): 15. *t. 17*, *fig. 3.* 1871.
Herrania atrorubens Hub. Bull. Soc. Genève II. **6**: 187. 1914.
Theobroma aspera (Karst. & Tr. ex Tr.) Van Hall,[4] Cacao. ed. 2. 49. 1932.

---

[4] This combination was made, but imperfectly so, by van Hall who, in a key, refers to "*T. aspera* (Karsten) Schumann". He refers to Schumann's account in Martius' Flora Brasiliensis where *aspera* is not mentioned under *Theobroma*, *Herrania* or *Brotobroma*; and there is no evidence that Schumann ever made the combination.

Herrania nitida (Poepp.) R. E. Schultes var. *aspera* (Karst. & Tr. ex Tr.) R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. **14**: 130. 1950, *pro parte*.

DISTRIBUTION: Widespread in the western half of the Amazon Valley and the Orinoco basin in Colombia.

Small tree, rather weak, graceful, probably up to 12 feet tall, with dark brown, roughened bark; the trunk usually less than 7 cm. in diameter at the base. Branches sparsely and minutely tomentose, becoming glabrous. Petioles subcomplanate, conspicuously striate-sulcate, ferruginous, very minutely closely appressed stellate-tomentulose, basally somewhat swollen, up to 40 cm. long, 5 mm. in diameter. Leaves grouped at the apex of the trunk, 7–9-digitate, long-petiolate, stipulate. Petiole usually slender, asperous, very minutely ferruginous-tomentulose, sometimes becoming subglabrous, terete but very deeply sulcate, up to about 40 cm. long, basally 4–5 mm. in diameter. Stipules linear, up to 2.5 cm. long, 1 mm. wide, usually brown stellate-setulose. Leaflets sessile or nearly so, unequal, lanceolate-oblong, acuminate, basally very long attenuate-decurrent, marginally entire, rigid-chartaceous to subcoriaceous, light green, shiny, glabrous above, glabrous or rarely with very sparse and deciduous minute stellate hairs remotely placed along the nerves beneath; the central leaflets 25–45 cm. long, 7–14 cm. wide; the lateral leaflets much smaller and often asymmetrical. Inflorescence fasciculate; often very numerous on the basal portion of the trunk, up to 30–40-flowered. Flowers cauline, pedicellate. Pedicels articulate, densely appressed, tomentulose with occasional strigose setae, 5 mm. long, less than 1 mm. wide. Calyx subcymbiform. Sepals 3, yellow-red, externally very coarsely stellate-setose, internally glabrous; outer sepal rounded-ovate, or triangular-ovate, up to 14 mm. long 10 mm. wide (but usually smaller); inner sepals elliptic, acute, up to 17 mm. long (but usually shorter) 6 mm. wide. Petals 5, broadly obovate, rotund, 4–5 mm. long, 4–5 mm. wide at the top, strongly cucullate, fleshy membranaceous, very densely muricate-papillose on both sides but especially without, glabrous, longitudinally marked with 5 or 6 dark red veins, yellowish-rose or rose-white, ligulate. Ligules linear, hanging, basally slightly contracted, apically slightly coiled, pink or scarlet, up to 80 mm. long, membranaceous, glabrous, longitudinally marked with five purple nerves. Staminal tube 5-parted, alternately 2- and 4-antheriferous with simple, flattened, free filaments. Staminodes conspicuous, petaloid, glabrous, muricate-granulose, elliptic, acute, marginally slightly undulating, dark blood-red without, yellowish-red within, 9 mm. long, 5 mm. wide. Ovary 5-locular, subcylindric, densely and very minutely stellate-pilose, yellow, about 1.8 mm. long, 1 mm. in diameter. Style strongly flattened, 3 mm. long, with a simple stigma. Fruit baccate, ovoid, acuminate, 11 cm. long, 5 cm. in diameter, dull, rich green, 10-costate, the 5 primary ribs thin, cultriform, basally up to 2.5–3 mm. and apically 1.5 mm. thick, 8–9 mm. high, the 5 secondaries similar but smaller, minutely and very densely beset with stinging hairs along the ribs; pericarp between the ribs usually smooth and not fibrous-rugose, very thin, sometimes with a few stinging hairs but becoming glabrescent. Peduncle short and strong, usually under

14 mm. long, 2.5 mm. in diameter. Seeds 30–40 or more, flattened, roughly triangular in outline, 9 mm. × 8 mm. × 5 mm., in a white pulp.

Brazil. AMAZONAS(?): *Glaziou 9635.* AMAZONAS: Rio Purus, varzea at Sobral, *Traill 64*; Rio Solimões, Santo Antonio do Iça, *Ducke 7618*; Benjamin Constant, *Fróes 20919*; Amaturá, *Ducke s. n.*

Colombia. AMAZONAS: Río Amazonas, La Victoria, *L. Williams 2816, 2843*; Leticia, alt. about 100 m., *Schultes 6000, 6016, 6141, 6142, 6143, 6144, 6145, 6146, 6147, 6149, 6192a*; Río Loretoyacu, *Schultes 6304, 6045, 6058, 6118, 6124, 6640, 6878, 8129, Schultes & Black 8286, 8377*; Río Apaporis, between Río Pacoa and Río Kananarí, region around Soratama, alt. 250 m., *Schultes & Cabrera 13628, 13630, 13632, 14880, 14882*; *Schultes & García-Barriga 14016*; Río Caquetá, La Pedrera, *Schultes 5876*; *Anglo-Colombian Cacao Collecting Expedition (Baker & Cope) 17, 19, 22, 24.* CAQUETÁ: Río Orteguaza, Tres Esquinas, *Schultes 3698*; upper Río Putumayo, Montclar, *Anglo-Colomb. Cacao Coll. Exped. (Cope & Holliday) 85*; Caucaya, *Anglo-Colomb. Cacao Coll. Exped. (Cope & Holliday) 87, 88*; Río Caucaya, Laguna Primavera, *Anglo-Colomb. Cacao Coll. Exped. (Cope & Holliday) 92*; Río Caguan, Arbolitos, *Anglo-Colomb. Cacao Coll. Exped. (Cope & Holliday) 100*; Camp Three, *Anglo-Colomb. Cacao Coll. Exped. (Cope & Holliday) 112*; Cartagena, *Anglo-Colomb. Cacao Coll. Expedition (Cope & Holliday) 106*; Río Caqueta, Camp Five, *Anglo-Colomb. Cacao Coll. Exped. (Cope & Holliday) 120.* PUTUMAYO: Río Putumayo, Puerto Ospina, alt. about 280 m., *Schultes 3405, Schultes & Cabrera 18933*; Río Caucaya, *Schultes 3730.* VAUPÉS: upper Apaporis basin, path between Río Itilla and Río Macaya, alt. 300 m., *Schultes 5351*; Río Macaya, Cachivera del Diablo, alt. 350 m., *Schultes 5491*; near confluence of Río Ajaju and Río Macaya, Puerto Hevea, alt. 350 m., *Schultes 5529*; middle Apaporis basin, Río Kananarí, Buenos Aires, alt. about 250 m., *Schultes 5685*; Río Apaporis, Jinogoje, *Anglo-Colomb. Cacao Coll. Exped. (Baker & Cope) 10*; Río Vaupés, Puerto Naré, *Schultes 5359*; near Miraflores, *Schultes 5715*; La Jirisa, *Schultes 5755*; near mouth of Río Kubiyú, *Schultes & Cabrera 14537*; Circasia, alt. 800 ft., *Schultes & Cabrera 19665*; between Mitú and Javareté, Igarapé, Murutinga, near Tipiaca, *Schultes & Cabrera 19284*; Río Kuduyarí, Cerro Yapobodá, *Schultes & Cabrera 14343*; near Irabasú, *Schultes, Baker & Cabrera 18439*; lower course of Río Kuduyarí, alt. 700–800 ft., near Yararacá, *Schultes, Baker & Cabrera 18553*; Río Paca, Wacaricuara, *Anglo-Colomb. Cacao Coll. Exped. (Bartley & Holliday) 55c*; Río Inirida, Caño Caribe, *Anglo-Colomb. Cacao Coll. Exped. (Bartley & Holliday) 67*; Río Papunawa, near junction with Río Inirida, *Anglo-Colomb. Cacao Coll. Exped. (Bartley & Holliday) 76.* META: Villavicencio, alt. 400 m., *Triana s. n., Killip 34247*; Llanos de San Martín, near Villavicencio, alt. 400 m., *Triana 5333*; Cordillera La Macarena, path between Río Guejar and Caño Guapayita, Cano Yerly, *Idrobo & Schultes 768, Schultes 11627*; savannahs near San Juan de Arama, Río Guejar, near landing strip "Los Micos", alt. about 500 m., *Idrobo & Schultes 1325.*

Ecuador. Río Pastaza, near Andrés, *Spruce 4969.*

Peru. [No precise locality], "*Herb. Pavon*". SAN MARTIN: Río Tocache, *Poeppig 1979* (Type). LORETO: Río Marañón, near Pongo de Manseriche, *Tessmann 4024*; Iquitos, alt. about 100 m., *Killip & Smith 27431, Murça Pires & Black 873*; lower course of Río Huallaga, between Yurimaguas and Balsopuerto, alt. 135–150 m., *Killip & Smith 28234*; Río Amazonas, Caballo Cocha, *L. Williams 2332*; upper course of Río Itaya, San Antonio, alt. 145 m., *L. Williams 3345*; Paraíso, alt. 145 m., *L. Williams 3364.*

Herrania nitida is the most widespread species in the genus, extending from the eastern slopes of the Andes in Colombia, Ecuador and Peru throughout the entire Amazon basin, being especially concentrated in the western half. As should be expected, therefore, there is evident considerable variation within the concept. It is undoubtedly the most variable species of *Herrania*, and further collections and studies will probably indicate that some of the variations are deserving of taxonomic recognition. To date, however, I have been able to separate out only one variant which is recognized now as a *forma*.

One can think of *Herrania nitida* as a kind of evolutionary center. It is in itself most distinct from all other species, but in certain respects some of its variants approach the variants of other species. Its foliage resembles that of *Herrania albiflora* and *H. purpurea* to a remarkable degree, but there are no floral or fruiting characters which point to even a remote relationship. *Herrania nitida* has often been confused with *H. Mariae*, usually because, in spite of its specific epithet, it has variants with leaflets softly tomentose (even though always sparsely so), especially in the central and eastern parts of the Amazon Valley. Indeed, one collection (*Krukoff 6085*) is so intermediate between these species that I have indicated (under *Herrania Mariae*) that it may possibly represent a hybrid of the two. Very significant floral characters (coloration, size and shape of the staminodes, form of the style, and placement of the anthers) serve easily to set the two apart; and the peculiar rhomboid-obovate leaflets of *Herrania Mariae* contrast strikingly with the lanceolate-oblong leaflets of *H. nitida*. We can see from the similarity in the fruit, however, that these two species are more closely allied than one would suspect from a study of the floral and vegetative parts.

The flower of *Herrania nitida* is one of the smallest and most delicate in the genus. Usually there is a general tendency in the staminodes and even in the petals for a yellowish tinge, with nerves which are the more conspicuous in these parts because of their dark purplish color against the yellow. The ligules are almost always yellowish or white in the upper half, but there are variants which have very dark scarlet ligules. The leaflets of *H. nitida* are generally drooping, a characteristic which I have not seen commonly in other species.

Herrania nitida prefers well-drained sloping soil, usually of a semi-lateritic consistency, and is rarely found where the annual flood of the rivers remains long enough and becomes deep enough to produce a drowning effect. It is most often rather abundant in the areas where it occurs.

In 1950, when I reduced *Herrania aspera* to a varietal status under *H. nitida*, I pointed out that there has been confusion in the presentation of this concept since 1857, when Karsten stated that it was found "in vallis Orenocensis marginibus ad pedem Andium bogotensium meridensiumque . . . et littora fluminis Magdalenae". It was difficult to accept the occurrence of the same species on both sides of the great Andean cordillera, and Karsten's assertion may have been based on the study of a sterile specimen of *Herrania albiflora* Goudot. Later, Triana and Planchon (Prodr. Novo-

Granat. 209. 1862) erroneously reduced *Herrania aspera* to synonymy under *H. pulcherrima* Goudot. A further confusion resulted with my treatment of *Herrania aspera* as a variety of *H. nitida.*

A study of the fruit and flowers of the Macarena material indicates that this plant, which represents a hitherto undescribed concept and which has, in part, been referred in the past to *H. aspera,* bears little relationship to *Herrania pulcherrima* and none to *H. nitida.* The confusion which has resulted in the past appears to be directly a result of two factors: incomplete material and Karsten's failure to cite a definite specimen which we could take as a type. The presumed type of *Herrania aspera* has been taken as *Triana 5333* from the llanos of Villavicencio. In view of the material now available and of field studies in the Macarena not far from the type locality of *Herrania aspera,* I am now reducing *H. aspera* to synonymy under *H. nitida* and am describing *H. tomentella* to accommodate the soft-pilose, large-leaved plant which is common in the western part of the Llanos and in the Macarena.

Herrania atrorubens is also herewith reduced to synonymy under *H. nitida.* When Huber described *Herrania atrorubens,* he cited his collection *7935* from the Alto Amazonas of Brazil as the type and only material of the concept. He stated that it differed from *Herrania Mariae* in being smaller and in having dark red flowers. In 1944, in treating this binomial (Caldasia 2: 329. 1944), I wrote, "I have been unable to examine the type of this concept. Without typical material, I have found it impossible to estimate its validity as a species, but it would seem that the colour character alone would hardly suffice for the creation of a new specific concept."

Now, having completed an extensive study of the classical material of the genus, I have been unable to locate the type of *Herrania atrorubens.* One would expect it to be preserved in the Museu Goeldi in Belém do Pará or in the Herbier Boissier in Geneva, but a search in these two institutions, as well as in other principal Brazilian and European herbaria has not uncovered Huber's material.

In the light of the experience gained during the study of a wide range of material, it would seem from an evaluation of the meager characters given by Huber and from the geographical data given for the type collection that *Herrania atrorubens* may be reduced safely to synonymy under *H. nitida.*

12a. **Herrania nitida** (Poepp.) R. E. Schultes f. **sphenophylla** R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. **14**: 131. 1950.

Herrania nitida (Poepp.) R. E. Schultes var. *sphenophylla* R. E. Schultes, Caldasia **2**: 20. 1943.

?Theobroma Mariae (Mart.) K. Schum. f. *minor* Diels, Notizbl. **15**: 48. 1940.

DISTRIBUTION: Western part of the Amazon Valley.

A small tree which differs from *Herrania nitida* principally in having smaller and lanceolate-elliptic or very narrowly obovate leaflets, in having a fewer-flowered inflorescence, in having flowers which are usually larger and redder (the ligules usually entirely red), in having a smaller fruit (7.5–8 cm. long, 4 cm. in diameter), and in being humbler in stature.

Brazil. AMAZONAS: Rio Jutahy, Riosinho Jurunema, *Fróes 21040.* **Colombia.** PUTUMAYO: Umbría, alt. 325 m., *Klug 1853.* AMAZONAS: Trapécio Amazónico, Río Loretoyacu, *Black & Schultes 46–331.* **Peru.** LORETO: Río Ucayali, *Tessmann 3287*; Guamitanacocha, Río Mazán, alt. 100–125 m., *Schunke 45* (Type).

The very striking difference in size between the leaves and nearly all other parts of *Herrania nitida* and *H. nitida* f. *sphenophylla* cannot be laid to ecological variation. When this difference was first noted (on the basis of *Schunke 45*) it was recognized as varietal. Later studies in the field, however, as well as information obtained through an examination of additional collections, indicate that the concept is probably better treated as a form, since little other than color and size differences, constant though they be, are evident.

In 1940, Diels described *Theobroma Mariae* f. *minor* from the Río Pastaza in eastern Ecuador. The type specimen seems to have been destroyed during the recent war. If we may judge from the few characters given in Diels' original description and from geographical distribution, it might be safe to assume that the concept represented either *Herrania nitida* or, more probably, *H. nitida* f. *sphenophylla.* In 1943, I pointed out this possibility (Caldasia **2**: 332. 1944), stating: "I have been unable to examine herbarium material or photographs of this form, and, until an opportunity to do so presents itself, I shall be unable to treat it critically. In most of the characters enumerated in the original description, it would seem that . . . it approaches *Herrania nitida* var. *sphenophylla*, although, of course, no mention is made of the fundamentally important character of leaf-pilosity."

13. **Herrania nycterodendron** R. E. Schultes, Caldasia **2**: 21. *tt. pag. 22, 26.* 1943; Bot. Mus. Leafl. Harvard Univ. **14**: *t. 35.* 1950.

DISTRIBUTION: Westernmost parts of the Amazon Valley.

Small, slender, graceful tree up to 25 feet tall, the trunk usually simple, erect, terete, apically leafy, up to 8–9 cm. in diameter at the base, covered with an ashy-yellowish, scrobiculate bark. Leaves large, 7-digitate, stipulate, very long petiolate. Stipules caducous, linear, acute, 2.5–4 cm. long, more or less 3 mm. wide, dry, tomentose. Petiole strong, terete but very obscurely sulcate, basally slightly swollen, subferruginous, extremely densely and softly tomentose, up to about 60 cm. in length, 8–9 mm. in diameter. Leaflets sessile, unequal lanceolate-oblong, with a rather acute cusp up to 2 cm. long, basally long- and gently decurrent-attenuate, entire (or minutely and obscurely subundulate) but often very conspicuously armed with the hirsute spinule (up to 1 mm. long) formed by the prolongation of the veins; firmly chartaceous or papyraceous, the central leaflets up to 60 cm. long, 22 cm. wide, above dark green and subnitid, subglabrous or very sparsely and minutely hirsute, minutely tomentulose along the principal veins, beneath pale green, softly stellate-pilose, very densely and softly ferruginous-tomentose along the main nerves; the veins prominently raised on both surfaces but especially so beneath. Inflorescence fasciculate, up to 40-flowered. Flowers cauline, long-pedicellate, in contracted racemes on the lower portions of the trunk. Pedicels very slender, appressed-tomentose, articulate, 2–2.5 cm. long, basally with a short, linear, apically acute bract which is densely tomentose and 3 mm. long. Bud subglobose, large, about 7–8 mm. in diameter, densely and minutely stellate-puberulent, brown. Calyx subcymbiform, divided almost to the base. Sepals 3, strongly unequal, thick, brownish-purple, valvate in the bud, externally minutely stellate-pilose, internally very minutely puberulent; the outer sepal broadly rotund-obovate, apically rotund-obtuse, entire, 19 mm. long, 15 mm. wide; the inner 2 elliptic, entire, apically subacute, about 15 mm. long, 7–8 mm. wide. Petals 5, basally sessile, widely rotund, concave, apically strongly cucullate, 10 mm. long, 8–9 mm. wide, glabrous, muricate-papillose on both surfaces but especially so on the outer, pale yellow with 7 purple nerves, ligulate. Ligules filiform, hanging, membranaceous, glabrous on both surfaces but basally minutely granulose, 2 mm. wide at base, up to 90–100 mm. long, dark purplish with prominent black nerves. Staminal tube 5-parted; stamens alternately 2- and 4-antheriferous, the filaments glabrous, slender and free. Staminodes conspicuous, petaloid, reflexed, lanceolate-elliptic, acute, entire, 19–21 mm. long, 7–9 mm. wide, muricate-granulose on both surfaces. Ovary sessile, ellipsoid, 10-costate and 5-locular, densely pilose, 3 mm. long, 2 mm. in diameter, yellow. Style filiform, glabrous, apically profoundly divided into 5 parts. Stigmas 5, thick. Fruit ellipsoid, 10–12 cm. long, 4–5 cm. in diameter, apically long and gradually attenuate, often slightly constricted near the tip, apically acute or often rotund-obtuse, basally indented and pedunculate (peduncle woody, up to 4–5 cm. long, 3–4 mm. in diameter), with an extremely dense and minute velvety-stellate indumentum on all parts, without stinging hairs, very profoundly 10-costate, with 5 thick and strongly blunt-rounded primary ribs and 5 similar but smaller secondary ribs; pericarp thick-crassulent, sublignose, ashy-yellow when ripe. Seeds up to about 100, triangular or triangular-ovate in outline, flattened, 9 mm. × 8 mm. × 2 mm. thick, in a white pulp.

Brazil. AMAZONAS: Rio Solimões, Fonte Boa, *Fróes 20578*.

Colombia. AMAZONAS: Trapécio Amazónico, Río Amazonas, Leticia, *Schultes 6017*; interior regions of Trapécio Amazónico, between Amazon and Putumayo watersheds, alt. about 400 m., *Schultes 6777*; path near Quebrada Agua Negra (headwaters of Río Hamacayacu), *Black & Schultes 46–389*; Río Loretoyacu, *Schultes 6335*; Río Caqueta, La Pedrera, *Anglo-Colomb. Cacao Coll. Exped.* (*Baker & Cope*) *14, 20.* CAQUETÁ: Río Caucaya, Laguna Primavera, *Anglo-Colomb. Cacao Coll. Exped.* (*Cope & Holliday*) *93*; Río Caguán, Cartagena, *Anglo-Colomb. Cacao Coll. Exped.* (*Cope & Holliday*) *108*; Camp Two, *Anglo-Colomb. Cacao Coll. Exped.* (*Cope & Holliday*) *110*; Camp Three, *Anglo-Colomb. Cacao Coll. Exped.* (*Cope & Holliday*) *113*; Camp Four, *Anglo-Colomb. Cacao Coll. Exped.* (*Cope & Holliday*) *109*; Río Caquetá, at confluence with

Río Caguán, *Anglo-Colomb. Cacao Coll. Exped.* (*Cope & Holliday*) *121*; Camp Six, *Anglo-Colomb. Cacao Coll. Exped.* (*Cope & Holliday*) *128*; Piedra Blanca, *Anglo-Colomb. Cacao Coll. Exped.* (*Cope & Holliday*) *131*.

Peru. LORETO: Río Putumayo, Remanso, alt. 180 m., *Schultes 4011* (Type); Florida, north of Río Zubineta, alt. 200 m., *Klub 2069*; "Corbata", opposite Isla Salamanca, alt. 180 m., *Schultes 4012*; near Caucaya, *Anglo-Colomb. Cacao Coll. Exped.* (*Cope & Holliday*) *97*; Río Amazonas, Mishayacu, near Iquitos, alt. 100 m., *Klug 1588*.

Herrania nycterodendron most closely resembles *H. Mariae* and *H. Cuatrecasana*. It is immediately set apart from these species, however, by its curious type of fruit. The fruit of *Herrania nycterodendron* has a dry, somewhat coarse and fibrous rind which is covered completely with a soft indument of velvety hairs; it lacks the stinging hairs which are usually present in this genus. The ribs of the fruit of *Herrania nycterodendron* are broad and rounded with deep furrows. The fruit is apically much more bluntly rounded, in most cases, than is that of related species.

Fróes 20578 is a sterile collection which has been referred to *Herrania nycterodendron* with some reserve.

The natives of the Peruvian bank of the Río Putumayo near Remanso, Isla Salamanca, refer to *Herrania nycterodendron* as "bat-tree" or "tree of the bats". This curious common name may be due, as several natives explained to me, to the fact that the soft, velvety indument of the fruit feels like the fur of small bats which are common in the vicinity. It may also be due to the fact that the fruits cluster on the basal portions of the stem in such a manner as to suggest bats which are accustomed to pass the day hanging from the lower parts of the trunks of small trees in the dark forests. The Witoto name, *mu-sĕ′-na*, is also applied to the *marraca* (*Theobroma glauca* Karst.), and *mu-sé-ge-ke*, the diminutive, is very commonly used to refer to *Herrania nycterodendron* and possibly also to *H. Mariae* var. *putumayonis*.

14. **Herrania pulcherrima** Goudot, Ann. Sci. Nat. III. 2: *232. t. 5, figs. 11, 12.* 1844.

Theobroma pulcherrima (Goudot) De Wildeman,[5] Pl. Trop. Grande Cult. 89. 1902.

DISTRIBUTION: The mountainous regions of Central Colombia.

Small tree up to 15–24 feet tall, with a simple, columnar trunk 15–25 cm. in diameter. Bark thin, ashy-brown, scrobiculate, glabrous except near the apex where it is covered with a ferruginous indument. Branchlets villose, obscurely sulcate. Leaves 10–15, large, digitate, very long-petiolate, 5–7-foliate. Petioles robust, terete or sulcate, very densely ferruginous-villose, as long as the leaflets, 7–10 mm. in diameter. Leaflets sessile, unequal, lanceolate-ovate, marginally coarsely and regularly sinuate towards

---

[5] This combination has been made independently by later workers, apparently unaware of the earlier publication. *Cf.* Pittier, Man. Pl. Usuales Venez. 147. 1926.

the apex, acuminate, basally attenuate, very coriaceous, mostly 45–60 cm. long (occasionally much longer), 19–35 cm. wide; above dark green, shining, coarsely muricate or minutely subtuberculate, glabrous (or extremely remotely armed with caducous hairs), the nerves minutely but densely tomentulose; beneath brownish green, densely and softly ferruginous stellate-pilose, softly and densely villose-sericeous along the veins. Stipules caducous, linear, tomentose, 3 cm. long. Inflorescence fasciculate, many-flowered (20–30). Pedicels 11 mm. long, 1.2 mm. in diameter, scabrid-hirtellous and minutely stellate-pilosiusculous. Buds ovoid, densely fulvo-tomentose, 10 × 6 mm. Flowers large, crimson-red. Calyx subcymbiform. Sepals 3, subchartaceous, broadly ovate or elliptic-ovate, entire, rounded or subacute, externally brownish red, stellate-tomentose and stellate-puberulent, internally glabrous and crimson-red, up to 19–20 mm. long, 12–13 mm. wide, valvate in the bud. Petals 5 or (usually) 6, sessile, obovate, concave, strongly cucullate muricate-papillose or granulose on both sides, but especially externally, longitudinally striate-veined, the 5 veins prominently purple or black internally, crimson or dark red, ligulate. Ligules pendulous, 80–110 mm. long, 2–3 mm. wide, glabrous, strongly marked with 3 dark red veins, basally strongly and abruptly contracted, dark purplish red. Stamen tube 5-parted with alternately 2- and 3-antheriferous stamens and simple, short, free filaments. Staminodes very conspicuous, petaloid, lanceolate-elliptic, apically 3-fid, marginally entire, muricate-granulose on both sides, dark purple-red, 23 mm. long, 7 mm. wide. Pistil up to 7.5 mm. long. Style slender, simple yellow, 3.5 mm. long, the stigmatic tip deeply 5-fid. Ovary sessile, 5-locular, ovoid, very densely pilose, pale yellow, 4 mm. long, 3 mm. in diameter. Fruit ellipsoid, attenuate-acuminate, 10-costate, with 5 large primary and 5 smaller secondary cultriform ribs, covered, especially along the ribs, with minute stinging stellate hairs, the rind very thin when dried but crassulent in life, yellow when ripe. Seeds probably about 50, compressed, triangular in outline, in a sweet white pulp.

Colombia. META: Iraca, San Juan [de Arama], Llanos Orientales, *Goudot s. n.* (Type). BOYACÁ: region of Mount Chapon, northwest of Bogota, El Umbo region, alt. 3,000 ft., *Lawrence 437*. CUNDINAMARCA: Municipio de El Peñon, Hacienda "Curiche," alt. 1000 m., *Jaramillo 202*.

The type specimen of *Herrania pulcherrima* has always been thought to be in Paris, but, as in the case of *H. albiflora,* there is material in Geneva which may well be the true type from which Goudot's description and illustrations (at least of the flowers) were made. Goudot spoke of the type plants as inhabiting the great forests situated between the Ríos Ariari and Guayabero, affluents of the upper Orinoco, in the Colombian *llanos*.

The Geneva material consists of two sheets. It is labelled in Goudot's hand, "*Herrania pulcherrima* mihi. An. Sc. Nat. 1844. Llanos del Orinoco, pueblo d'Iraca, San Juan, Flos: Dec." One sheet consists of a piece of golden-tomentose stem about one foot long, a very young leaf, and young capsules. One of the envelopes has the native Coreguaje Indian name (reported by Goudot in the original description): "*cacao cahouai* — Llanos". Another envelope, on the outside of which Goudot has written "C N. 2 theobroma affinis *Herrania pulcherrima*," has a completely and beautifully dissected flower, the separate parts glued to the inside of the envelope. There can be no doubt but that Goudot made his drawing of the flower of *Herrania pulcherrima* (loc. cit. *t. 5, figs. 11, 12*) from this same dissection.

The leaf which is preserved at Geneva could not have served as a basis for Goudot's excellent description, but a study of the material and the description would seem to indicate that the Paris material represents that from which the original description of the leaf was drawn.

It may be of value to publish a few notes on Goudot's dissection of the flower. The three sepals are laid flat, the very slightly puberulent inner surface exposed. Two are rather broadly ovate, about 15 mm. long and 5 mm. wide (all measurements taken dry), apically rounded; the third, somewhat elliptic, 18 mm. long and 4 mm. wide, apically bluntly pointed. The five petals are all about equal, strongly cucullate, very densely muricate-papillose or granulose externally, papillose internally in six longitudinal lines, the ligules up to 90 mm. long, 2.5 mm. wide immediately above the constriction at its junction with the petal. The staminodes are lanceolate-elliptic, 15 mm. long, 4–4.5 mm. wide, muricate-granulose, and apically so strongly trifid that the tip appears to be mucronate. This was noted by Goudot when he described the staminodes as apically "mucronés et échancrés;" but, in his drawing, he indicated the tip as extremely acute. The ovary is very densely yellowish tomentose.

It is unusual to find a species of *Herrania* which occurs both east and west of the Andes, as well as in the valley between the several Andean chains in Colombia. Yet that appears to be the distribution of *Herrania pulcherrima*. Goudot said that he had found it in the deep valleys of the eastern Andean chain, near Savana-Grande and Payme where, however, it seemed to be rare and isolated. I have seen no Goudot specimen from this locality, but it is very significant, I think, to note that all earlier and a number of the later collections were made not in the eastern llanos but within the *Andean* cordillera.

Vegetatively, *Herrania pulcherrima* can easily be confused (and has been confused) with *H. tomentella*, a species growing in the eastern llanos at the foothills of the Andes where the type of *H. pulcherrima* was collected. The differences between these two species are discussed under *Herrania tomentella*.

The earliest reference to *Herrania pulcherrima* is Eloy Valenzuela's minute description of the plant written in Mariquita in the Departamento del Tolima, Colombia, in 1784, while he was engaged in the work of the Mutis Botanical Expedition in New Granada. For historical reasons, this description has been reproduced in full under the generic description at the beginning of the synopsis.

In the collection of Mutis plates, there is a most strikingly beautiful and accurate water-color of a section of *Herrania pulcherrima* in full flower.

A number of diagnostic characters of this species are most clearly shown: the congested, many-flowered inflorescences, the very abbreviated pedicels, and the long and membranaceous ligules with alternate scarlet and whitish bands. Of this colored plate, there are two copies in black and white. No foliage seems to have been drawn. A search in the Mutis collection of plants in Madrid has failed to produce a specimen of *Herrania pulcherrima.*

The specific name *pulcherrima*, meaning "very beautiful," could not be more appropriate. It recalls Valenzuela's picturesque remark, which I have used as a theme for this synopsis; that the flower of *Herrania pulcherrima* or *cacao esquinado* "could be considered as the greatest marvel of the plant kingdom, and one can hardly believe that nature, as frugal and simple as she is, would have used so many ribbons and so much ornamentation to adorn herself almost as ostentatiously as in the fashions".

14a. **Herrania pulcherrima** Goudot var. **pacifica** R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. **14**: 131. *t. 28, lower fig.* 1950.

Herrania pacifica Cuatr. Rev. Acad. Col. Ciénc. Exact. Físic. Nat. 7. **27**: 307. 1947. Nomen nudum.

DISTRIBUTION: Pacific coastal slope of Colombia and northern Ecuador and the Gulf of Urabá in Colombia.

A small tree up to 25 feet tall, differing from *Herrania pulcherrima* chiefly in having strongly membranaceous leaflets which are minutely stellate-pilose and not muricate or subtuberculate above; lateral leaflets usually strongly oblique; flowers which are commonly much smaller, with the petals and ligules yellow or white; and smaller fruit (11.5 cm. long, 7 cm. in diameter).

Colombia. ANTIOQUIA: north of Dabeiba, road to Turbo, *Univ. Calif. 3rd Bot. Exped. Andes 1942 (Metcalf & Cuatrecasas) 30173*; near Guapá, 53 km. south of Turbo, alt. about 50 m., *Haught 4607*; Urabá, Municipio de Mutatá, Villa Arteaga, alt. about 150 ft., *Schultes & Cabrera 18707a.* VALLE: Pacific Coast, Río Yurumangui, Caimanero, *Cuatrecasas 16010*; Río Calima, Quebrada La Brea, alt. 30–40 m., *Schultes 7324.* CHOCÓ: Río San Juan, vicinity of Palestina, alt. 0–30 m., *Cuatrecasas 21337*; Río Andaquedá, Lloro, *Anglo-Colomb. Cacao Coll. Exped. (Bartley & Holliday) 174.* **Ecuador.** PICHINCHA: Santo Domingo de los Colorados, alt. 800 m., *Acosta-Solis 10923*; "foot of western cordillera", alt. 100 m., *Rimbach 48.*

This concept, as indicated by the varietal epithet, would seem to represent a western or Pacific coastal variant of *Herrania pulcherrima*, a species which, in its typical form, is endemic to the Cordilleras of Colombia.

15. **Herrania purpurea** (Pitt.) R. E. Schultes, Caldasia **2**: 333. 1944; Caldasia **3**: 23. *t. pag. 24, fig. 1, 2.* 1944; Bot. Mus. Leafl. Harvard Univ. **13**: 282. 1949.

Theobroma purpureum Pitt., Fedde Rep. Sp. Nov. **13**: 319. 1914; Standl. Contr. U. S. Nat. Herb. **27**: 262. *t. 51.* 1928; Standl., Contr. Arnold Arb.

5: 104. 1933; Standl., Field Mus. Nat. Hist. Bot. Ser. Publ. 392: 688. 1937; León, Inst. Interam. Ciénc. Agríc. Bol. Técn. 2: 6. 1949.

DISTRIBUTION: Costa Rica, Nicaragua, Panama and northwesternmost Colombia.

Small tree up to 10 feet tall, without branches along the trunk, except near the apex, with grey bark becoming glabrous but densely yellow-villose when young. Leaves usually 5-digitate, stipulate. Stipules linear, acute, dark purple, more or less stellate-villose, caducous, up to 5 cm. long, 3 mm. wide. Petioles terete, obscurely sulcate, somewhat ferruginous-villose, strong, basally rather swollen, 30–45 cm. long. Petiolules strong, very short, up to 5 mm. long. Leaflets unequal, obovate-oblong, basally cuneate, apically broadly and obtusely acuminate, entire or very obscurely sinuate, thin-chartaceous, glabrous above, sparsely and minutely stellate-villose beneath (the nerves densely stellate-villose on both surfaces), almost as long as the petioles, 22–35 cm. long, 6–13 cm. wide. Inflorescences fasciculate, 5–8-flowered. Flowers cauline, in contracted racemes on the lower and middle portions of the trunk, dark purple, pedicellate. Pedicels terete, articulate, brown-tomentose, about 4 mm. long, basally subtended by a short, linear, naviculiform bract which is densely brown-tomentose externally, glabrous internally. Buds globose, 7–9 mm. in diameter, villose. Calyx patelliform. Sepals 3 (rarely 4), united for half their length, broadly ovate or (rarely) elliptic-ovate, obtuse, entire, 12 mm. long, 9 mm. wide, brownish purple, glabrous within, ferruginous, densely stellate-tomentose without. Petals 5, sessile, obovate, strongly cucullate, up to 8 mm. (frequently less) long, 4 mm. wide, muricate-papillose on both sides but denser externally (especially along the nerves), pale purple without, veins deep purple within, longitudinally striate-nerved, 5-veined, ligulate. Ligules linear, very narrowly lanceolate, basally emarginate, acute, hanging, dark purple, about 15 mm. long, 1.8–2 mm. wide. Staminal tube 5-parted, short, 3 mm. long; stamens alternately 1- and 2-antheriferous; filaments simple, short, free; anthers about 1.5 mm. long, longitudinally dehiscent, yellow. Staminodes petaloid but not very conspicuous, ovate, apically acute, reflexed, densely muricate-granulose, red-purple, 9 mm. long, 8 mm. wide. Ovary ovoid, 10-sulcate, villose, 2.5 mm. long, 1.3 mm. in diameter. Style glabrous, 5-parted. Fruit not numerous, elliptic-ovoid, often irregularly twisted, up to 9 cm. long, 5 cm. in diameter, apically rotund-obtuse, slightly constricted near the apex, basally hardly indented, with a strong, comparatively long, peduncle, 10-costate, the 5 primary and the 5 secondary ribs almost equal, blunt-rounded, 5 mm. and 4 mm. high, respectively, and very densely armed with stinging stellate hairs, between the ribs striate-fibrous and armed with stinging hairs; pericarp crassulent-coriaceous or subligneous, yellow when ripe. Seeds 25, obtusely rhomboid, flattened, about 1 cm. long, 1.3 cm. wide and up to 0.6 cm. thick.

Colombia. ANTIOQUIA: Golfo de Urabá, region around Turbo, road between Turbo and Río Grande, *Schultes 5754*; Río Micurí, *Schultes 5755*; Municipio de Pavorandocito, outskirts of Pavorandocito, alt. 80 m., *Gutiérrez 2000*; Municipio de Mutatá, Villa Arteaga, alt. about 150 ft., *Schultes & Cabrera 18653, 18593*; *Schultes & López 10464*; *Anglo-Colomb. Cacao Coll. Exped.* (*Bartley & Holliday*) *164, 169, 170.*

Costa Rica. Palmar, Río Grande de Terraba, *Pittier & Durand 3926, 6721*; Pacific Coast, Boca Culebra, alt. 50 m. *Pittier 12158.* LIMÓN: La Colombiana Farm of United Fruit Company, alt. about 70 m., *Standley 36832*; Finca Montecristo, Río Reventazón, below Cairo, alt. about 25 m., *Standley & Valerio 48421, 48545, 48584*; Hamburg Finca, Río Reventazón, below Cairo, *Standley & Valerio 48792*; hills above tramline, Los Negritos Farm near Río Reventazón, *Dodge & Neverman 7178.* GOLFO DULCE: Playa Blanca, *Valerio 461.*

Nicaragua. *Seemann s. n.*

Panama. Monte Lirio, *Hayes 398.* CANAL ZONE: Near El Paraíso, alt. 30–100 m., *Pittier 2574*; forests along Río Indio de Gatún, *Maxon 4835*; Valley of Masambí, road to Las Cascadas Plantation, alt. 20–100 m., *Pittier 2675*; Barro Colorado Island, Gatún Lake, *Maxon, Harvey & Valentine 6804, Kenoyer 443*; Gatún Lake, *Standley 31319*; alt. 120 m., or less, *Standley 40911*; Armour House to second bay north, *Bangham 549, Bailey & Bailey 31, Shattuck 198*; near end of Fairchild Trail, *Wetmore & Abbe 73*; hills north of Frijoles, *Standley 27434*; Gamboa, *Standley 28416*; near Fort Randolph, *Standley 28647*; Obispo, *Standley 31722*; near Madden Dam, *Alston 8861.* CHIRIQUÍ: Progreso, *Cooper & Slater 283.* BOCAS DEL TORO: Laguna de Chiriquí and vicinity, *Hart 96, von Wedel 1112*; Changuinola Valley, *Dunlap 448, von Wedel 976, 1721, Lucas 2.* DARIEN: trail between Pinogana and Yavisa, alt. 15 m., *Allen 282.* PANAMÁ: vicinity of Caña, alt. 900 m., *Goldman 1974*; Changuinola, *Cooper & Slater 12a*; Changuinola and Sixaola, *Rowlee & Stock 1029*; Marraganti and vicinity, alt. 10–200 ft., *R. S. Williams 662.*

Herrania purpurea is obviously most closely allied to *H. albiflora*, a relationship which is discussed under *H. albiflora.* Both species are alone in the genus in having a curious patelliform calyx and extremely short ligules which give the flowers an entirely different appearance from those of all other species which have a subcymbiform calyx, usually with very long, filiform ligules. *Herrania albiflora* and *H. purpurea*, therefore, are considered to form a distinct section of the genus.

Further study may indicate that *Herrania purpurea* might better be treated as a variety of *H. albiflora*; but, at the present state of our understanding, the two would seem to represent well established specific concepts which geographically are sharply delineated.

Herrania purpurea is the only species of the genus known to occur outside of South America. It has its main center of distribution in lower Middle America but it is represented in the adjacent part of Antioquia (and probably in the northern Chocó) — the northwesternmost corner of Colombia.

The binomial *Herrania purpurea* was published as a *nomen nudum* in the first edition of Thomas Belt's "The Naturalist in Nicaragua" (1874, p. 116). Belt wrote: "About here grows a cacao (*Herrania purpurea*) differing from the cultivated species (*Theobroma Cacao*)." I have been unable to discover a description of the plant or a publication of the binomial prior to 1874. In the preface of his book, Belt stated that "Prof.

D. Oliver of Kew has kindly named for me some of the plants." In the collection of *Herrania* at Kew, I did not find any specimen from Nicaragua collected prior to 1874 and annotated with this binomial. Dr. N. Y. Sandwith of Kew has kindly searched through the archives and reports that he can find nothing which might suggest that Oliver had published the binomial.

Pittier's description of *Theobroma purpureum* was based upon a Panamanian collection, and he made no mention of a prior publication of this specific epithet. There is no doubt that the binomial which Belt published refers to the same concept which Pittier later and independently described and for which he used the identical specific epithet. In accordance with the International Code of Botanical Nomenclature, therefore, we must consider Pittier's *Theobroma purpureum* as the first valid use of the specific epithet.

According to Pittier (Fedde Rep. Sp. Nov. **13**: 319. 1914; Standley, Field Mus. Nat. Hist. Bot. Ser. **18** (Publ. 392): 688, 1937), the Bribrí Indians of Costa Rica employ the roasted seeds for preparing a bitter drink.

16. **Herrania tomentella** R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. **16**: 205, 213. *t. 32.* 1954.

Herrania nitida (Poepp.) R. E. Schultes var. *aspera* (Karst. & Tr. ex Tr.) R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. **14**: 130. 1950, *pro parte*.

DISTRIBUTION: Eastern foothills of the Andes in the Orinoco drainage area of Colombia.

A small tree, slender and graceful, commonly up to 12 feet in height. Trunk erect, about 3 inches in diameter, covered with blackish bark, sparsely branched near the top or unbranched. Branches tomentose. Branchlets densely villose, with golden-rust-colored and persistent hairs. Leaves very large, digitate, 7-foliate, very long-petiolate. Petioles round, somewhat constricted at the base, very densely and softly golden or ferruginous, tomentellous, up to 60 cm. long, 9–10 mm. in diameter. Stipules persistent, linear, densely rough-tomentellous, up to 3 cm. long, 2 mm. wide. Leaflets sessile, oblanceolate or broadly lanceolate-ovate, erect, strongly unequal, membranaceous to papyraceous, acuminate, basally attenuate, the margin both regularly and lightly sinuate-dentate in the upper half but especially towards the apex and everywhere armed with cilia-like stellate hairs, 30–50 cm. long, 13–20 cm. wide, above rough to the touch with sparse, single, brown hairs, beneath rather softly and densely tomentellous with long golden-rust-colored stellate hairs. Inflorescence fasciculate, relatively few-flowered, growing from the lower portion of the trunk. Pedicels articulate, 7 mm. long, 1.5 mm. in diameter, densely stellate-pilose. Buds globose, 15 mm. in diameter, densely stellate-pilose. Calyx 3-parted, divided almost to the base, subcymbiform. Sepals commonly unequal, rather carnose in life, dark purplish, strongly valvate in the bud, externally rather coarsely stellate-pilose, internally very minutely granulose-pulverulent; the 2 interior sepals round-ovate, the margins entire, apically perfectly rounded, about 14 mm. long, 10 mm. wide; the exterior sepal usually triangular-elliptic, the margin entire, apically subacute, 13–14 mm. long, basally 6–7 mm. wide. Petals 5, basally sessile, obovate or ovate, apically very strongly concave-cucullate, about 8 mm. long, 7 mm. (often up to 8 mm.) wide, dark blood-red with purple nerves, externally minutely muricate-verrucose, ligulate. Ligules linear, about 70 mm. long, basally 3 mm. wide, filiform near the apex, dark blood-red but near the tip pinkish. Staminal tube 5-parted with stamens bearing 1 and 2 anthers alternately and with short, free filaments. Staminodes petaloid, dark blood-red, membranaceous, elliptic, marginally entire, acute, 14–15 mm. long, 6–7 mm. wide, somewhat verrucose on both surfaces. Fruits not numerous, ellipsoid, up to 9 cm. long, 4 cm. in diameter, long-attenuate but near the tip slightly constricted, the tip itself obtuse and frequently twisted, basally not indented, pedunculate, with remnants of the persistent sepals; peduncle articulate, 3 cm. long, 4 mm. in diameter, everywhere densely and very minutely velvety-pilose, soft to the touch and without stinging hairs, very deeply 10-costate, the 5 primary ribs thick and bluntly rounded, 8 mm. high, the 5 secondary ribs similar but smaller, 4–5 mm. high, transversely rather fibrous-rugose, the pericarp thick, almost woody, reported to ripen yellow. Seeds about 60, embedded in a white pulp.

A description of the pollen grain of *Herrania tomentella* is given under the generic description at the beginning of this monograph.

Colombia. [No precise locality], *Rocha s. n.* META: Villavicencio, alt. 300 m., *Triana s. n.*; *Sprague 135*; Sierra de la Macarena, Playa Bonita, alt. 400 m., *Philipson, Idrobo & Fernández 1420*; Caño Entrada, alt. 550 m., *Philipson, Idrobo & Jaramillo 2199*; Sabanas de San Juan de Arama, Río Guëjar, near landing-field Los Micos, alt. about 500 m., *Idrobo & Schultes 612, 721*; path between Río Guëjar and Caño Guapayita, alt. about 500–600 m., *Idrobo & Schultes 787, 1192* (Type); Caño Yerly, *Schultes 11629*; Sabanas de San Juan de Arama, Río Guëjar, *Schultes 11821.*

Herrania tomentella resembles, in its foliage, *H. pulcherrima* and *H. Cuatrecasana.* It differs from the former in having a much more finely sinuate margin, in having a smooth (instead of a rather muricate-subtuberculate) upper surface, in being more finely tomentose beneath, and in being membranaceous (rather than coriaceous) and generally smaller. From the latter, it can be distinguished by differences in the shape and margin of the leaflets: those of *Herrania Cuatrecasana* are conspicuously long attenuate-decurrent towards the base and have very remotely and obscurely crenate-denticulate margins.

In form of the fruit, *Herrania tomentella* approaches *H. Cuatrecasana* more closely than *H. pulcherrima.* The capsule of *Herrania pulcherrima* has strongly cultriform ribs with stinging hairs, whereas that of *H. tomentella* has broadly rounded ribs without stinging hairs. Furthermore, floral differences between *H. pulcherrima* and *H. tomentella* are marked, especially in the staminodes which are apically trifid in the former but acute in the latter.

Although there are a number of resemblances between the capsule of *Herrania tomentella* and that of *H. Cuatrecasana,* the soft indumentum and lack of stinging hairs in the former are in sharp contrast to the condition in the latter where, except for stinging hairs along the ribs, the surface is glabrous or glabrescent. There are likewise several floral differences.

The leaflets of *Herrania tomentella* are borne in a partly erect position. This is also true of *Herrania Cuatrecasana* and *H. pulcherrima* and possibly of all species which have a noticeably swollen callus at the base of the leaflets. In this erect position of the leaflets, *Herrania tomentella* differs strikingly in habit from the only other species known in the Macarena, *H. nitida*, which has leaflets which tend to be rather reclinate.

A study of the fruit of the material from the Macarena has clarified a confusion of long standing. Although in the past specimens of *Herrania tomentella* have been referred to *H. pulcherrima* or to *H. nitida* (as *H. aspera* or *H. nitida* var. *aspera*), a study of the capsule, until recently unknown, shows conclusively that *H. tomentella* has its relationships in other directions. The history of the confusion between *Herrania tomentella* and *H. aspera* has been discussed in detail under the heading of *H. nitida.*

17. **Herrania umbratica** R. E. Schultes, Caldasia 2: 261. *t. pag. 263, figs. a–d.* 1943; R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. 17: 86. *t. 24.* 1955.

DISTRIBUTION: Department of Santander, Colombia.

Small, slender, graceful tree up to about 16 feet in height, with the branches grouped at the top of the trunk. Trunk erect, up to 15–18 cm. in diameter, the bark probably brownish black; the root long, fusiform. The branchlets densely ferruginous-tomentose. Leaves very large, 7-digitate, very long-petiolate, stipulate. Stipules membranaceous, 3–6 cm. long (according to the collector). Petioles strong, sub-terete but obscurely sulcate, slightly swollen near the base, rusty, densely but softly tomentose, up to about 60–65 cm. long, basally 10 mm. and apically 4–5 mm. in diameter. Leaflets unequal, sessile, papyraceous, lanceolate-oblong, rather acutely cuspidate with a tip about 2 cm. long, basally subattenuate-cuneate, entire; above dark green and almost glossy glabrous, minutely and obscurely ferruginous-tomentose along the main veins, beneath of almost the same color, very minutely and sparsely stellate-pilose, the nerves prominent and rather more densely stellate-pilose; the central leaflet 55–60 cm. (according to the collector, 40–70 cm.) long, 20–22 cm. wide; the lateral leaflets smaller. Inflorescence fasciculate, many-flowered. Flowers cauline, arising from the lower part of the trunk in abbreviated racemes, short-pedicellate. Buds globose in anthesis, 18–22 mm. in diameter. Pedicels up to 5 mm. long, densely fulvo-tomentose, articulated basally and subtended by a minute, linear bract. Buds globose, mostly 10–12 mm. in diameter. Calyx patelliform, obscurely 2-parted. Sepals very fleshy, 2, connate most of their length, subequal, rotund-ovate, entire, apically rounded, more or less 22 mm. long, 22 mm. wide, glabrous and purple within, without yellow-brown and very densely and minutely stellate-pilose and sparsely and coarsely stellate pilose. Petals 5, sessile, thick, blood-red, concave, obovate, mostly 9 mm. long, 8 mm. wide, apically stongly cucullate, within with 5 thick-callused, purple, muricate-papillose veins, glabrous between the nerves but near the thickened margin densely muricate-papillose. Ligules linear, 19 mm. long, 2 mm. wide at base, the base strongly and abruptly contracted, spirally twisted in the bud but in flower erect, yellowish red, minutely granulose. Staminal tube 5-parted, the stamens 2- and 4-antheriferous, with short, free, strongly flattened filaments; anthers 2-locular, the locules 1.5 mm. long, 0.6 mm. wide, yellow. Staminodia thick, conspicuously petaloid, yellowish, strongly deflexed, hiding the petals and anthers, oblanceolate-elliptic, entire, apically subacute, 20 mm. long, 10 mm. wide, densely papillose-granular on both surfaces. Ovary sessile, elongate-ovoid, 10-costate and 5-locular, reddish golden, very densely stellate-pilose, 3 mm. in diameter. Style fleshy-terete, simple, yellow, apically conspicuously 5-parted into a stigma, 1 mm. long. Fruits numerous, up to 45 to a tree; elongate-ellipsoid, conspicuously irregular, mostly 11–14.5 cm. (according to the collector, up to 17 cm.) long, 4.5–5 cm. (according to the collector up to 8 cm.) in diameter, apically rotund-obtuse, not constricted near the apex, basally obtuse (not indented) and pedunculate (with a woody, articulated peduncle up to 10 mm. long, 4 mm. in diameter), with 10 subequal ribs, the 5 primary ribs thick, irregular, blunt-rounded, 6–8 mm. high, 5 mm. wide, the secondary ones similar but rather smaller, about 5 mm. high, 5 mm. wide, somewhat striate-fibrous between the ribs, very sparsely and rather grossly beset with simple, white, probably stinging hairs up to 1.5 mm. long, lacking a velvety indumentum; pericarp crassulent-leathery or subligneous, 3–4 mm. thick; bright yellow when ripe. Seeds 45, triangular or angular-ovate in outline, flattened, 13 mm. × 10 mm. × 3 mm., in a white pulp, measuring 18 mm. × 15 mm. × 7 mm. with the pulp.

Colombia. SANTANDER: Municipio de Girón, region of Capitancitos, alt. 695 m., *Ortíz Méndez s. n.* (Type). NORTE DE SANTANDER: Río Tibú, above Beltrania, *Anglo-Colomb. Cacao Coll. Exped. (Bartley & Holliday) 179*; Río Orú, *Anglo-Colomb. Cacao Coll. Exped. (Bartley & Holliday) 180*; Río Nuevo, *Anglo-Colomb. Cacao Coll. Exped. (Bartley & Holliday) 182.* **Trinidad.** Imperial College of Tropical Agriculture, *Baker s. n.*

When *Herrania umbratica* was originally described, the resemblance of its fruit to that of *H. nycterodendron* led to the suspicion of some relationship between the two concepts. Further investigation, however, has indicated that *Herrania umbratica* and *H. albiflora* are probably very closely allied.

The vegetative differences between *Herrania umbratica* and *H. albiflora* are slight. *Herrania albiflora* f. *titanica* would seem to represent, in some respects, a link between the two species. Exact relationship, however, cannot be established, until complete flowers of *Herrania umbratica* and additional fruits of *H. albiflora* are found. In the present state of our knowledge, we may say that the fruit of *Herrania umbratica*, similar in some respects to that of *H. nycterodendron*, differs from the fruit of *H. albiflora* (as represented in Goudot's line drawing published with the original description of *H. albiflora* and as known for *H. albiflora* f. *titanica*) in being irregularly contorted (instead of very regular); in having the primary and secondary ribs nearly equal and so thick that there is little flat intercostate area (instead of having the primary ribs twice or more higher and much thicker than the secondaries and extensive flat areas between the ribs); in being apically extremely thick and blunt (instead of having a slender, somewhat attenuate tip which is but slightly obtuse); and in having the peduncle much stouter than that of *H. albiflora*.

Further investigation and additional collections may possibly indicate that *Herrania umbratica* would better be considered as a variety of *H. albiflora*, but a complete understanding of the floral structure of *H. umbratica* must be had before any definite decisions can be made in this respect.

The collector of the type of *Herrania umbratica* records that this same species is found in townships in the vicinity of Girón, the type locality: San Vicente, Lebrija, Zapatoca, and Betulia. There are, however, no specimens from these localities. Regarding the habitat of *Herrania umbratica*, Ortíz Méndez wrote in his field notes: ". . . loose sandy, sandy-clay soils . . . the normal growth of the plant occurs in rather wet situations . . . it grows and develops in the shade of the trees which are known in the region by the names *juanblanco*, *canalete*, *guarumo*, *guamo*, *anaco*, *barba de mono*, *cocotinajo*, *qualanday*, etc." Of diseases which attack *Herrania umbratica*, he reported: "The trunk and branches are completely healthy. There are sporadic cases of insect attack to the fruits, but these attacks do not harm the seeds. Fungal attack is absolutely negative. The leaves are attacked slightly by *crisomélidos* and *minadores*."

PLANTS OF UNCERTAIN POSITION

THEOBROMA MARIAE (Mart.) K. Schum. f. MINOR Diels, Notizbl. **15**: 48. 1940. The possible position of this concept is discussed under *Herrania nitida* f. *sphenophylla*.

THEOBROMA MONTANA Goudot ex Bernoulli, Neue Denkschr. allg. Schweiz. Gesell. gesam. Naturw. **24**: 15. 1871, nomen nudum. Under the caption: "species mihi ignotae," Bernoulli published this name without a description and without the citation of specimens. It may represent a species of *Herrania*, for Bernoulli commented: "Vero similiter *Herraniae* species."

HERRANIA GUIANENSIS Sagot ex K. Schum. Mart. Fl. Bras. **12**(3): 75. 1886. Nomen in syn. French Guiana. "Karouany", *Sagot* (?) *s. n.* When K. Schumann published as a synonym of *Theobroma speciosum* Willd. ex Spreng. Sagot's manuscript name *Herrania guianensis*, he cited Sagot *1206*, a collection from French Guiana consisting merely of flowers. In the Utrecht herbarium, I found specimen number 000030 to be a collection of flowers only. They represent *Theobroma speciosum*, but on the outside of the packet there is a handwritten annotation: "*Herrania guianensis* Sagot". This is probably part of the Sagot collection cited by Schumann.

COMMON AND NATIVE NAMES KNOWN FOR THE SPECIES OF HERRANIA

In compiling the following enumeration of names used for *Herrania* in Middle and South America, I have included all orthographical variants which have been found in the literature. The list is made up from the literature, from labels on herbarium specimens and from my own ethnobotanical observations in the field. In each case, the country or countries in which the name is employed has been indicated. Some of the names reported are taken from the Indian languages, in which cases it has almost always been possible to designate the specific tribe.

abare	Venezuela: (Musuchíes Indians)	*H. lemniscata*
a-no-kwa	Colombia: (Kubeo Indians)	*H. nitida*
a-wa-ka-de-ro	Colombia: (Kuripako Indians)	*H. nitida*
awarivacabariyek	Venezuela	*H. lemniscata*
bee-ay-o	Colombia: (Makuna Indians)	*H. nitida*
be-se-o-wa	Colombia (Tanimuka Indians)	*H. nitida*
boscacao	Dutch Guiana	*H. kanukuensis*
bur-oo-ma	British Guiana: (Arawak Indians)	*H. lemniscata*
cacahuillo	Perú	*H. nitida*
cacahuio	Perú	*H. nitida* f. *sphenophylla*
cacaíta	Venezuela	*H. albiflora*
cacao cahouai	Colombia	*H. pulcherrima*
cacao cahouit	Colombia	*H. pulcherrima*
cacao cahousí	Colombia	*H. pulcherrima*
cacao caimán	Colombia	*H. Mariae, H. nitida*
cacao canaludo	Colombia, Ecuador	*H. Cuatrecasana*
cacao cimarrón	Costa Rica	*H. purpurea*
cacao cuadrado	Colombia	*H. pulcherrima*
cacao de andirá	Brazil	*H. Mariae* var. *putumayonis*
cacao de ardilla	Panamá	*H. purpurea*
cacao de chimbe	Colombia, Perú	*H. nycterodendron*
cacao de cintillas	Colombia	*H. laciniifolia*
cacao de macaco	Brazil	*H. Camargoana*
cacao de mico	Costa Rica	*H. purpurea*
	Colombia	*H. Camargoana*
cacao de monte	Brazil	*H. Mariae*
	Colombia	*H. albiflora* & f. *titanica, H. breviligulata, H. Cuatrecasana, H. Dugandii, H. laciniifolia, H. Mariae, H. nycterodendron, H. tomentella*
	Ecuador	*H. balaensis, H. pulcherrima* var. *pacifica*
	Panamá	*H. purpurea*
	Perú	*H. nitida, H. nycterodendron*
cacao de murcielago	Colombia, Perú	*H. nycterodendron*
cacao esquinado	Colombia	*H. pulcherrima*
cacao maní	Panama	*H. purpurea*
cacao montarás	Colombia	*H. albiflora*
cacao montaráz	Colombia	*H. albiflora*
cacao jacaré	Brazil	*H. Camargoana, H. Mariae, H. Mariae* var. *putumayonis*

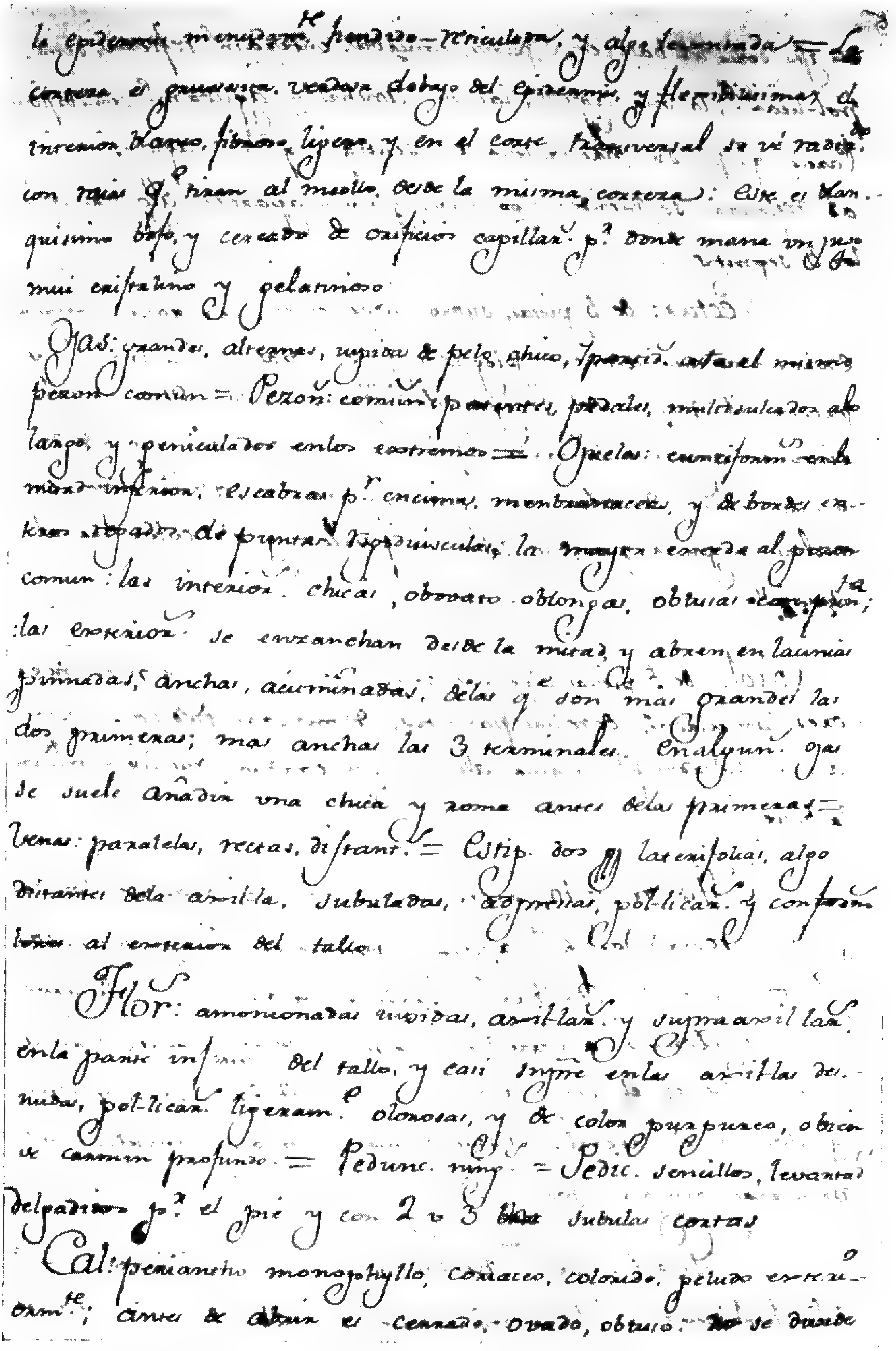
cacao quadrado	Brazil	*H. Mariae*
	Colombia	*H. pulcherrima*
cacao silvestre	Colombia	*H. laciniifolia*, *H. Mariae* var. *putumayonis*, *H. nitida*
	Perú	*H. nitida*, *H. nycterodendron*
cacao simarrón	Colombia	*H. albiflora*
cacao symarrón	Colombia	*H. albiflora*
cacaoito de monte	Colombia	*H. nitida*, *H. pulcherrima*
cacaorana	Brazil	*H. Mariae*
caca-ú	Brazil	*H. Mariae*
cacau de quina	Brazil	*H. nycterodendron*
cacauí	Brazil	*H. Mariae*
cacau-jacaré	Brazil	*H. Mariae*
cacau-rana	Brazil	*H. Mariae*
cahouit	Colombia	*H. pulcherrima*
cha-te-ra	Colombia, Perú: (Tikuna Indians)	*H. nitida*
chocolatillo	Panamá	*H. purpurea*
coco del monte	Panamá	*H. purpurea*
ee-so-pe-ke	Brazil: (Tukano Indians)	*H. Camargoana*
hee-ree-la-na-pee-ta-re	Colombia: (Yukuna Indians)	*H. nitida*
he-me-ka-ra	Colombia: (Taiwano Indians)	*H. nitida*
jo-kee-kee-yo-ke	Colombia: (Kubeo Indians)	*H. nitida*
ko-kee-ot-chu	Colombia, Ecuador: (Kofán Indians)	*H. Cuatrecasana*, *H. nitida*
ku-ra-ta	Colombia: (Karijona Indians)	*H. nitida*
maipoilie doron doron	Dutch Guiana: (Karib Indians)	*H. kanukuensis*
ma-mi-ree	Colombia: (Kabuyari Indians)	*H. nitida*
maripoele kakaoeleo	Dutch Guiana: (Karib Indians)	*H. kanukuensis*
matayaka	Venezuela: (Maquiritare Indians)	*H. lemniscata*
mi-to-ro-re	Colombia: (Karijona Indians)	*H. nitida*
mu-se-ge-ke	Colombia, Perú: (Witoto Indians)	*H. Mariae* var. *putumayonis*, *H. nycterodendron*
mu-se-na	Colombia, Perú: (Witoto Indians)	*H. Mariae* var. *putumayonis*, *H. nycterodendron*
o-so-pee-ko	Brazil: (Tukano Indians)	*H. Camargoana*
o-yaw-pee-ka-ye	Colombia: (Desano Indians)	*H. nitida*
palo de chimbe	Colombia, Perú	*H. nycterodendron*
palo de murciélago	Colombia, Perú	*H. nycterodendron*
pan y cacao	Colombia	*H. albiflora*
rus-ub	Panamá: (Bribrí Indians)	*H. purpurea*
sacha cacao	Colombia: (Inga Indians)	*H. breviligulata*, *H. Cuatrecasana*
so-pee-ja-ke	Colombia: (Gwanano Indians)	*H. nitida*
tach-ko-au	Colombia: (Miraña Indians)	*H. nitida*
toot-choo	Colombia: (Yurutí Indians)	*H. nitida*
wild cacao	Panamá: Canal Zone	*H. purpurea*
wild cacao	British Guiana	*H. lemniscata*

INDEX TO EXSICCATAE

For purposes of facility in consulting material of *Herrania* in our herbaria, the following list summarizing the collections which have been consulted in the preparation of this synopsis is offered. The list is arranged alphabetically by the last name of the collector. Numbers in parentheses refer to the corresponding species in the text.

13630, *13632*, *14343*, *14537*, *14880*, *14882*, *18933*, *19284*, *19665* (12); *18707a* (14a); *18652*, *18693* (12)
Schultes & López *8758*, *8759*, *8762*, *8763*, *8956*, *9144*, *9162*, *9205*, *9240*, *9416b*, *9619*, *9722*, *9747*, *9869* (4); *10464* (15).
Schultes & Murça Pires *8978*, *9130* (4)
Schultes & Smith *2050* (3)
Schunke *45* (12a)
Scolnik, Araque Molina & Barkley *195001* (10)
Seemann *s.n.* (15)
Shattuck *198* (15)
Smith *3541* (7)
Sprague *135* (16)
Spruce *4969* (12)
Stahel & Gonggrijp *3015* (7)
Standley *27434*, *28416*, *28647*, *31319*, *31722*, *36832*, *40911* (15)
Standley & Valerio *48421*, *48545*, *48584*, *48792* (15)
Steyermark *60558* (10)
Tejera *268* (1)
Tessmann *4024* (12); *3287* (12a)
Traill *64* (12); *65* (11a)
Triana *s.n.*, *5333*, *s.n.* (12)
Ule *5031* (11)
Univ. Calif. 3rd Bot. Gard. Exped. Andes *30173* (14a)
Valerio *461* (15)
Von Wedel *976*, *1112*, *1721* (15)
Wetmore & Abbe *73* (15)
L. Williams *11339* (10); *2332*, *2816*, *2843*, *3345*, *3364* (12)
R. S. Williams *662* (15)
Collector unknown [Hort. Trinidad] *s.n.* (1)

BOTANICAL MUSEUM
HARVARD UNIVERSITY



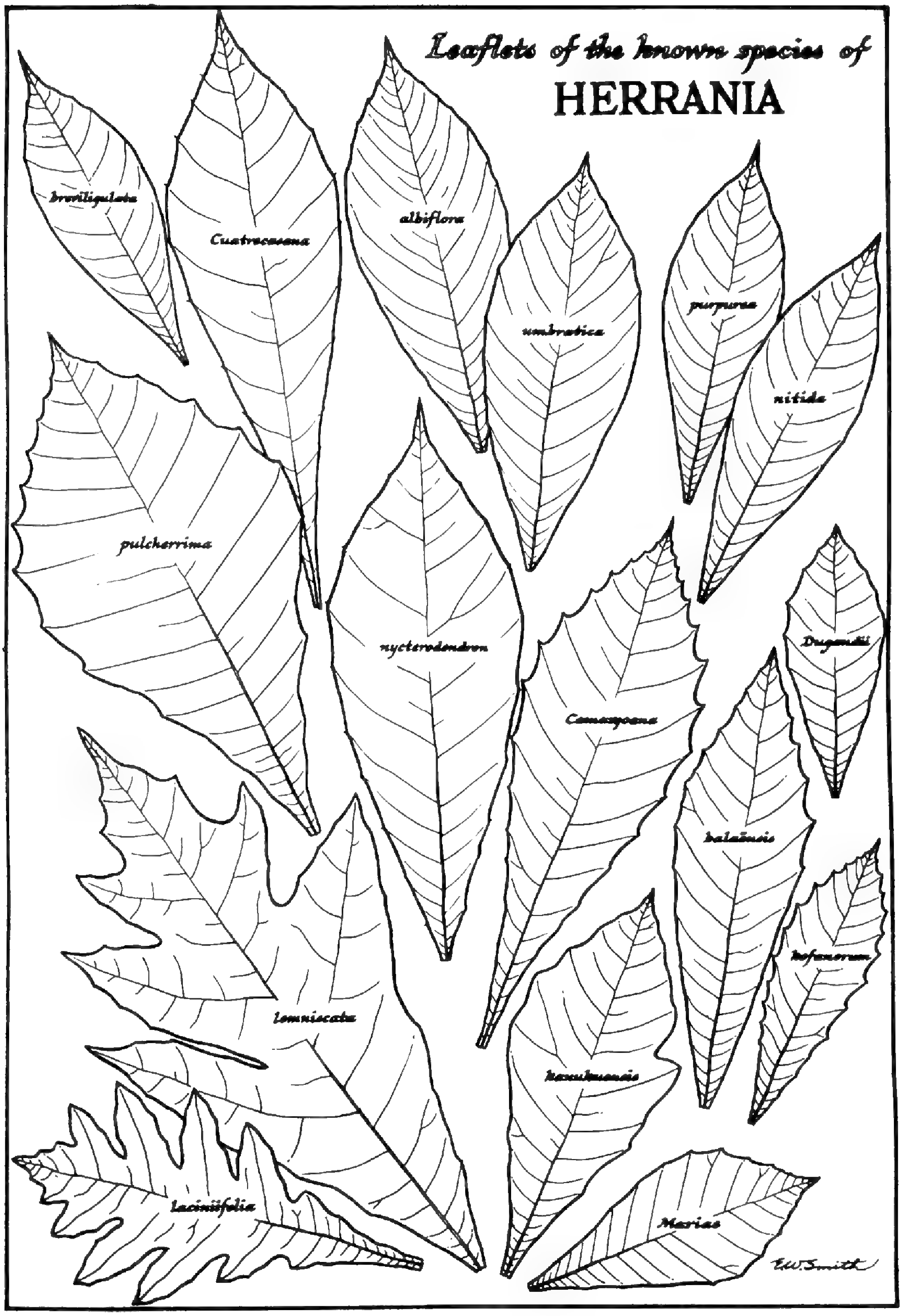
la epidermis menudam.te [illegible]-reticulada, y algo [illegible] = La
corteza es gruesecita, verdosa debajo del epidermis, y flexibilisima; de
interior blanco, fibroso, ligero, y en el corte transversal se vé radia-
do con rayas q.e tiran al meollo desde la misma corteza: Este es blan-
quisimo, bofo, y cercado de orificios capillar.s p.r donde mana un jugo
mui cristalino y gelatinoso

Ojas: grandes, alternas, unidas de pelo [illegible], sostenid. [illegible] el mismo
pezon comun = Pezon: comun, patentes, pedales, multisulcados alo
largo, y geniculados enlos extremos = Ojuelas: cuneiformes enla
mitad inferior, escabras p.r encima, membranaceas, y de bordes en-
teros sembrados de puntas tuberculosas; la mayor excede al pezon
comun: las interior. chicas, obovato oblongas, obtusas [illegible];
:las exterior. se ensanchan desde la mitad, y abren en lacinias
pinnadas, anchas, acuminadas, delas q.e son mas grandes las
dos primeras; mas anchas las 3 terminales. En alguna ojas
se suele añadir una chica y roma antes delas primeras =
Venas: paralelas, rectas, distant. = Estip. dos [illegible] laterifolias, algo
distantes dela axilla, subuladas, adpresas, pel-lican. y conform-
[illegible] al crecer del tallo.

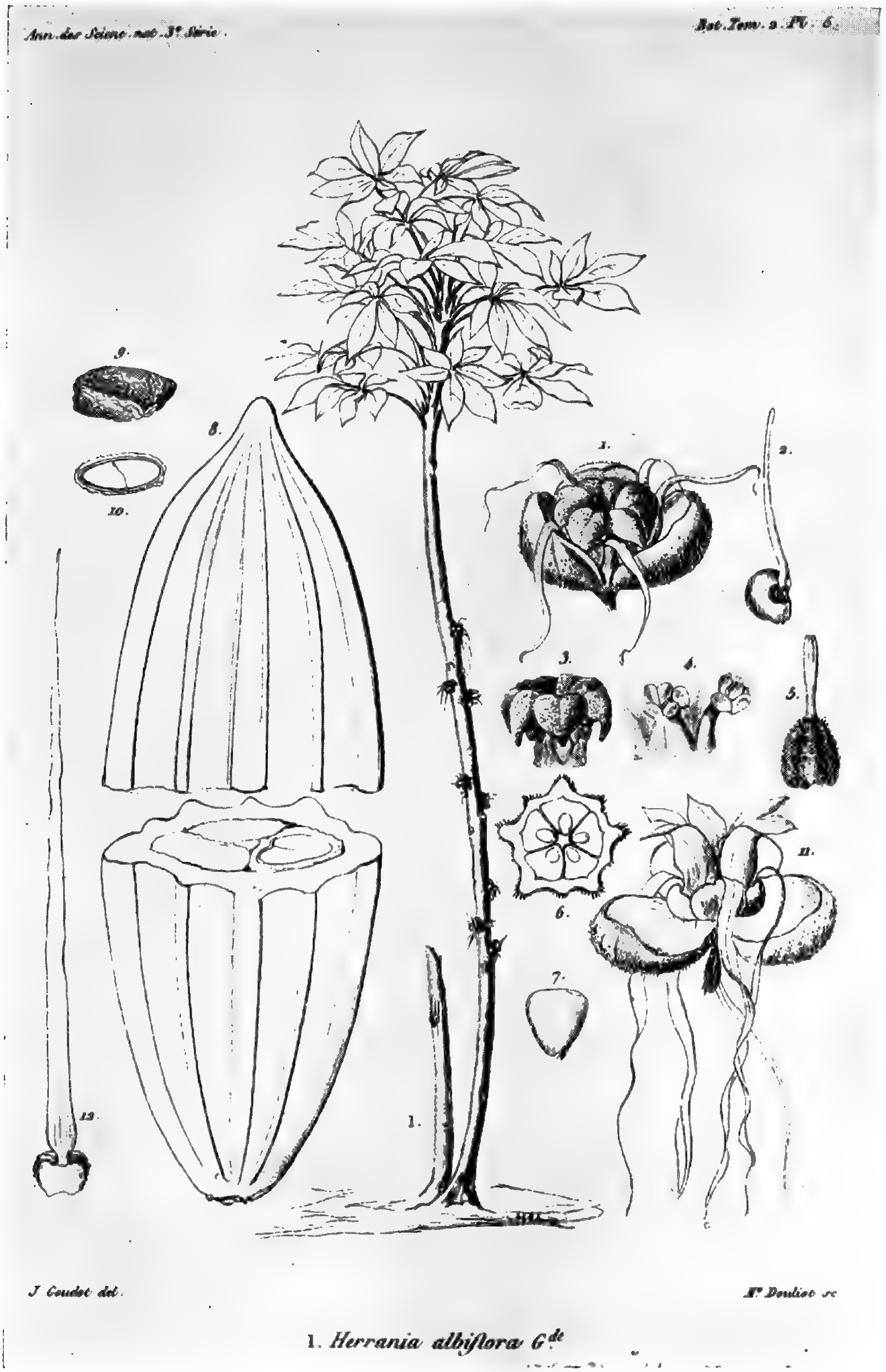
Flor: amontonadas unidas, axillar. y supraaxillar.
enla parte inf.r del tallo, y casi siempre enlas axillas des-
nudas, pel-lican. ligeram.te olorosas, y de color purpureo, obscu-
ro carmin profundo = Pedunc. ning. = Pedic. sencillos, levantad.
delgaditos p.r el pie y con 2 ó 3 [illegible] subulas cortas

Cal: perianthio monophyllo, coriaceo, colorido, peludo exteriu-
orm.te; antes de abrir es cerrado, ovado, obtuso: [illegible] se divide

Page of manuscript of Valenzuela's *Diario de la Expedición Botánica al Reino de Nueva Granada* in which the detailed description of *cacao esquinado* (*Herrania pulcherrima*) is set down.

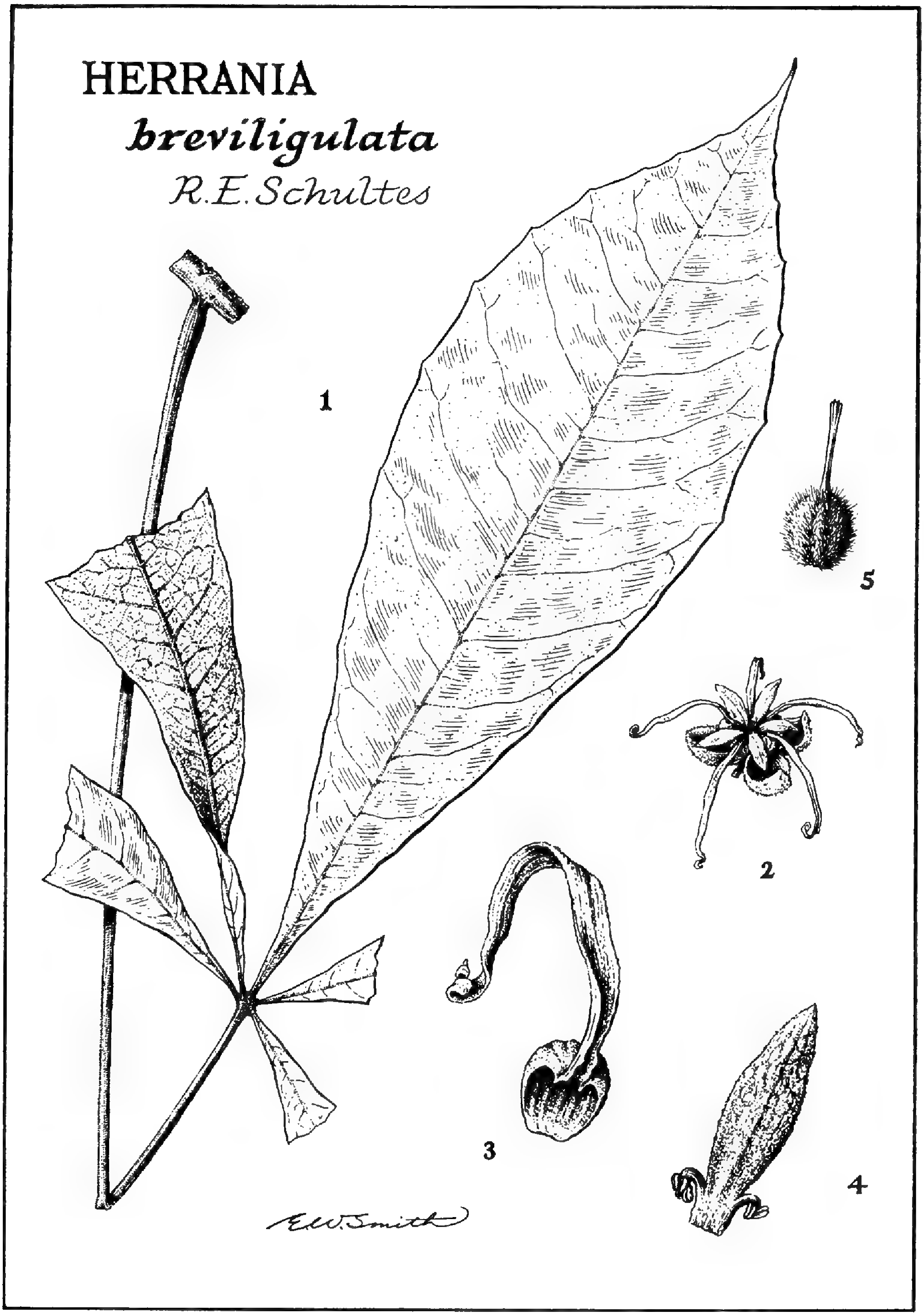


Forms of the leaflets of sundry species of *Herrania*.



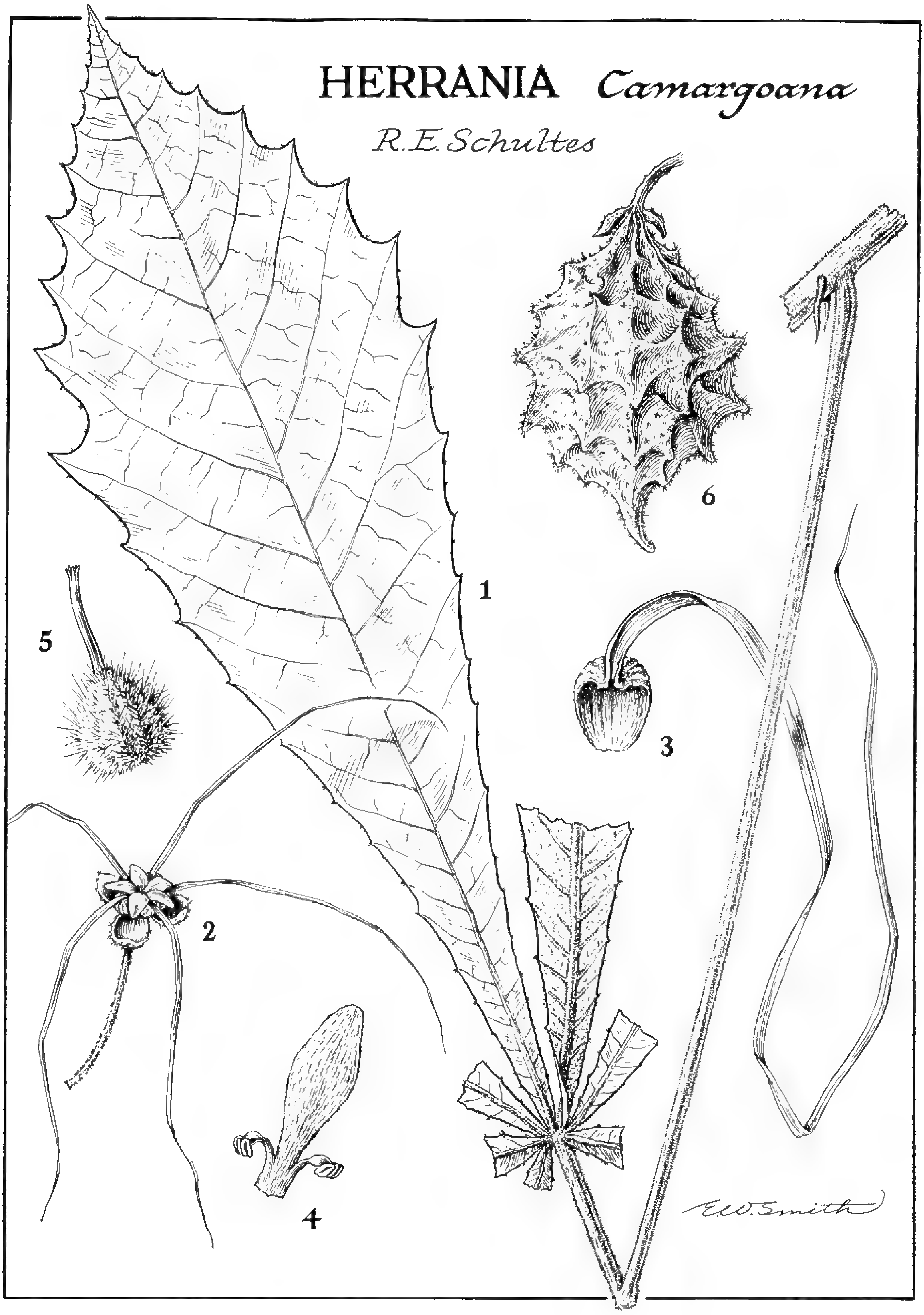
Drawing of *Herrania albiflora* from Goudot's original description of the genus and species.

Flower and buds (left) and stipules (right) of *Herrania albiflora*.



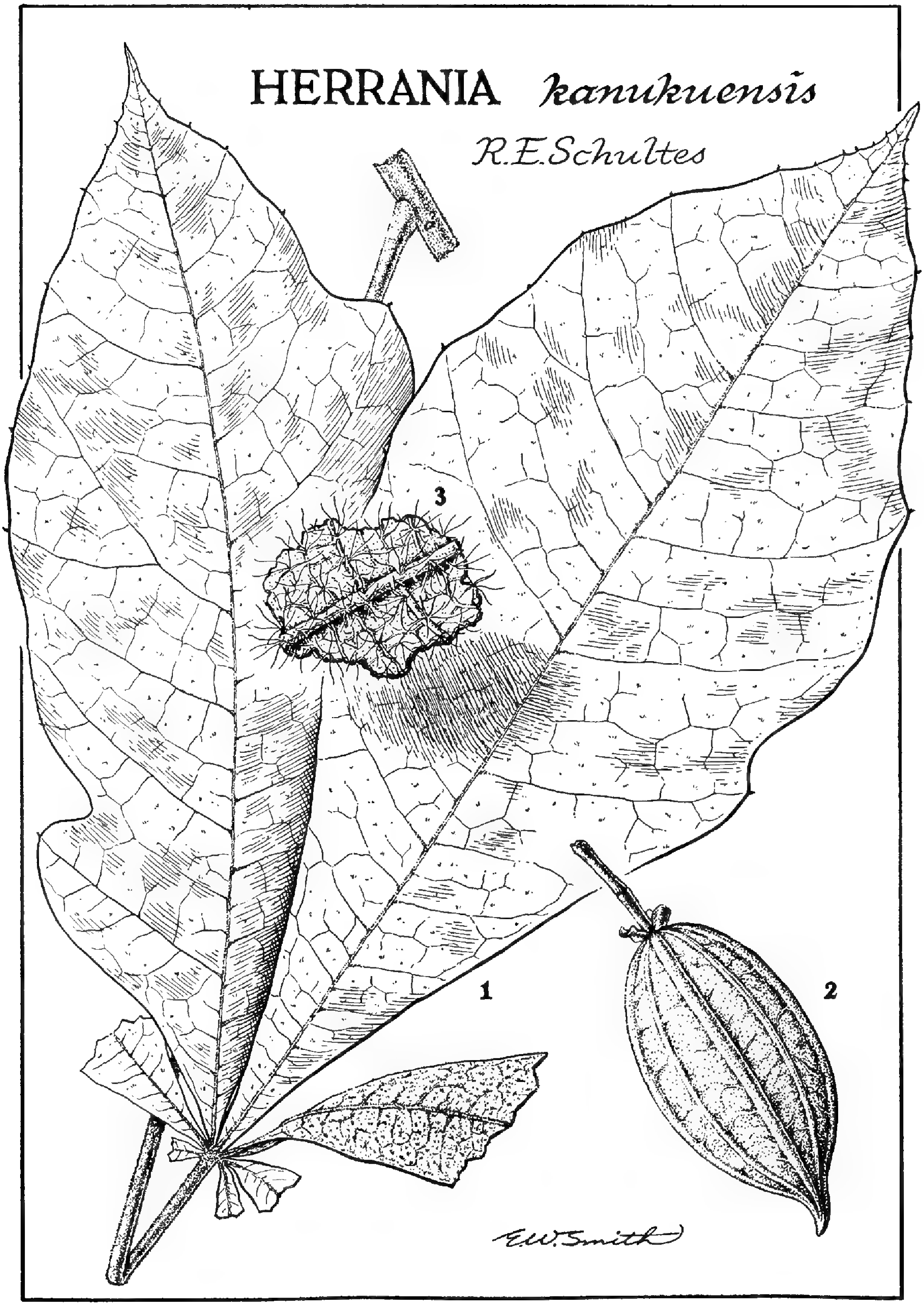
Herrania breviligulata. FIG. 1. Leaf, × 1/3. FIG. 2. Flower, × 1/2. FIG. 3. Petal, × 2. FIG. 4. Staminode and anthers, × 2. FIG. 5. Ovary and style, × 4.

Fruits of *Herrania breviligulata.*



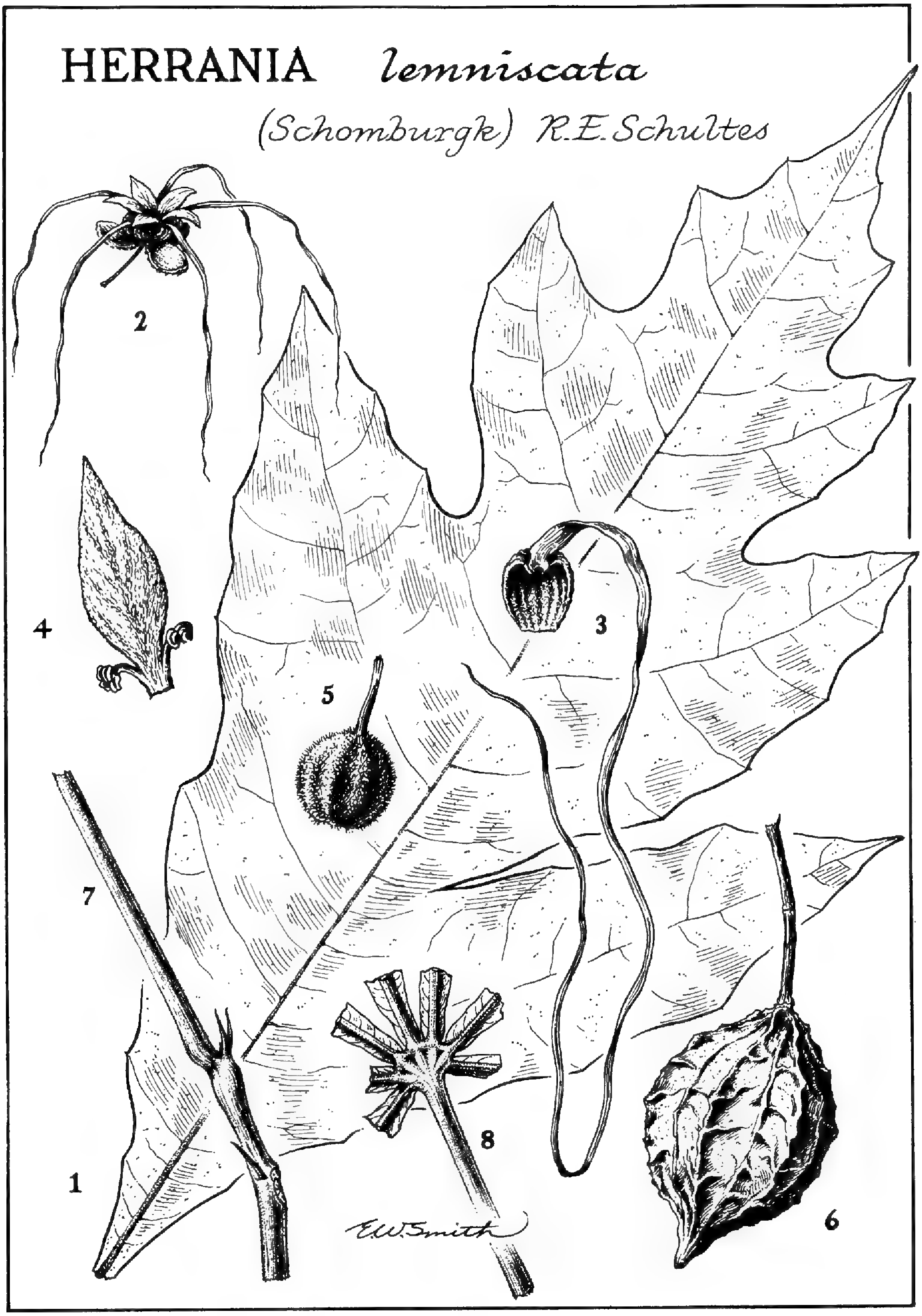
Herrania Camargoana. FIG. 1. Leaf, × 1/4. FIG. 2. Flower, × 1/2. FIG. 3. Petal, × 2. FIG. 4. Staminode and anthers, × 2. FIG. 5. Ovary and style, × 4. FIG. 6. Fruit, × 1/2.

Inflorescences of *Herrania Camargoana.*



Herrania kanukuensis. FIG. 1. Leaf, × 1/6. FIG. 2. Fruit, × 1/2. FIG. 3. Portion of lower surface of leaflet, showing pilosity, × 4.

Herrania kofanorum. FIG. 1. Leaf, × 1/2. FIG. 2. Flower, × 1/2. FIG. 3. Petal, × 2. FIG. 4. Staminode and anthers, × 2. FIG. 5. Ovary and style, × 4.

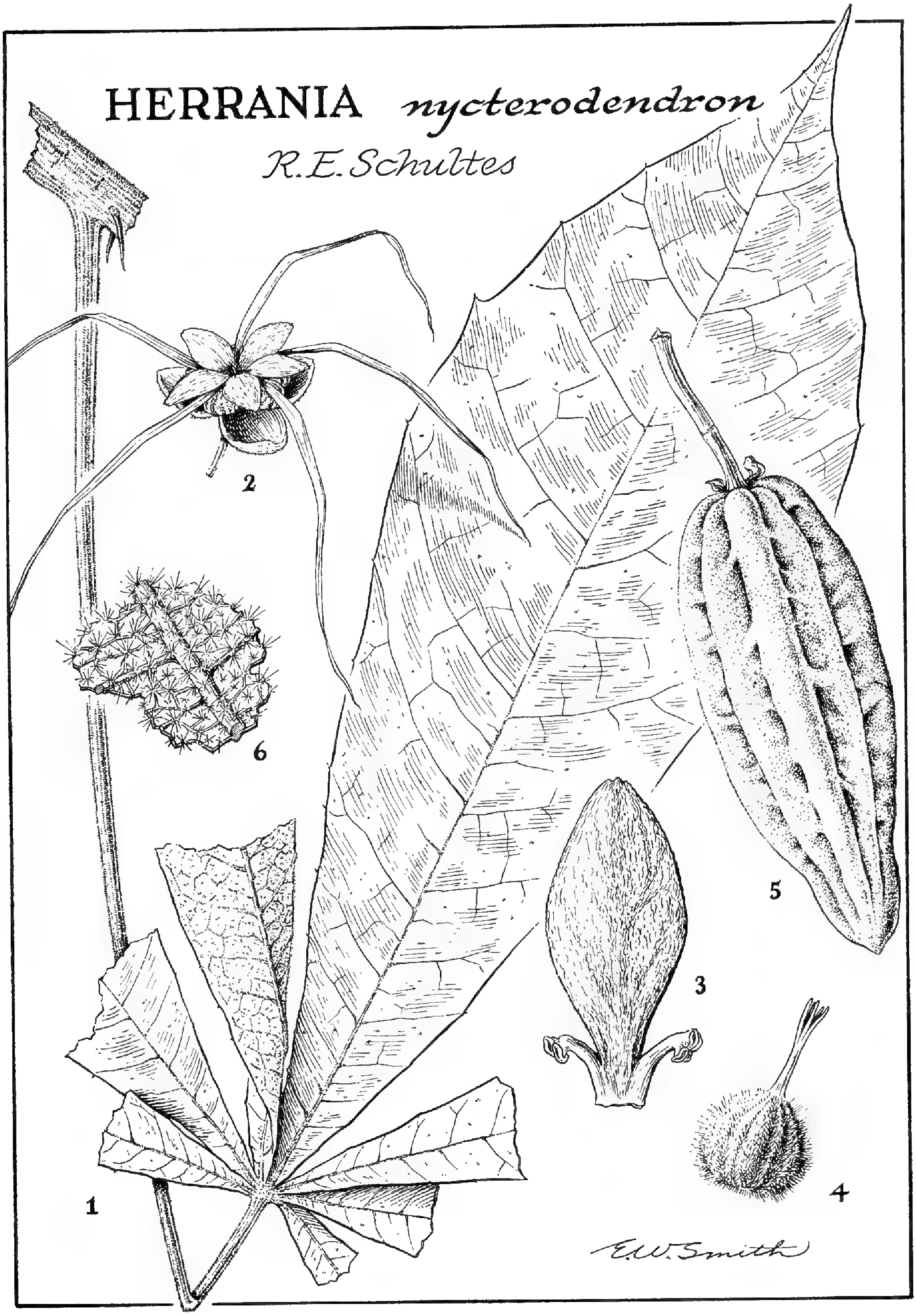


Herrania lemniscata. FIG. 1. Leaflet, × 1/5. FIG. 2. Flower, × 1/3. FIG. 3. Petal, × 2. FIG. 4. Staminode and anthers, × 2. FIG. 5. Ovary, × 2. FIG. 6. Fruit, × 1/2. FIG. 7. Petioles and stipules. FIG. 8. Base of leaflets.

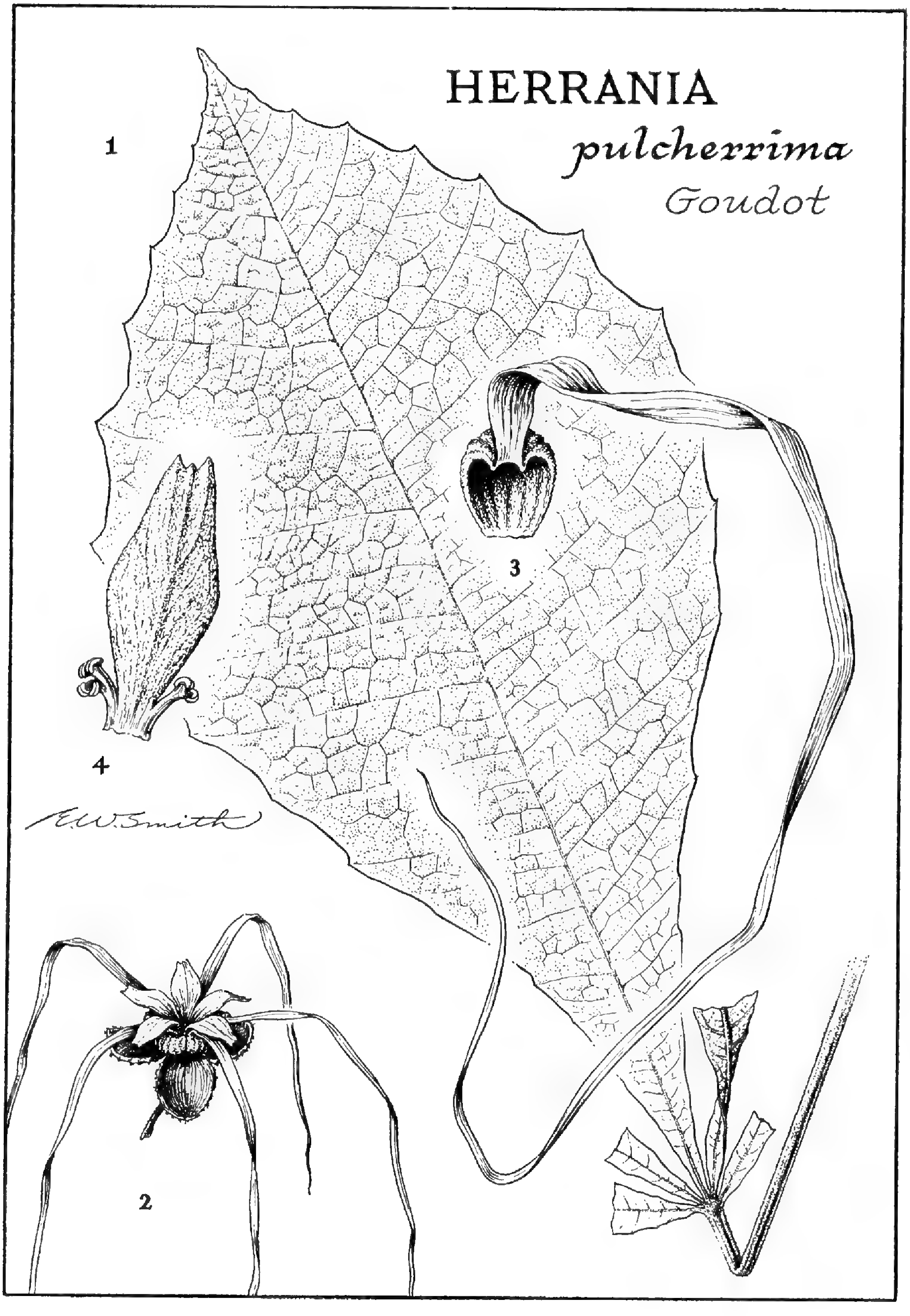
Herrania lemniscata. Schomburgk's field painting of *Lightia lemniscata, Tab.* XLI in the Schomburgk collection of water-colors in the British Museum (Natural History).

Flowers and buds of *Herrania Mariae* var. *putumayonis*.

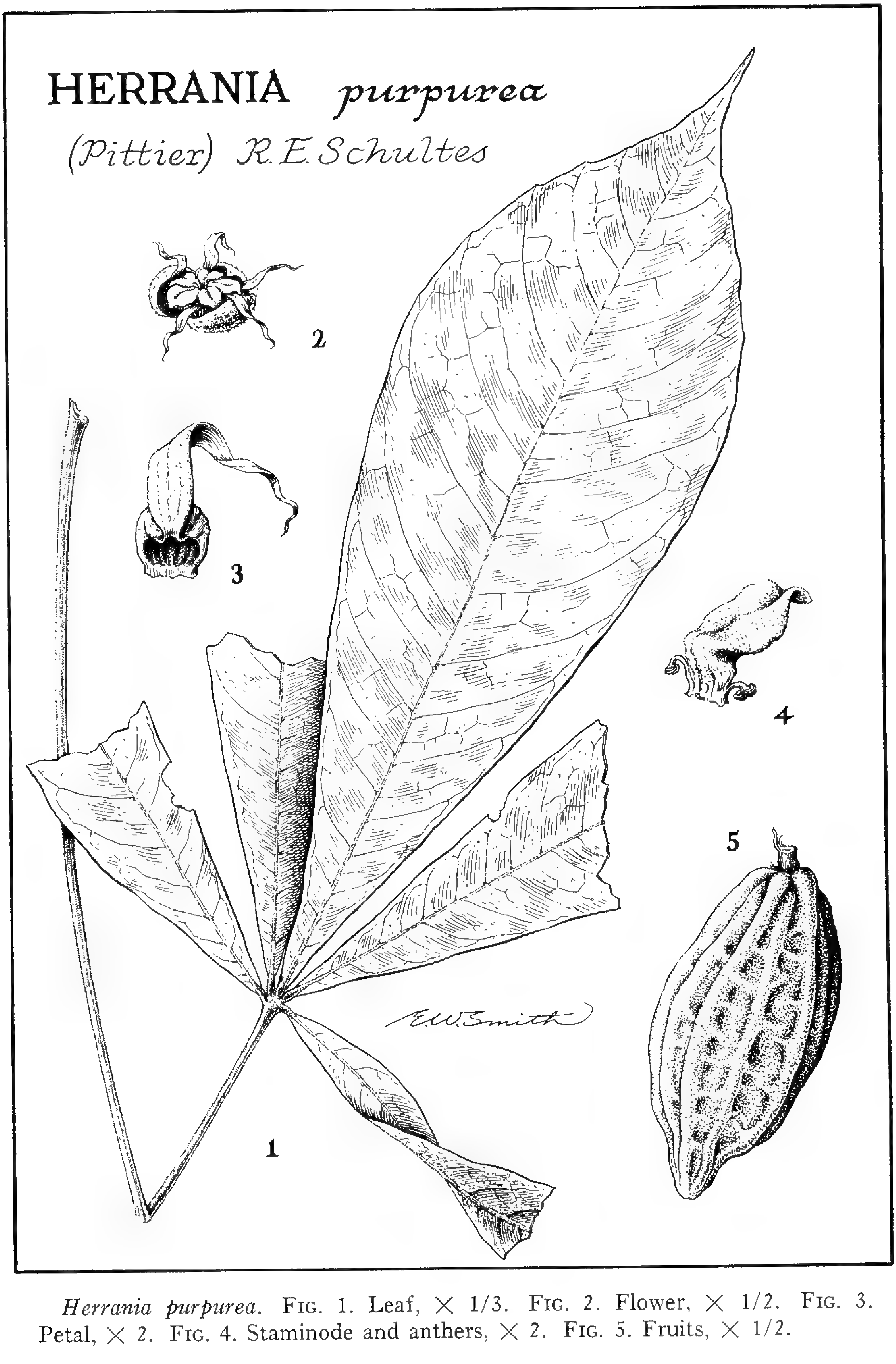
Fruits of *Herrania nitida*.



Herrania nycterodendron. FIG. 1. Leaf, × 1/4. FIG. 2. Flower, × 1/2. FIG. 3. Staminode and anthers, × 2. FIG. 4. Ovary and style, × 4. FIG. 5. Fruit, × 1/2. FIG. 6. Portion of lower surface of leaf, showing pilosity, × 4.



Herrania pulcherrima. FIG. 1. Leaf, × 1/4. FIG. 2. Flower, × 1/2. FIG. 3. Petal, × 2. FIG. 4. Staminode and anthers, × 2.



Herrania purpurea. FIG. 1. Leaf, × 1/3. FIG. 2. Flower, × 1/2. FIG. 3. Petal, × 2. FIG. 4. Staminode and anthers, × 2. FIG. 5. Fruits, × 1/2.

THE GENERA OF THE WOODY RANALES IN THE SOUTHEASTERN UNITED STATES

CARROLL E. WOOD, JR.

THE TREATMENTS PRESENTED BELOW of the sixteen genera of seven woody ranalian families which occur in the southeastern United States have been prepared as part of a generic study of the seed plants of that area. This work has been undertaken as a joint project of the Gray Herbarium and the Arnold Arboretum and has been made possible through the interest and support of George R. Cooley and through a grant from the National Science Foundation. In view of the co-operation and interest others have shown in this undertaking it seems worth while to publish our treatments of at least some of the families in advance of the completed work. In this way some of the material brought together in the course of these studies will be made available, and we should hope to have constructive criticisms from other botanists as the work progresses.

In attempting a generic treatment of the approximately 1300 genera of seed plants known to occur within the area bounded by and including North Carolina and Tennessee, on the north, and Arkansas and Louisiana, on the west, the objectives are toward a review and reorganization of familial and generic lines (often obscured in Small's *Manual of the Southeastern Flora*) and, especially, toward bringing together at least a part of the vast botanical literature which bears upon the plants of this rich area. The work is being done by taxonomists and is both taxonomic and floristic, but the approach, as well as the scope, is intended to be somewhat broader than is usual in a regional manual. The basic scheme is biological with the intent of including material from all branches of botany and of underscoring the biosystematic aspects of each genus and family, insofar as possible. In such an approach more problems may be raised than are solved but, in at least some instances, some of the difficulties which must be resolved before the plants of our area can be understood adequately become evident when the literature of a particular genus or family is brought together. Of course, with the existing information such a large goal is impossible for all genera (or even most) but a biological or biosystematic viewpoint is that which we are attempting to maintain throughout these studies.

The difficulties and weaknesses of this undertaking are apparent to no one more clearly than to those of us who have planned and worked on this project. More than a year and a half were spent on the tedious but basic chore of drawing together a file of more than 50,000 references arranged by families and genera which provided the starting point for the work. The large number of references and their wide distribution in the botanical literature of the world point up the almost incredible amount of information which is rather effectively "lost" to most botanists and even to authorities on particular groups of plants. The amount of material published about some genera of plants (cf. *Magnolia* and *Liriodendron*) is very large, while that concerning others is so scattered and fragmentary that it seems almost impossible to retrace. The matters of locating references, attempting to deal with information from a number of fields, culling, and trying to synthesize in a few choice words the "essence" of the genus sometimes seems to be (and probably is) a nearly hopeless task. The degree of success undoubtedly varies considerably from one group to another, and both sins of omission and commission will be evident. However, the work is absorbing and it is difficult to set aside one group for another, leaving behind many unsolved problems. It is to be hoped that others may take an interest in some of these problems and that the notes and references included will prove to be useful to students and researchers. One thing is certain: there are enough botanical problems in the Southeastern flora to supply all possible workers for a long time to come.

Although the general scheme being followed throughout this work will be apparent in the treatments below, a few explanatory comments will be apropos. It should be noted especially that the descriptions of families and genera are based mainly upon the species which occur in the southeastern United States and are not necessarily wholly applicable to those beyond this area. However, additional information which may provide a more balanced concept of the genus may sometimes be included in brackets. Although each description is regional, the concept of the genus is broader, with an attempt being made to delimit the group more in terms of all its species. Such an approach is essential, for many genera are represented in our area by only a few outlying species which often belong to different sections or subgenera. Were the viewpoint essentially regional these might be placed in different genera to the obscuring of true interrelationships (and to the ensuing confusion of all). This viewpoint is, in general, a conservative one which stresses similarities, rather than differences. In many instances it would seem far better at this stage of our knowledge to point out a problem than to attempt a solution which may only cause ultimate confusion.

The notes included vary widely with the group. Not all branches of botany will be found to be equally well represented: the training and background of the present investigators leads to the emphasis of taxonomic and biosystematic materials, although an attempt has been made to include as much other information as possible. Pathology and palaeobotany, each a large field with its own special and extensive literature, are likely to be represented least well. Limitations of space prohibit the inclusion of the source of each item of information, but a series of selected references will provide many of these. References included are primarily to journals. Many standard texts have been consulted but, rather than to cite each of these repeatedly, it is planned to include a list in the final work. Many references have been annotated as to content, especially when the title is not self-explanatory. Abbreviations used for journals follow the clear and useful general principles followed by Schwarten and Rickett (Bull. Torrey Bot.

Club 74: 348–356. 1947, and a much amplified list now in press) which are in accordance with the recommendations of the Madison Botanical Congress of 1893 and the International Code of Botanical Nomenclature, 1956. Those references which we have not seen are followed by an asterisk (*).

The illustrations are by Dorothy H. Marsh (Mrs. Stephen Marsh) who has worked meticulously in depicting the details upon which the accuracy of scientific illustrations depends. Since the adequate illustration of more than a thousand genera is likely to be quite impossible, the drawings have been planned on the assumption that, even though few in number, illustrations which provide some insight into the details of the plant are far more desirable in a work at the generic level than a larger number of "recognition" drawings. These more detailed drawings, which eventually will represent genera scattered throughout the whole range of families, are being made mostly from fresh or preserved materials as these become available. A number of kind individuals have been most helpful in their efforts in this direction, and the living collections of the Arnold Arboretum, which include many woody plants of authentic southern origin, have provided invaluable material.

The project is under the direction of Dr. Reed C. Rollins and the writer. Dr. Kenneth A. Wilson is working with us at the present time and we have had as our other excellent collaborators Dr. R. B. Channell, now of Vanderbilt University, and Dr. C. W. James, now of the University of Georgia. All three have worked conscientiously on the many tasks directly concerned with the studies on the Southeastern flora: the preparation of files of references, the identification of specimens, the preparation of generic treatments and the supervision of drawings of groups which they have studied. The basic plan of the generic treatments has been modified through the ideas, trials and efforts of all of us. In these studies a great many friends and colleagues from the staffs of our respective institutions, from many parts of the United States, and from other countries, as well, have brought us appreciated assistance. The appropriate time has not yet come, nor would there be here sufficient space to mention each one individually, but to each I am personally most grateful for his help.

The order Ranales, including as it does the most primitive of known living angiosperms, is one of particular interest from an evolutionary point of view. In recent years, the studies of Professor I. W. Bailey and his numerous collaborators and students have elucidated many aspects of the woody members of this group and have stimulated a renewed interest not only in these plants as a group but in the "complete" approach to problems of the interrelationships of higher categories through the use of information from all parts of the plant, rather than that from a single organ obtained by a single discipline. This approach not only has pointed out the many remarkable primitive structures in various members of this order but has emphasized again and again the very different rates at which structures or organs of a plant may have evolved. Hence, any evolutionary arrangement of families must be an attempt to sum up the degree of relationship with other groups as well as the over-all level of specialization.

The ranalian families included here are those characterized by their predominantly woody habit and by the possession of the characteristic ranalian ethereal oil cells in the tissues of the plant. In our flora this group includes the Magnoliaceae, Annonaceae, Illiciaceae, Schisandraceae, Canellaceae, Calycanthaceae, and Lauraceae. In spite of investigations on these and other ranalian families by numerous authors, a number of families remain to be studied carefully. The interrelationships of all the families of the order are still far from certain, although various related groups have been pointed out. Thus, the Degeneriaceae, Magnoliaceae, Annonaceae, and Himantandraceae form a group of related families within the order; Illiciaceae and Schisandraceae another; Austrobaileyaceae, Trimeniaceae, Amborellaceae, Monimiaceae, Calycanthaceae, Gomortegaceae, Lauraceae, and Hernandiaceae yet another. The relationships of the Canellaceae are undoubtedly with the ranalian complex (presumably with that group of families having monocolpate pollen and tri-lacunar nodes — perhaps Myristicaceae), instead of with the Parietales where they are placed in the Englerian system, but exactly where remains to be seen. I have not attempted to deal at all with the matter of splitting the Ranales (sensu lato) into other orders, retaining all of these families together, instead, and only arranging these groups in this rough way pending the outcome of studies now under way at several institutions.

In connection with these ranalian families Professor I. W. Bailey has given freely and most helpfully of his knowledge of these more primitive angiosperms and Dr. C. E. Kobuski has most kindly read the entire manuscript with a practiced editorial eye. The flowering material used in the illustration of *Illicium floridanum* came through the kindness of Mrs. J. Norman Henry from plants cultivated at the Henry Foundation, Gladwyne, Pennsylvania, and the fruiting specimens through that of Dr. R. B. Channell from Gallman, Mississippi.

MAGNOLIACEAE (MAGNOLIA FAMILY)

Deciduous or evergreen trees or shrubs with simple, alternate, stipulate leaves with pinnate venation, the stipules inclosing the bud and leaving conspicuous encircling scars at each node. Flowers solitary, terminal [or axillary], perfect [except *Kmeria*], all parts free [in ours]. Perianth of 9–15 green, yellow or white tepals in whorls of threes, the outermost whorl sometimes partially differentiated as a "calyx." Stamens numerous, spirally arranged on the elongated receptacle below the carpels, [7–]3(2 or 1)-veined, often poorly differentiated into "anther" and "filament" with four microsporangia (often confluent as two), dehiscing longitudinally; pollen ellipsoidal, monocolpate, the germinal furrow distal. Gynoecium of numerous conduplicate carpels, free [in ours], spirally arranged on the upper part of the receptacle and so closely imbricated and packed as to appear syncarpous [in ours], the style elongate, vascularized, the ovaries 1-loculed, in both our genera with 2 anatropous 2-integumented ovules at the inner angle of the locule, back to back with the funiculi adjacent. Fruit cone-like [in ours], composed of the imbricated follicles or samaras which are clearly distinct at maturity; seeds 2 in each carpel, each with abundant endosperm and a minute embryo; embryo sac development normal in all known cases; basic chromosome-number 19 throughout the family.

A family of about 200 species in 6–10 genera, the generic lines not well agreed upon, but including *Magnolia*, *Talauma*, *Michelia*, *Manglietia* and *Liriodendron*. The family is bicentric in distribution: all of the genera occur in eastern or southeastern Asia and *Magnolia*, *Talauma* and *Liriodendron* also occur in the New World. Although many of the 80 fossil "species" of *Magnolia* and the 25 of *Liriodendron* are doubtful, the record is sufficient to show that these two genera were formerly of wide distribution in the Northern Hemisphere but have become extinct over most of this area.

The family as here considered does not include *Schisandra*, *Kadsura*, *Illicium*, *Drimys* and its relatives, *Trochodendron*, *Tetracentron*, *Austrobaileya* and other genera which the studies of I. W. Bailey, his collaborators and students have shown clearly to belong elsewhere. Magnoliaceae (sensu stricto) seems to be most closely related to *Degeneria* and *Himantandra*. (See also Annonaceae.) Canright notes, ". . . the tissues and organs of the Magnoliaceae reveal many transitions between the more primitive Degeneriaceae and the slightly more specialized Himantandraceae; yet all three families undoubtedly form a compact alliance within the woody Ranales."

With their woody habit, wood with some primitive features, mostly perfect flowers, numerous and mostly free floral parts with hypogynous and partially spiral insertion, sporophyll-like stamens, monocolpate pollen and ethereal oil cells, the Magnoliaceae are often considered to be among the most primitive living angiosperms. Bailey & Nast in concluding their studies on the Winteraceae (1945) wrote, however, ". . . it is unfortunate that so much attention has been focused upon the Magnoliaceae (sensu stricto) in discussions concerning the origin of the angiosperms, for the seedlings, stems, roots, leaves, stamens, and carpels of these plants all exhibit a relatively high degree of morphological specialization. More primitive and significant ranalian structures are retained by such families as the Winteraceae, Degeneriaceae, Himantandraceae, Trochodendraceae, etc." The detailed studies of Canright bear this out and he concludes, in part, ". . . the evidence in support of the postulated primitiveness of the Magnoliaceae is in some tropical stamen types, plus the occurrence of distal-furrowed monocolpate pollen."

It may be added that Sect. *Tasmania* of *Drimys* (Winteraceae) appears to combine more numerous primitive features than any other known group of angiosperms. However, in spite of its more advanced position on a world-wide basis, *Magnolia* is probably the most primitive genus within the Southeastern flora.

REFERENCES:

BAILEY, I. W., AND COLLABORATORS. See the very important series of papers dealing with related groups in Jour. Arnold Arb. **23–38.** 1942–1957, especially BAILEY & NAST, The comparative morphology of the Winteraceae VII. Summary and conclusions. **26:** 37–47. 1945.

CANRIGHT, J. E. The comparative morphology of the Magnoliaceae. Doctoral Dissertation. Widener Library, Harvard University. May, 1949. [With the exception of data on carpels and seedlings, most of the material covered is included in the three published papers.]

———. The comparative morphology and relationships of the Magnoliaceae. I. Trends of specialization in the stamens. Am. Jour. Bot. **39:** 484–497. 1952. II. Significance of the pollen. Phytomorphology **3:** 355–365. 1953. IV. Wood and nodal anatomy. Jour. Arnold Arb. **36:** 120–140. 1955. [The most comprehensive survey; extensive bibliography.]

DANDY, J. E. The genera of Magnolieae. Kew Bull. **1927:** 257–264. 1927. [Key to the genera of family, sensu stricto.]

———. Magnoliaceae. Inst. Paranaense Bot. Cat. Estat. Gên. Bot. Fan. **11:** 1, 2. 1956. [List of genera with synonymy; estimate of no. of spp.]

——— & R. D'O. GOOD. Magnoliaceae Jaume. Pflanzenareale **2:** 35–38. Maps 41–43. 1929.

D'IPPOLITO, G. Contributo all'anatomia comparata del caule delle Magnoliacee in relazione specialmente alla struttura anatomica del legno secondario. Malpighia **15:** 438–460. 1901. [Includes *Magnolia*, *Michelia*, *Illicium*, *Kadsura*, *Drimys*, *Schisandra*.]

GARRISON, R. Studies in the development of axillary buds. Am. Jour. Bot. **42:** 257–266. 1955. [Includes *Magnolia stellata* var. *rosea*, *Liriodendron Tulipifera*, *Schisandra chinensis*, among others.]

GOOD, R. D'O. The past and present distribution of the Magnolieae. Ann. Bot. **39:** 409–430. 1925.

GRÖPPLER, R. Vergleichende Anatomie des Holzes der Magnoliaceen. Biblioth. Bot. **31:** 1–49. 1894.

JOHNSON, M. A. Relationship in the Magnoliaceae as determined by the precipitin reaction. Bull. Torrey Bot. Club **80:** 349–350. 1953.

———. The precipitin reaction as an index of relationship in the Magnoliaceae. Serol. Mus. Bull. **13:** 1–5. 1954. [*Magnolia*, *Michelia*, *Talauma* closely related; *Liriodendron* more isolated; *Illicium* unrelated.]

LEMESLE, R. De l'ancienneté des caractères anatomiques des Magnoliacées. Revue Gén. Bot. **45:** 341–355. 1933.

———. Les caractères histologiques du bois secondaire des Magnoliales. Phytomorphology **3:** 430–446. 1953. [See Canright, 1955.]

MCLAUGHLIN, R. P. Systematic anatomy of the woods of the Magnoliales. Trop. Woods **34:** 3–39. 1933. [Magnoliaceae, Schisandraceae, Winteraceae, Trochodendraceae, Cercidiphyllaceae, Lactoridaceae, Himantandraceae.]

———. Some woods of the Magnolia family. Jour. Forestry **26:** 665–677. 1928. [A key to their structural identification, gross and microscopic; Magnoliaceae sensu lato.]

MANEVAL, W. E. The development of *Magnolia* and *Liriodendron*, including a discussion of the primitiveness of the Magnoliaceae. Bot. Gaz. **57:** 1–30. 1914. [*M. virginiana*, *L. Tulipifera*.]

MATSUDA, S. On the anatomy of Magnoliaceae. Jour. Coll. Sci. Imp. Univ. Tokyo **6:** 115–149. 1893. [Magnoliaceae, sensu lato.]

OZENDA, P. Structure du noeud foliaire des Magnoliacées et des Anonacées. Compt. Rend. Acad. Sci. Paris **224:** 1521–1523. 1947.

PARMENTIER, P. Histoire des Magnoliacées. Bull. Biol. France Belgique **27:** 159–337. 1895.*

PLOUVIER, V. Sur la recherche du pinitol chez quelques Caryophyllacées, Magnoliacées et plantes de familles voisines. Compt. Rend. Acad. Sci. Paris **244:** 382–385. 1957.

U. S. DEP. AGR., FOREST SERV. Woody Plant Seed Manual. U. S. Dep. Agr. Forest Serv. Misc. Publ. **654.** 1948. [*Liriodendron*, 222, 223; *Magnolia*, 232–234.]

WEEVERS, T. Das Quercetin bei den Magnoliaceae und seine Verbreitung im Pflanzenreiche. Proc. Roy. Acad. Amsterdam **33:** 778–785. 1930.*

WHITAKER, T. W. Chromosome number and relationship in the Magnoliales. Jour. Arnold Arb. **14:** 376–385. 1933. [Undocumented counts.]

WORSDELL, W. C. A study of the vascular system in certain orders of the Ranales. Ann. Bot. **22:** 651–682. 1908. [Mostly petiole; includes Magnoliaceae sensu lato; bibliography.]

KEY TO THE GENERA OF MAGNOLIACEAE

Leaves entire, acute to cordate-auriculate at the base; petals white, green or yellow; stamens without distinct filaments, introrse or latrorse; styles deciduous; the numerous carpels in fruit forming a cone-like follicetum; carpels opening on the abaxial surface, the seeds pendulous by threads, with a fleshy scarlet to pink outer coat. .... 1. *Magnolia*.

Leaves with 4 or 6 lobes, truncate-emarginate at the tip; petals greenish-yellow with an orange band near the base; stamens with distinct, although thick filaments, extrorse; styles persistent, flat and wing-like; the numerous carpels maturing as a cone-like mass of samaras, each of which falls separately. .... 2. *Liriodendron*.

Tribe MAGNOLIEAE DC.

1. **Magnolia** L. Sp. Pl. 1: 535. 1753; Gen. Pl. ed. 5. 240. 1754.

Trees, or sometimes shrubs, mostly with showy and large flowers, the leaves deciduous to evergreen, entire or sometimes cordate-auriculate at the base. Tepals 9–15, in series of 3, white or green to yellow [pink or purple], similar or the outer 3 sometimes partially differentiated, deciduous. Stamens with filament and connective hardly differentiated, the latter produced into a blunt point [in ours] beyond the anther-sacs (sporangia); anther-sacs 4, linear, opening introrsely or latrorsely. Styles recurved, deciduous, the stigma along the inner face. Fruit a cone-like follicetum of the more or less fleshy imbricated carpels, the individual follicles at maturity clearly separate, dehiscent along the outer (abaxial side), the two seeds hanging by a delicate silky thread of unrolled spiral vessels (from the funiculus and placenta); seeds with a fleshy scarlet to pink outer layer and a hard bony inner layer, both derived from the outer integument. $2n = 38, 76, 114$. (Including *Tulipastrum* Spach.) TYPE SPECIES: *M. virginiana* L. (Named in honor of Pierre Magnol, 1638–1715, Professor of Botany at the botanical garden at Montpellier, France.) — MAGNOLIA, BAY, CUCUMBER-TREE.

An ancient genus with about 75–80 species, in two centers: about 50 in the Old World (Japan to the eastern Himalayas, south to Java) and about 25 in the New World (eastern U.S., the Greater Antilles, and Mexico to southeastern Venezuela). Dandy divides the genus into 2 subgenera and 11 sections; both subgenera and 4 sections are represented by the 8 species, including 5 varieties, of our area.

Subgenus MAGNOLIA. Anthers dehiscing introrsely; flowers neither precocious nor with a much reduced outer whorl of tepals; leaves evergreen or deciduous. Eight sections, 5 entirely Asiatic, 2 entirely American.

Sect. RYTIDOSPERMUM Spach includes 3 species of Asia and 4–6 of America, all white-flowered and deciduous, with the leaves crowded together near the tips of the branches. *Magnolia tripetala* L., *M. Fraseri* Walt., *M. pyramidata* Bartr., *M. macrophylla* Michx. and *M. Ashei* Weatherby represent this group in our area. *Magnolia macrophylla* and *M. Ashei* are very similar, differing principally in size of plant and shape of fruit, and probably are only varietally distinct. It is also notable that the Mexican *Magnolia dealbata* Zucc., of the mountains of Veracruz to Oaxaca, is hardly distinguishable from *M. macrophylla* and may well be only disjunct populations of that species. All of the species of the section, except *M. pyramidata* and the Mexican plant (as yet uncounted), have been determined to be diploid ($2n = 38$).

Sect. MAGNOLIA (*Magnoliastrum* DC.) includes only *M. virginiana*, the Sweet Bay, of wide distribution from eastern Massachusetts to southernmost Florida, eastern Texas and Arkansas. The species, a diploid ($2n = 38$), is notable for the adnate stipules, leaves glaucous beneath, and very fragrant, small white flowers. Two geographical varieties (var. *virginiana* and var. *australis* Sarg.), based primarily on size of plant and pubescence of branchlets, peduncles and leaves, are currently recognized but need further study.

Sect. THEORHODON Spach is composed of about 15 American evergreen species with stipules free from the petioles. All are tropical in distribution, with the exception of the exceedingly handsome *M. grandiflora* ($2n = 114$) which ranges from southern Florida northward on the coastal plain to eastern North Carolina and eastern Texas and Arkansas. *Magnolia grandiflora* is widely cultivated throughout our region and has escaped in some areas; the exact limits of its native occurrence need to be determined more carefully. Its closest relationships seem to be with the group of species which includes *M. Schiediana* Schlecht., also with 114 chromosomes, and others of Central America southward to the isolated table-top mountains of southeastern Venezuela. The 8 species of Cuba, Hispaniola and Puerto Rico are all closely related, on the other hand, and form a separate subsection. *Magnolia Hamori* Howard, of Hispaniola, is a diploid; other chromosome numbers are unknown.

Subgenus PLEUROCHASMA Dandy. Anthers dehiscing laterally or sublaterally; flowers precocious and/or with a much reduced (calyx-like) outer whorl of tepals; leaves deciduous. Three sections, two entirely Asiatic.

Sect. TULIPASTRUM (Spach) Reichb., with the outer whorl of tepals reduced to a small "calyx," includes only the green- or yellow-flowered *M. acuminata* L. (sensu lato), of eastern North America, and the purple-flowered *M. liliflora* Desrouss., of eastern China. Both are tetraploids, $2n = 76$. *Magnolia acuminata,* the most variable of our species, appears to be composed of three more or less well defined geographical varieties (var. *acuminata*, var. *cordata* (Michx.) Sarg., and var. *ozarkensis* Ashe), but some aspects of its variation deserve further study. (See Hardin.)

No wild hybrids have been found in the genus, although garden hybrids are common. No hybrids between subgenera have been obtained but a number of intersectional hybrids are known, including *M.* × *Thompsoniana* (Loud.) C. de Vos (*M. tripetala* × *virginiana*) and *M. virginiana* × *grandiflora*. The best known hybrid is the intersectional *M.* × *Soulangiana* Soulange-Bodin (*M. denudata* × *liliflora*) ($2n = 95, 114$), which is widely grown in a number of cultivars. All species appear to be proterogynous, the stigmas being receptive just before the flowers open.

Although *Magnolia* retains relatively primitive sporophyll-like stamens, especially in some of the tropical Asiatic species of Sect. *Gwillimia*, the genus is advanced within the family in respect to carpellary features, being surpassed only by *Liriodendron* which has both more specialized stamens and carpels. *Magnolia* is most closely related to *Talauma*: some of the tropical Asiatic species are so similar in flower that fruit is necessary for proper identification.

REFERENCES:

AFANASIEV, M. A physiological study of dormancy in seed of *Magnolia acuminata*. Cornell Agr. Expt. Sta. Mem. **208:** 1–37. 1937.*

ANDREWS, F. M. Karyokinesis in *Magnolia* and *Liriodendron*, with special reference to behavior of chromosomes. Bot. Centr. Beih. **11:** 134–142. 1901.

BRUSH, W. D. Southern magnolia (*Magnolia grandiflora* Linnaeus). Am. Forests **52:** 32–33. 1946.

———. Our native magnolias. Am. Forests **62:** 31–32, 58–59. 1956.

COKER, W. C. *Magnolia cordata* Michaux. Jour. Elisha Mitchell Sci. Soc. **59:** 81–88. 1943. [Taxonomy, distribution.]

CRUM, P. Chelating agents for the control of lime-induced chlorosis in southern magnolia (*Magnolia grandiflora*). Proc. Nat. Shade Tree Conf. **30:** 267–270. 1954.*

DANDY, J. E. A survey of the genus *Magnolia* together with *Michelia* and *Manglietia*. *In* Camellias and Magnolias. Roy. Hort. Soc. Conf. Rep. 64–81. London, 1950.

———. Key to the species of *Magnolia*. Jour. Roy. Hort. Soc. **52:** 260–264. 1927.

DAUMANN, E. Das Blütennektarium von *Magnolia* und die Fütterkörper in der Blüte von *Calycanthus*. Planta **11:** 108–116. 1930.

EARLE, T. T. Embryology of certain Ranales. Bot. Gaz. **100**: 257–275. 1938. [*M. grandiflora, Cimicifuga racemosa.*]

———. Origin of the seed coats in *Magnolia*. Am. Jour. Bot. **25**: 221, 222. 1938. [*M. grandiflora*; corroborates Gray's observations.]

EVANS, C. R. Germination behavior of *Magnolia grandiflora*. Bot. Gaz. **94**: 729–754. 1933.

FARR, C. H. Cell division by furrowing in *Magnolia*. Am. Jour. Bot. **5**: 379–395. 1918. [*M. tripetala* and cultivated spp. not specified, Jamaica.]

FLANDERS, B. C. Reliability of growth rings in *Magnolia grandiflora* as indicators of age. Quart. Jour. Fla. Acad. **13**: 77–109. 1950. [False growth rings.]

FREEMAN, O. M. A new Magnolia hybrid. Nat. Hort. Mag. **16**: 161–162. 1937. [*M. virginiana* ♀ × *grandiflora* ♂.]

———. New Magnolia hybrids. Loc. cit. **30**: 132–135. 1951. [*M. acuminata* × *cordata* and reciprocal; cultivated plants.]

GIBSON, H. H. American forest trees — 39. Cucumber tree, *Magnolia acuminata* Linn. Hardwood Rec. **23**: 16, 17. 1906.

GRAY, A. A short exposition on the structure of the ovule and seed-coats of *Magnolia*. Jour. Linn. Soc. **2**: 106–110. 1858. [*M. tripetala.*]

GRIER, N. M. Note on fruit of mountain Magnolia. Rhodora **19**: 256. 1917. [Misshapen cones of *M. acuminata.*]

GRIESEL, W. O. Retardation of maturation in *Magnolia* flowers by maleic hydrazide. Science **119**: 843–845. 1954.

———. Cytological changes accompanying abscission of perianth segments of *Magnolia grandiflora*. Phytomorphology **4**: 123–132. 1954.

HARDIN, J. W. An analysis of variation within *Magnolia acuminata* L. Jour. Elisha Mitchell Sci. Soc. **70**: 298–312. 1954. [3 vars. recognized.]

HARPER, F. Two more available plant names of William Bartram. Bartonia **21**: 6–8. 1942. [*M. pyramidata* Bartr.; see also MERRILL, E. D., In defense of the validity of Bartram's binomials. Bartonia **23**: 10–35. 1945.]

HAUPT, A. W. The stem of *Magnolia* as a laboratory type. Science **61**: 469. 1925.

HOWARD, R. A. The morphology and systematics of the West Indian Magnoliaceae. Bull. Torrey Bot. Club **75**: 335–357. 1948. [*Magnolia* and *Talauma.*]

JOHNSON, H. W., AND C. W. EDGERTON. A heart rot of magnolia caused by *Fomes geotropus*. Mycologia **28**: 292–295. 1936.

JOHNSON, M. A. The precipitin reaction as an index of relationship in the Magnoliaceae. Serol. Mus. Bull. **13**: 1–5. 1954. [Mostly comparison of sp. in different sections; *M. tripetala* and *M. obovata* show close correspondence.]

JOHNSTONE, G. H. Asiatic Magnolias in cultivation. 160 pp. Roy. Hort. Soc., London, 1955.

KENNEDY, G. G. Some historical data regarding the sweet bay and its station on Cape Ann. Rhodora **18**: 205–212. 1916. [*M. virginiana* at its northernmost locality, e. Mass.]

KURZ, H., AND K. WAGNER. *Magnolia* associations in northern Florida. (Abs.) Jour. Tenn. Acad. **27**: 207. 1952.

MEEHAN, T. On the stipules of *Magnolia Fraseri*. Proc. Acad. Phila. **1887**: 155. 1887.

MILLAIS, J. G. Magnolias. 251 pp. London, 1927.

OZENDA, P. Sur la vascularisation des carpelles et du pistil chez les *Magnolia*. Compt. Rend. Acad. Sci. Paris **217**: 31–33. 1943.

PLOUVIER, V. Sur la presence de rutoside dans les fleurs de quelques *Magnolia*. Compt. Rend. Acad. Sci. Paris **216**: 459–461. 1943.

———. Sur l'huile des graines de *Magnolia macrophylla* Michx. (Magnoliacée). Loc. cit. **222**: 1009–1011. 1946.

REED, R.A. Nuclear phenomena in the tapetum of *Magnolia grandiflora*. Wasmann Collect. **7**: 1–15. 1947.

SANTANTARAI, B. A note on the induction of roots on the twigs of *Magnolia grandiflora* L., with the aid of synthetic hormones. Indian Jour. Hort. **12**: 32–33. 1955.*

SAWADA, K. Oriental magnolias in the South. Nat. Hort. Mag. **29**: 54–57. 1950.

WEATHERBY, C. A. A new *Magnolia* from west Florida. Rhodora **28**: 35–36. 1926. [*M. Ashei*; see also SMALL, J. K. A magnolia as a new border plant. Jour. N. Y. Bot. Gard. **34**: 150–152. 1933.]

Tribe LIRIODENDREAE Reichb.

2. **Liriodendron** L. Sp. Pl. 1: 535. 1753; Gen. Pl. ed. 5. 239. 1754, "*Liriodendrum*."

Large, deciduous trees with long-petioled leaves with conspicuous stipules and very characteristic leaf-blades with 2 lateral lobes near the base (and sometimes 2 smaller above) and 2 at the apex which appears as if cut off abruptly by a broad, shallow notch. Perianth segments 9, deciduous, the 3 outer ones sepaloid, green, glaucous, reflexed, the 6 inner ones in 2 whorls making a campanulate, tulip-like corolla, greenish-yellow, each with an orange band near the base. Stamens numerous (± 30), the filaments stout, narrowed to the broader, apiculate, extrorse anther. Gynoecium of numerous spirally arranged carpels tightly imbricated into a cone-like column as long as the petals; style elongated, broad, flattened and winglike, constricted to a small, recurved stigmatic crest. Fruit a spindle-shaped cone of closely appressed 2-seeded samaras, these falling separately at maturity leaving the persistent receptacle; seeds with a thin, dry, and leathery testa. TYPE SPECIES: *L. Tulipifera* L. (The name from Greek, *lirion*, lily or tulip, and *dendron*, tree, from the tulip-like flowers.) — YELLOW-POPLAR, TULIP-POPLAR, TULIP-TREE.

An ancient genus formerly of wide distribution in the Northern Hemisphere, now reduced to two very similar species, *L. Tulipifera*, of eastern North America, and *L. chinense* (Hemsl.) Sarg., of a small area in central China (parts of Kweichow, Chekiang, Hupeh, Kiangsi, and Wushan Provinces).

Liriodendron Tulipifera ($2n = 38$), a very handsome and important timber tree, reaches its best development in the rich, hardwood forests of the Appalachians, attaining a maximum height of 200 ft. and a circumference of almost 35 ft. It is distributed from western Massachusetts and southern Vermont to southernmost Ontario, southern Michigan, Indiana, southeastern Missouri, eastern Arkansas, and Louisiana to central Florida.

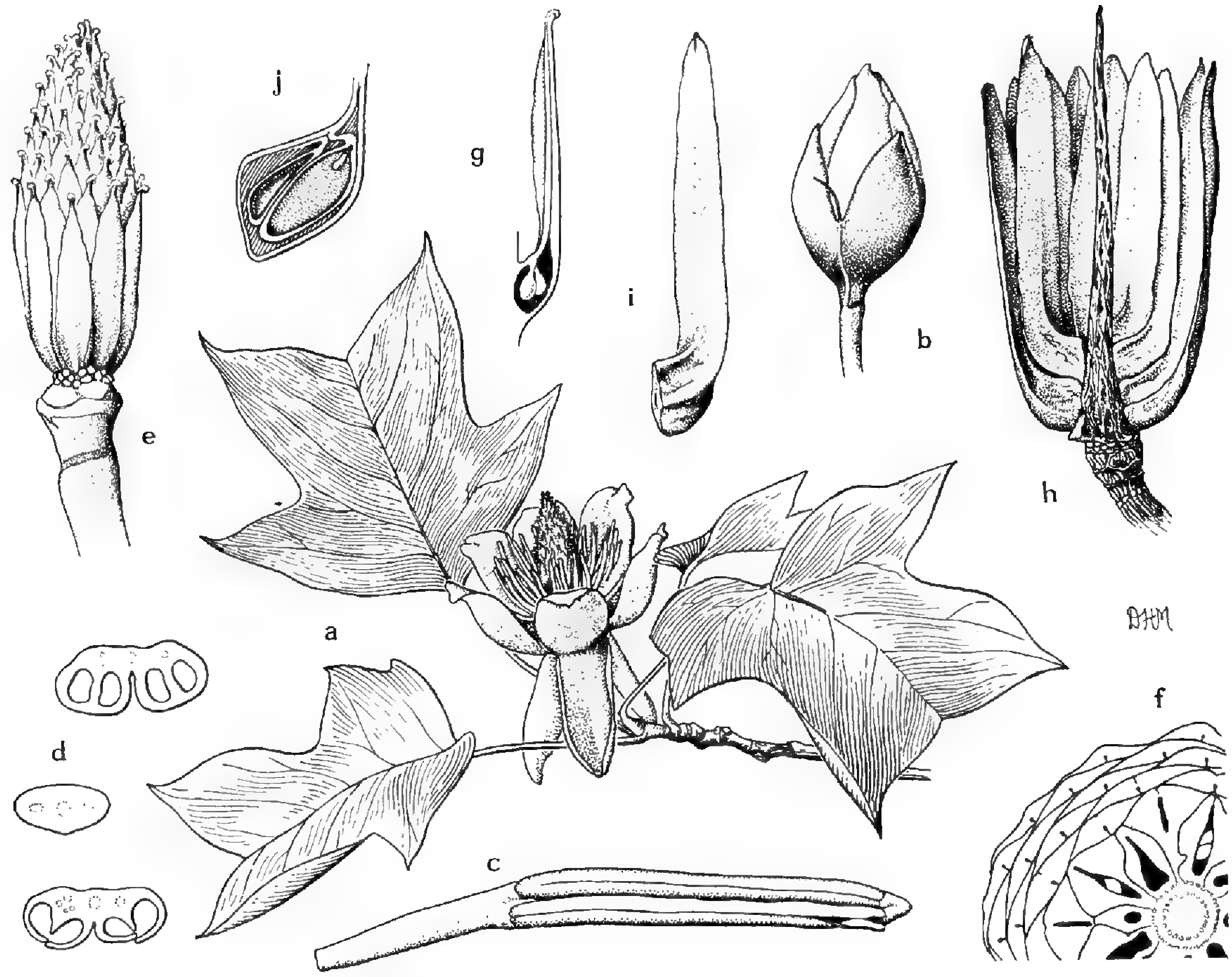


FIG. 1. **Liriodendron.** a–j, *L. Tulipifera*: a, flowering branchlet, × 1/4; b, flower-bud with stipular bud-scales, × 1/2; c, stamen, abaxial view, × 2; d, unopened anther, filament, and anther after anthesis, cross-sections, pollen omitted, × 6; e, gynoecium, with sepals, petals, and stamens removed, × 1; f, gynoecium, portion of cross-section, with spirally arranged imbricated carpels, ovaries adnate to axis to lower right, increasingly flattened styles toward outside, the locules and stylar canals in black, × 3; g, carpel at anthesis, vertical section, × 1; h, mature gynoecium with many samaras already shed from axis, × 1; i, samara, × 1; j, lower part of samara, vertical section, with aborted ovule (left) and seed with bony coats, abundant endosperm and small embryo, × 2; d, f, g, j, semi-diagrammatic.

The leaves although always unmistakable are extremely variable and most of those described for 25 fossil species may be matched from the existing populations. The faintly fragrant proterogynous flowers of *L. Tulipifera* are provided with copious watery nectar at anthesis, but seem to be visited primarily by bees collecting the abundant pollen.

Liriodendron chinense ($2n = 38$) seems to be generally a smaller tree, (ca. 50 ft.) with slightly different leaves, smaller flowers and smaller and slightly different fruit. The plant is not nearly so hardy as our native species. Apparently no crosses between the two species have been made; such hybridizations should be of great interest in view of the geographic isolation of the parental species and in comparison with similar crosses in *Catalpa* and *Platanus*.

Liriodendron is isolated within the Magnoliaceae with no close relatives.

It is the only genus in the group with a definitely localized stigma, and the manner of vascularization of the ovules is unique in the family.

REFERENCES:

ANDREWS, F. M. Karyokinesis in *Magnolia* and *Liriodendron*, with special reference to behavior of chromosomes. Bot. Centr. Beih. **11:** 134–142. 1901.

BARRACHINA Y ALMEDA, J. Tulipero de virginia estudio botanico selvicola e industrial. Mem. Acad. Cien Artes Barcelona **23:** 39–66. 1932.*

BERRY, E. W. The origin of stipules in *Liriodendron*. Bull. Torrey Bot. Club **28:** 493–498. 1901.

———. Notes on *Liriodendron* leaves. Torreya **1:** 105–107. 1901.

———. Notes on the phylogeny of *Liriodendron*. Bot. Gaz. **34:** 44–63. 1902.

———. Additional notes on *Liriodendron* leaves. Torreya **2:** 33–37. 1902.

———. *Liriodendron* notes. Torreya **3:** 129–132. 1903.

———. *Liriodendron* in the Miocene of America and Eastern Asia. Torreya **41:** 82–84. 1941.

BETTS, H. S. Yellow-poplar (*Liriodendron tulipifera*). U. S. Forest Serv. Am. Woods. 8 pp. Washington, 1954.

CHAPMAN, A. G. Some effects of varying amounts of nitrogen on the growth of tulip poplar seedlings. Ohio Jour. Sci. **33:** 164–181. 1933.

CREASY, W. D. Secondary succession and growth of yellow poplar. Castanea **19:** 81–87. 1954.

CURTIS, C. C. Second flowering of the tulip-tree. Jour. N. Y. Bot. Gard. **2:** 136–138. 1901.

DRIVER, C. H. Morphology of mycorrhizae of *Liriodendron tulipifera* L. (Abs.) Jour. Tenn. Acad. **25:** 224. 1950.

FRASER, J. *Liriodendron chinense*. Gard. Chron. III. **88:** 109. 1930.

GIBSON, H. H. American forest trees — Poplar or whitewood, *Liriodendron Tulipifera* Linn. Hardwood Rec. **19:** 14, 15. 1905.

GUARD, A. T. The development of the seed of *Liriodendron tulipifera* L. Proc. Indiana Acad. **53:** 75–77. 1943. (1944).

HEPTING, G. H., AND G. G. HEDGCOCK. Decay in merchantable oak, yellow poplar, and bass wood in the Appalachian region. U. S. Dept. Agr. Tech. Bull. **570:** 1–29. 1937.

HOLLICK, A. Wing-like appendages on the petioles of *Liriophyllum populoides* Lesq. and *Liriodendron alatum* Newb., with description of the latter. Bull. Torrey Bot. Club **21:** 467–471. 1894.

———. A new fossil *Liriodendron* from the Laramie at Walsenberg, Colo. and its significance. (Abs.) Proc. Am. Assoc. Adv. Sci. **43:** 225. 1895.

———. Appendages to the petioles of *Liriodendra*. Bull. Torrey Bot. Club **23:** 249–250. 1896.

———. The tulip tree and its ancestors. Proc. Nat. Sci. Assoc. Staten Island **5:** 80. 1896.*

HOLM, T. On the validity of some fossil species of *Liriodendron*. Bot. Gaz. **20:** 312–316. 1895.

———. Notes on the leaves of *Liriodendron*. Proc. U. S. Nat. Mus. **13:** 15–25. 1890.

———. Medicinal plants of North America. 30. *Liriodendron tulipifera* L. Merck's Rep. **18:** 198–201. 1909.*

HUCKENPAHLER, B. J. Auxins fail to stimulate rooting of yellow-poplar cuttings. Bot. Gaz. **117**: 73–75. 1955.

JOHNSON, T. W., and others. Observations on yellow-poplar (*Liriodendron tulipifera*) dieback. Forest Sci. 3(1): 84–89. 1957.

LI, H. L., AND J. W. WRIGHT. The Chinese tuliptree (*Liriodendron chinense*) in northeastern United States. Morris Arb. Bull. **5**: 34–35. 1954. [Notes on history, distribution, introduction into U. S., hardiness and chromosome-number.]

LIMSTROM, G. A., AND R. F. FINN. Seed source and nursery effects on yellow-poplar plantations. Jour. Forestry **54**: 828–831. 1956.

MEYER, B. S. The daily periodicity of transpiration in the tulip poplar, *Liriodendron tulipifera* L. Ohio Jour. Sci. **32**: 104–114. 1932.

MILLINGTON, W. E., AND J. E. GUNKEL. Structure and development of the vegetative shoot tip of *Liriodendron tulipifera* L. Am. Jour. Bot. **37**: 326–335. 1950.

PRAY, T. R. Foliar venation of angiosperms I. Mature venation of *Liriodendron.* Am. Jour. Bot. **41**: 663–670. 1954. II. Histogenesis of the venation of *Liriodendron.* Loc. cit. **42**: 18–27. 1955.

SCHWERIN, F. GRAF VON. Angeblicher Atavismus bei *Liriodendron.* Mitt. Deutsch. Dendr. Ges. **28**: 135–143. 1919.

VOIGT, J. W. A preliminary investigation of the effect of the descaling of winter buds on their growth in east central Illinois. Trans. Ill. State Acad. Sci. **35**(2): 78–80. 1942. [Incl. *Liriodendron, Betula nigra, Tilia europea.*]

WEISSE, A. Über die Blattstellung von *Liriodendron tulipifera.* Ber. Deutsch. Bot. Ges. **20**: 488–493. 1902.

ANNONACEAE (CUSTARD-APPLE FAMILY)

Trees, shrubs [or vines] with alternate, exstipulate, simple, entire leaves with pinnate venation; buds naked, the leaves conduplicate; oil glands present, the plants aromatic. Flowers perfect [in most], hypogynous, regular, axillary [or terminal], usually nodding. Perianth trimerous, generally of 3 small sepals and 6 petals in 2 whorls of 3, the inner smaller [or sometimes lacking]. Stamens numerous, spirally inserted on the receptacle, filament and anther poorly or not at all differentiated, the sterile tip variously modified; sporangia 4, extrorse, opening longitudinally; pollen in tetrads [or single], monocolpate [to acolpate], the germinal furrow proximal. Carpels many–1, usually free but sometimes united by the ovaries at anthesis [and rarely more completely syncarpous]; stigmas terminal; ovules many–1, in 1 or 2 rows along the adaxial wall or basal, anatropous, 2-integumented. Carpels free in fruit and berry-like, or coalescent, forming a fleshy syncarp. Seeds arillate (in ours), with ruminate endosperm and a small embryo. Embryo-sac development normal (Polygonum type) [insofar as investigated], endosperm development cellular.

A tropical family with 75–120 genera and more than 1000 species, many poorly known, and the classification of the family not yet well agreed upon. Represented in our area by *Asimina,* the only extra-tropical genus, and by *Annona,* which reaches subtropical Florida.

The family is distinguished by the exstipulate, simple leaves, the 3 whorls of 3 perianth segments, the numerous more or less fleshy spirally inserted stamens (each with a single vein), the usually numerous carpels, the fleshy fruits, the large seeds with ruminate endosperm, the tri-lacunar nodes with tripartite median trace, and the monocolpate (or derived) pollen with proximal germinal area (evident in those species in which the pollen is shed in tetrads). Anatomical features of wood, stem and leaf are remarkably uniform throughout the family.

It has been agreed generally that the affinities of the group are with the Ranales (sensu lato) but more precise relationships have been a matter of speculation. The anatomical evidence brought together by Vander Wyk and Canright strongly supports the view that the Annonaceae should be most closely allied with Degeneriaceae, Magnoliaceae and Himantandraceae, on a level of specialization above the Magnoliaceae and perhaps roughly comparable with Himantandraceae.

REFERENCES:

ADATIA, R. D., AND D. B. CHOKSHI. The chromosome numbers in the family Anonaceae. Cur. Sci. Bangalore **20:** 102. 1951.*

ASANA, J. J., AND R. D. ADATIA. The chromosome numbers in the family Anonaceae. Cur. Sci. Bangalore **14:** 74–75. 1945.*

———. Contributions to the embryology of the Annonaceae. Jour. Bombay Univ. B, Biol. Sci. II. **16**(3): 7–21. 1947.*

BOWDEN, W. M. Chromosome numbers in the Annonaceae. Am. Jour. Bot. **35:** 337–381. 1948. [7 sp. *Asimina* $2n = 18$; 5 sp. *Annona*, $2n = 16$; and others.]

CORNER, E. J. H. The annonaceous seed and its four integuments. New Phytol. **48:** 332–364. 1949.

DIELS, L. Die Gliederung der Anonaceen und ihre Phylogenie. Sitzungsb. Preuss. Akad. Wiss. **1932:** 77–85. 1932.

FRIES, R. E. Einige Gesichtspunkte zur systematischen Gruppierung der amerikanischen Annonaceen-Gattungen. Ark. Bot. **30A**(8): 1–31. 1943.

———. Revision der Arten einiger Anonaceen-Gattungen. I–V. Acta Horti Berg. **10:** 1–341. 1931; **12:** 1–220, 289–577. 1939.

———. Verstreute beobachtungen hinsichtlich der familie Annonaceae. Ark. Bot. II. **3:** 35–42. 1955. [Old world genera.]

GARRATT, G. A. Bearing of wood anatomy on the relationships of the Myristicaceae. Trop. Woods **36:** 20–44. 1933. [Many data on Annonaceae.]

HUTCHINSON, J. Contributions toward a phylogenetic classification of flowering plants. II. The genera of Annonaceae. Kew. Bull. **1923:** 241–261. 1923.

LICOPOLI, G. Sull anatomia a fisiologia del frutto nell' *Anona reticulata* e nell' *Asimina triloba*. Atti Accad. Napoli II. **1:** 1–9. 1887.*

OZENDA, P. Structure du noeud foliaire des Magnoliacées et des Anonacées. Compt. Rend. Acad. Sci. Paris **224:** 1521–1523. 1947.

PERIASAMY, K. On the floral biology of some members of the Anonaceae. Jour. Madras Univ. **24:** 7–12. 1954.*

RUSBY, H. H. The custard-apple family in Florida. Jour. N. Y. Bot. Gard. 36: 233–239. 1935. [*Asimina* and *Annona*.]

VANDER WYK, R. The comparative morphology of the Annonaceae. Doctoral Dissertation. Widener Library, Harvard Univ. 1950. [Stem, wood, node and petiole, leaf, cotyledon, and pollen, especially, in comparison with Degeneriaceae, Magnoliaceae, Himantandraceae, Myristicaceae, Eupomatiaceae, Canellaceae, Calycanthaceae.]

——— AND J. E. CANRIGHT. The anatomy and relationships of the Annonaceae. Trop. Woods **104**: 1–24. 1956. [Stem and wood anatomy.]

VOIGT, A. Untersuchungen über Bau und Entwicklung von Samen mit ruminiertem Endosperm aus den Familien der Palmen, Myristicaceen und Anonaceen, Ann. Jard. Bot. Buitenzorg **7**: 151–190. 1888.

WESTER, P. J. Annonaceous possibilities for the plant breeder. Philipp. Agr. Rev. **6**: 312–321. 1913.

1. **Asimina** Adans. Fam. Pl. 2: 365. 1763.

Trees (to 40 ft.), shrubs or subshrubs (ca. 2 ft.). Flowers nodding, axillary on greatly reduced branches, solitary or in pairs, borne on the wood of the preceding season or on the growth of the year, ill-scented or fragrant. Sepals 3 (rarely 4), small, valvate in the bud. Petals usually 6(–8 or sometimes 12), in 2 (or more) series of 3, the outer largest (often very much larger), imbricated, brown or purplish, greenish, white or yellowish, often increasing greatly in size during anthesis. Stamens numerous–10, inserted on the subglobose to nearly flat receptacle; pollen in tetrads. Carpels 15–1, distinct, the styles short, the stigma small; ovules many–6, in two rows or one. Carpels berry-like in fruit (usually one 1–4 maturing) free, banana-shaped or somewhat torulose to ellipsoid or ovoid, the flesh aromatic; seeds flattened to round, many–4, inclosed in a pulpy membranaceous aril. (Including *Pityothamnus* Small and *Deeringothamnus* Small.) TYPE SPECIES: *A. triloba* (L.) Dunal. (The name from *asiminier,* an early French-colonial name for *A. triloba,* this, in turn, from the Indian name *assimin*). — PAWPAW.

Perhaps 10 species, all of eastern North America. *Asimina triloba* (northern Florida to Texas, north to New Jersey, western New York, southern Ontario, Michigan, Illinois, southeastern Iowa and southeastern Nebraska) and *A. parviflora* (Michx.) Dunal (Piedmont and Coastal Plain, northern Florida to Mississippi, north to southeastern Virginia) have the widest ranges; the others are mostly confined to Florida. The genus includes the only truly extra-tropical species in the family. According to Fries, the only close relative is *Stenanona* Standl., of Panama and Costa Rica.

Although the species of *Asimina* range from deciduous trees reaching 40 ft. (*A. triloba*) to low, fusiform-rooted shrubs with dimorphic stems and partly persistent leaves and, although there is considerable diversity in flower-color and petal-shape, -size, and -sculpturing, the group appears to be a natural one. The differences used by Small in segregating *Pityothamnus* and *Deeringothamnus* seem trivial as generic distinctions. The chromosome-numbers of species of the former group are the same as those of *A. triloba* and *A. parviflora* ($2n = 18$) and, even more significantly, vigorous hybrids have been obtained between *A. triloba* and at least "*A.*

obovata" (= A. *grandiflora* (Bartr.) Dunal?) and "*A. angustifolia*" (= *A. pygmaea* (Bartr.) Dunal?), two very different species assigned to *Pityothamnus*. The former hybrid is known to be fully fertile. No such data are available for the two species placed in *Deeringothamnus* (*A. pulchella* (Small) Rehd. & Dayton, of sw. Florida, and *A. Rugelii* Robins., of ne. Florida). Although differing in the nearly flat receptacle (correlated with reduced numbers of stamens and carpels), in the narrow, hardly fleshy petals of nearly equal size, and in the lack of bracts on the peduncles of the flowers, these plants appear to be only the most specialized members of the genus, standing at the opposite extreme from *A. triloba* but connected to it through the "Pityothamnus" group.

Although apparently rather stable in its vegetative and floral morphology, *A. triloba* shows a wide variation in size, color and palatability of fruits. Two general types have been observed: (1) large, yellow-fleshed, highly flavored, early ripening and (2) small to large, white-fleshed, mild-flavored, late or very late ripening fruits. A number of selected clones, propagated by grafting, are in cultivation.

The flowers of all species are proterogynous. The brown or purple flowers of *A. triloba* and *A. parviflora* are reputed to be ill-scented, while those of the white-flowered species, especially *A. pulchella* and *A. Rugelii*, are fragrant. Beetles appear to be involved in pollination. Most species set few fruit; hand-pollination seems to be necessary to obtain a good fruit-set in *A. triloba*.

REFERENCES:

BOWDEN, W. M. Triploid mutants among diploid seedling populations of *Asimina triloba*. Bull. Torrey Bot. Club **76**: 1–6. 1949. [5 triploids among 205 seedlings in 23 collections.]

——— AND B. MILLER. Distribution of the Papaw, *Asimina triloba* (L.) Dunal, in southern Ontario. Canad. Field-Nat. **65**: 27–31. 1951.

DEMING, W. C. Papaw (*Asimina triloba*) notes. North. Nut Growers Assoc. Ann. Rep. (1945) **36**: 98. 1946.*

EXELL, A. W. William Bartram and the genus *Asimina* in North America. Jour. Bot. **65**: 65–69. 1927. [Includes key to species.]

FRIES, R. E. Revision der Arten einiger Annonaceen-Gattungen. V. Acta Horti Berg. **12**: 289–577. 1937. [*Asimina*, *Deeringothamnus*, 546–554.]

GRAY, ASA. The genus *Asimina*. Bot. Gaz. **11**: 161–164. 1886.

HERMS, W. B. Contribution to the life history of *Asimina triloba*. Ohio Nat. **8**: 211–217. 1907. [Embryo sac; embryology.]

LAMPTON, R. K. Developmental morphology of ovule and seed in *Asimina triloba* Dunal. (Abs.) Jour. Tenn. Acad. **28**: 182–183. 1953. [See also Diss. Abs. **13**: 290, 291. 1953.*]

LEVERETT, F. The northern limit of the papaw tree. Science **23**: 919, 920. 1906. See also other authors, loc. cit. **23**: 920; **23**: 749–751. 1906; **24**: 48. 1906.

LOCKE, F. J. Microsporogenesis and cytokinesis in *Asimina triloba*. Bot. Gaz. **98**: 159–168. 1936.

NASH, G. V. Revision of the genus *Asimina* in North America. Bull. Torrey Bot. Club **23**: 234–242. 1896.

POPENOE, P. Where are the best papaws? Jour. Hered. **7**: 291–296. 1916.

———. The best papaws. Loc. cit. **8:** 21–33. 1916. [Includes information on propagation, fruits, largest trees, etc.]

REHDER, A. AND W. A. DAYTON. A new combination in *Asimina.* Jour. Arnold Arb. **25:** 84. 1944. [*A. pulchella*; *Deeringothamnus* discarded.]

SMALL, J. K. *Deeringothamnus pulchellus.* Addisonia **11:** 33–34. 1926. See also Bull. Torrey Bot. Club **51:** 390. 1924. *Deeringothamnus Rugelii.* Loc. cit. **15:** 17–18. 1930.

———. A new pawpaw from Florida. Torreya **26:** 56. 1926. [*A. tetramera.*]

SMITH, G. H. Vascular anatomy of Ranalian flowers II. Ranunculaceae (continued), Menispermaceae, Calycanthaceae, Annonaceae. Bot. Gaz. **85:** 152–177. 1928. [*Asimina triloba.*]

SOBAJMA, Y. Studies on the pawpaw (*Asimina triloba* Dunal). III. On the time of flower bud differentiation and bearing habit. (In Japanese.) Saikyo Univ. Facul. Agr. Sci. Rep. **7:** 81–86. 1955.* [English summary.]

——— AND N. KUNIMURA. Studies on the pawpaw (*Asimina triloba* Dunal). I: (1) Flowering season and microsporogenesis in pawpaw, (2) Insect visitors on the flowers of pawpaw. (In Japanese.) Saikyo Univ. Facul. Agr. Sci. Rep. **5:** 33–46. 1953.* II. On the fruit setting by the self pollination and the germination test of pollen. (In Japanese.) Loc. cit. **6:** 29–37. 1954.*

UPHOF, J. C. T. Die nordamerikanischen Arten der Gattung *Asimina.* Mitt. Deutsch. Dendr. Ges. **45:** 61–76. 1933.

ZIMMERMAN, G. A. Hybrids of the American pawpaw. Jour. Hered. **32:** 83–91. 1941. [Notes on *A. triloba* and interspecific hybrids.]

2. **Annona** L. Sp. Pl. 1: 536. 1753; Gen. Pl. ed. 5. 241. 1754.

Trees (deciduous with us) with rather coriaceous 2-ranked leaves, nodding flowers borne on axillary or supra-axillary branches (which may abort producing the effect of either terminal or axillary flowers), and fleshy syncarpous fruits. Sepals small, valvate in the bud; petals rather thick and fleshy, generally whitish or yellowish, the outer whorl larger and alternate with the sepals and valvate, the inner smaller or very much reduced [or lacking] and valvate [or imbricate]. Stamens club-shaped, the tip modified, generally broad and truncate, very numerous and tightly packed, inserted on the hemispherical receptacle; pollen grains in columns of tetrads. Carpels sessile, numerous, on the receptacle, the ovaries free or united at anthesis, the styles generally club-shaped, fleshy, and conspicuous; ovules solitary in each ovary (rarely 2), erect. Carpels coalescent, forming a many-seeded syncarp with a smooth, squamulose or muricate surface, the individual carpels being indicated on the surface by more or less distinctly outlined areoles. Seeds ovate or elliptical, with a thin outer coat and a thin aril. TYPE SPECIES: *A. muricata* L. (The name from *anon* or *hanon*, the native Hispaniolan name for *A. muricata*, but changed by Linnaeus to Latin *annona*, a year's harvest, in preference to the use of a "barbarous" name, but so that the sound might be kept.) — CUSTARD-APPLE.

A genus of about 110 species assigned to 17 sections, most species tropical American, but about 10 in Africa; several species widely cultivated and naturalized in tropical regions; one species native, one sparingly naturalized and several cultivated in subtropical Florida.

Sect. PHELLOXYLON Saff., with ovate petals, the inner valvate, and ovaries connate at anthesis, includes only *Annona glabra* L. ($2n = 28$), the most widespread species in the genus (West Indies, north to the Bahamas and southern Florida, south to southern Brazil, Mexico to Equador; also in Africa from Senegal to the Belgian Congo). Always at low altitudes and associated with abundant moisture, the Pond-apple or Alligator-apple occurs in Florida in the Everglades and coastal areas in shallow ponds, along the borders of small fresh-water streams or on swampy hummocks; in other areas it seems sometimes to be associated with mangroves. The leaves appear in March–April and flowers in April; the edible but not very palatable fruits ripen in November.

Sect. ANNONA, cauliflorous, but also with ovate petals, the inner imbricate, and with free ovaries, is represented in cultivation by *A. muricata* L., the Guanabana or Sour-sop, a favorite tropical fruit only precariously hardy in Florida.

Sect. ATTA Mart., with elongate petals, the inner greatly reduced, includes *A. squamosa* L. (Sweet-sop or Sugar-apple), *A. reticulata* L. (Bullock's Heart) and *A. Cherimola* Mill. (Cherimoya), all in cultivation in tropical Florida, the first naturalized on some of the Florida Keys.

All species are proterogynous. At the time of pollination a sticky fluid exudes from the stigmas, gluing the styles together and providing a receptive medium for the pollen. The members of sect. *Atta* seem to be cross pollinated (by beetles?) but *A. muricata* may be self-pollinated, at least in some areas. Artificial hybrids have been obtained at least between *A. squamosa*, *A. reticulata*, and *A. Cherimola,* and between these species and *A. glabra*. The Atemoya (*A. squamosa* × *Cherimola*) is regarded as a very promising tropical fruit combining the better features of both parents. The chromosome numbers of the 4 cultivated species above have been reported as both 14 and 16. Numerous cultivars, perhaps involving hybridization, are known in various areas of the tropics. Other species are being introduced and tested for their horticultural possibilities.

According to Fries the genus is most closely related to the American genera *Raimondia*, *Rollinia* and *Rolliniopsis*.

REFERENCES:

FRIES, R. E. Revision der Arten einiger Anonaceen-Gattungen II. Acta Horti Berg. **10:** 129–341. 1931. [American spp. of *Annona*, 197–315.]

ISLAM, A. S. Preliminary report on the colchicine-induced tetraploids of *Anona squamosa* L. Cur. Sci. Bangalore **22:** 118–120. 1953.*

JULIANO, J. B. Morphological contribution on the genus *Anona*. Philipp. Agr. **24:** 528–541. 1935.*

KUMAR, L. S. S., AND K. RANADIVE. A cytological study of the genus *Anona*. Jour. Univ. Bombay **10B:** 1–8. 1941.* [*A. muricata, A. reticulata, A. squamosa, A. Cherimola,* $2n = 14$.]

LEÓN, HNO., AND HNO. ALAIN. El genero *Annona* en Cuba. Revista Soc. Cuba. Bot. **3:** 116–124. 1946. [15 spp.]

MEIJER, T. M. The alkaloids of *Anona muricata* Linn. Buitenzorg Lab. voor Scheikundig Onderzoek Meded. **94:** 1–8. [undated]; reprinted from De Ingenieur in Nederlandsch-Indië, no. 6. 1941, Rubriek VII.*

NOONAN, J. C. Review of investigations on the *Anona* species. Proc. Fla. State Hort. Soc. **66:** 205–210. 1953.*

PIJL, L. VAN DER. On the flower biology of some plants from Java with general remarks on fly-traps. Ann. Bogor. **1:** 77–99. 1953. [Includes self-pollination in *A. muricata.*]

POPENOE, W. Anona culture in Florida. Am. Eagle **41**(6): 1, 3. 1946.*

PREST, R. L. Custard apples pollination. Queensl. Fruit & Veg. News 2(8): 29–30. 1952. See also Queensl. Prod. 33(24): 14. 1951.*

ROBYNS, W., AND J. GHESQUIÈRE. Essai de révision des espèces africaines du genre *Annona* L. Bull. Soc. Roy. Bot. Belg. **67**(1): 7–50. 1934. [All except *A. glabra* belong to the otherwise S. Am. sect. *Helogenia.*]

SAFFORD, W. E. Classification of the genus *Annona*, with descriptions of the new and imperfectly known species. Contr. U. S. Nat. Herb. **18:** i–xii + 1–68. 1914.

———. The genus *Annona*: the derivation of its name and its taxonomic subdivisions. Jour. Wash. Acad. **1:** 118–120. 1911. See also SPRAGUE, Jour. Bot. **59:** 158. 1921, and Kew Bull. **1928:** 114. 1928.

SANTOS, A. C. Alkaloid from *Anona reticulata* Linnaeus. Philipp. Jour. Sci. **43:** 561–564. 1930. [Anonaine from bark.]

SAMUELSSON, G. Über die Pollenentwicklung von *Anona* und *Aristolochia* und ihre systematische Bedeutung. Sv. Bot. Tidskr. **8:** 181–189. 1914. [*A. Cherimola.*]

SCHROEDER, C. A. Fruit morphology and anatomy of the Cherimoya. Bot. Gaz. **112:** 436–446. 1951. [*A. Cherimola.*]

———. Hand pollination of cherimoya practical method for improving fruit set for better yields. Calif. Agr. (Calif. Sta.) **1**(8): 2. 1947.*

SIMONS, J. S. La guanábana y su cultivo. Puerto Rico Agr. Exp. Sta. Río Pedras Agriculture Exp. **2**(3): 7–8. 1942.*

STURROCK, D. Tropical fruits for southern Florida and Cuba and their uses. 131 pp. Arnold Arb., 1940. [*Annona*, 43–50.]

WESTER, P. J. Pollination experiments with Anonas. Bull. Torrey Bot. Club **37:** 529–539. 1910. [*A. reticulata, A. squamosa, A. Cherimola, A. glabra.*]

———. Hybridization of Annonas. Philipp. Agr. Rev. **8:** 177–181. 1915.*

———. A contribution to the history and vernacular nomenclature of the cultivated Anonas. Philipp. Jour. Sci. (Bot.) **7:** 109–123. 1912.

ILLICIACEAE (ANISE-TREE FAMILY)

A single genus, *Illicium* L., of southeastern Asia and southeastern North America. Although often placed near *Drimys* (Winteraceae) or associated with the Magnoliaceae, its closest relatives are undoubtedly *Schisandra* and *Kadsura* with which it shares similar pollen, the ranalian type of ethereal oil cell, cambiform "mucilage" cells in the phloem, unilacunar nodes, and similar cuticles, stomata and chromosomes, a combination of characters unique within the Ranales. The total evidence from morphology, anatomy and cytology suggests the inclusion of these three genera either in a single family or in two closely related families; it further provides a strong obstacle to the association of these genera with either Magnoliaceae or Winteraceae. According to the A. C. Smith, "The three genera will probably be treated by future phylogenists as composing a sub-order of the Ranales, coördinate with suborders composed of the (1) Magnoliaceae, Himantandraceae, and Degeneriaceae, (2) Winteraceae, (3) Trochodendraceae and Tetracentraceae, (4) Eupteleaceae, and other combinations of families . . . not yet sufficiently investigated."

Illicium stands apart from the Schisandraceae in its shrubby or arborescent habit, unmodified receptacle, free stamens, vascularized style, comparatively few carpels in a single whorl, single ovule, fruit a single whorl of follicles, unilacunar nodes with a single trace, pseudo-siphonostelic arrangement of the primary tissues, lack of crystal-bearing sclerenchyma, and a specific combination of primitive and specialized anatomical features in the secondary xylem and phloem.

1. **Illicium** L. Syst. Nat. ed. 10. 1050. 1759.

Glabrous evergreen shrubs or small trees with thin-coriaceous, exstipulate, entire, alternate or distally clustered leaves, the blades decurrent on the petioles. Flowers solitary or 2 or 3 together in minute glomerules, axillary or sub-terminal and appearing crowded among leaves toward the tips of branchlets, sometimes bracteolate, subtended by several caducous bracts. Flowers perfect, hypogynous, the parts free. Receptacle convex to short-conical, usually concealed by carpel-bases. Perianth segments numerous (12–15 or 21–33 in ours), several seriate. Stamens numerous (6–7 or 30–38, rarely –50, in ours), 1-seriate or 2- or 3-seriate, erect, with fleshy filaments and basifixed 4-sporangiate anthers introrsely dehiscent by longitudinal slits; pollen tricolpate. Carpels 11–15(–20), free, in a single whorl, each composed of a laterally flattened ellipsoid ovary distally attenuate into an acute style; style vascularized, conduplicate, stigmatic along the upper side along all or most of its length; ovary unilocular, with a single anatropous ovule on the adaxial side near the base. Fruit a folliceturn of a single whorl of free, spreading follicles 10–18 mm. long, these dehiscing along the upper side. Seed with a sub-basal hilum, ellipsoid and laterally flattened, 5–7 mm. long, brownish, glossy; endosperm copious, oily; embryo minute, near the hilum. TYPE SPECIES: *I. anisatum* L. (The name Latin, *illicium*, an allurement, in reference to the fragrance of the fruits of *I. verum* Hook f., an economically important species confused by Linnaeus and others with *I. anisatum*.) — ANISE-TREE.

A genus of some 37 species of southeastern Asia and 5 of southeastern North America. Two species, representing each of the 2 sections, occur entirely within our area. Our species are easily recognized by the fragrant (when crushed), thin-coriaceous, more or less evergreen leaves, the red to yellow relatively small flowers with numerous perianth segments, and the very characteristic star-shaped fruit, a ring of follicles.

Section ILLICIUM (*Badiana* Spach), with 13 species in which the inner

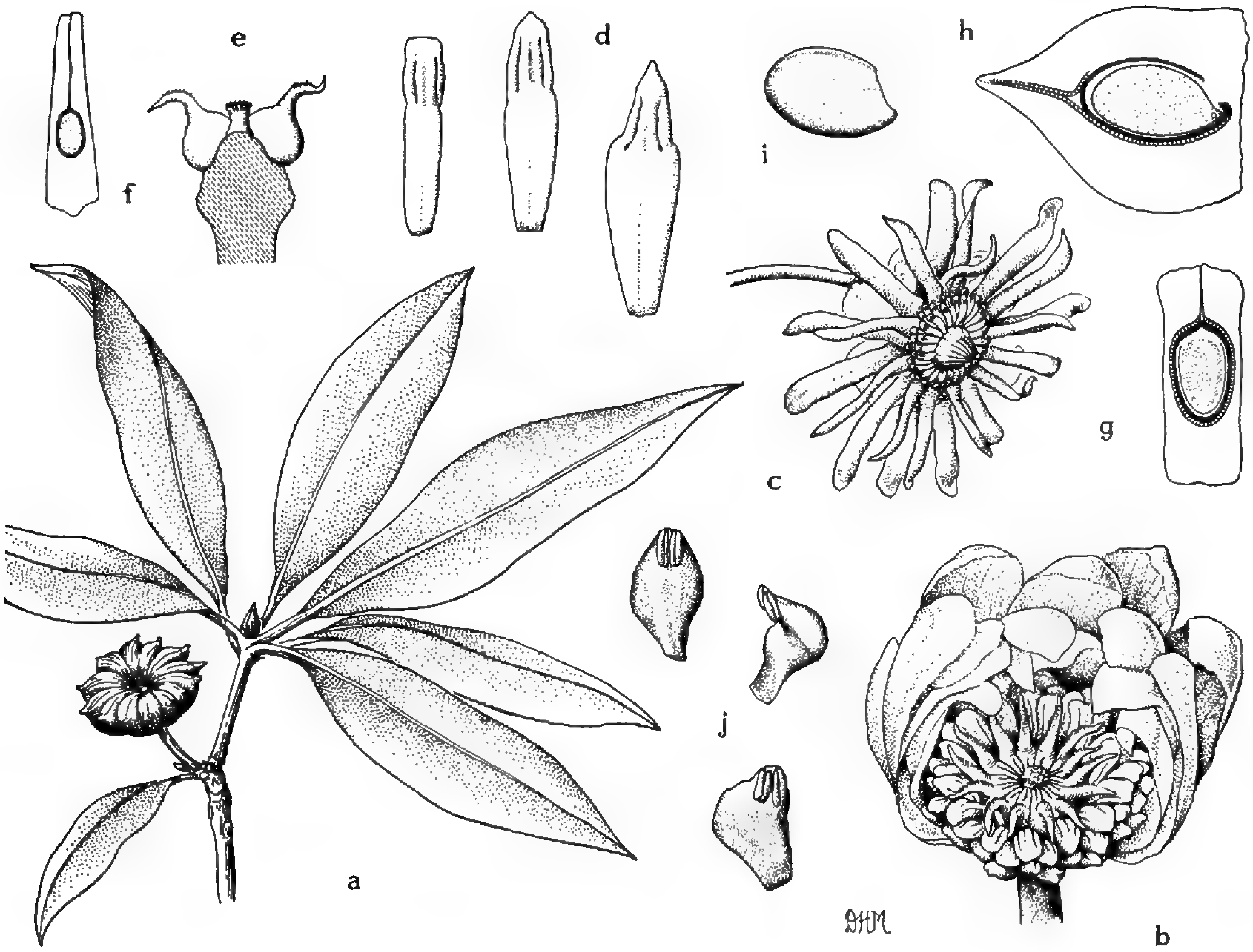


FIG. 2. **Illicium.** a–i, *I. floridanum*: a, fruiting branchlet, × 1/3; b, opening bud with carpels receptive to pollen, × 3; c, flower, later stage at shedding of pollen, the carpels connivent, × 1; d, stamens, inner, outer, and an unusual sub-tepaloid form, adaxial views, × 5; e, two carpels on axis, other flower parts removed, × 3; f, carpel, vertical section, to show folded, unfused sporophyll with single ovule, × 10; g, mature carpel, in section, with horny endocarp (striped) and seed with horny outer seed-coat (black) and endosperm (dotted), × 2; h, mature carpel, cross-section, the mature embryo at micropylar end of seed (to right), × 2; i, seed, × 2; f, g, h, semi-diagrammatic. j, *I. parviflorum*: stamens, adaxial view, × 5.

perianth segments are thin, narrowly oblong or ligulate or lanceolate and somewhat lax at anthesis, is represented with us by *I. floridanum* Ellis ($2n = 28$), a very well marked species which ranges from northwestern Florida to eastern Louisiana and northward to central Alabama at low elevations, especially in wet areas (e.g., around bay-heads). The only close relative of this species is the very similar and perhaps conspecific *I. mexicanum* A. C. Smith, of Veracruz and Tamaulipas. Both plants differ from Old World members of the section in their comparatively long pedicels, numerous stamens and brightly colored perianth segments.

The proterogynous flowers of *I. floridanum*, borne from March to May, are showy, deep red or purple, with an intensely unpleasant odor, both features suggestive of pollination by carrion flies. The species is hardy as far north as Philadelphia where, however, it may lose its usually evergreen habit. The leaves were used with those of *Ilex Cassine* as a tea by the Indians of western Florida.

Section CYMBOSTEMON (Spach) A. C. Smith, with 29 species in which the inner perianth segments are fleshy to paper-like, usually ovate to suborbicular and not lax at anthesis, occurs in our area as *I. parviflorum* Michx. ex Vent., a shrub or small tree which appears to be restricted to a few counties (Lake, Marion, Seminole and Volusia) at the headwaters of the St. Johns River in northeastern Florida. With its obtuse leaves, small, yellowish flowers produced in May and June and reduced number of stamens (6 or 7), this species is unlikely to be confused with *I. floridanum.* Beyond our area the section is represented in the New World by *I. cubense* A. C. Smith, of eastern Cuba, and *I. Ekmanii* A. C. Smith, of western Hispaniola.

Illicium verum, Star anise of southeastern China and adjacent Indo-China, provides a volatile oil used as a medicine, a condiment, or in flavoring liqueurs such as absinthe and anisette. The seeds of *I. anisatum* L. ($2n = 28$), of Japan, contain a poisonous alkaloid.

REFERENCES:

BAILEY, I. W., AND C. G. NAST. Morphology and relationships of *Illicium, Schisandra* and *Kadsura.* I. Stem and leaf. Jour. Arnold Arb. **29:** 77–89. 1948.

GRAY, A. Magnoliaceae. Genera Pl. U. S. **1:** 52–64. *pl. 21–25.* 1848. *I. floridanum.*

LEMESLE, R. Les ponctuations aréolées des fibres des genres *Schizandra* L., *Kadsura* J., *Illicium* L. et leur rapports avec la phylogenie. Compt. Rend. Acad. Sci. Paris **221:** 113–115. 1945.

OSWALD, F., JR. Beiträge zur Kenntniss der Bestandtheile der Früchte des Steranis, *Illicium anisatum.* 47 pp. Marburg, 1887.

SCHLOTTERBECK, J. O., AND C. R. ECKLER. The structure and development of the fruit of *Illicium floridanum.* Proc. Am. Pharm. Assoc. **49:** 485–589. 1901; Pharm. Arch. **4:** 201–205. 1901.*

SMITH, A. C. The families Illiciaceae and Schisandraceae. Sargentia **7:** 1–224. 1947. [A complete monographic treatment.]

SZE, Y. C. *Illicium religiosum* Siebold, Mang Tsao, a phytochemical study. Am. Jour. Pharm. **101:** 505–574, 622–637, 687–716. 1929.* [*I. anisatum.*]

TIEGHEM, P. VAN. Sur les dicotylédones du group des Homoxylées. Jour. de Bot. (Morot) **14:** 259–297, 330–361. 1900. [349–354, anatomical features of *Illicium*, which should not be included in Winteraceae.]

WHITAKER, T. W. Chromosome number and relationship in the Magnoliales. Jour. Arnold Arb. **14:** 376–385. 1933. [Includes undocumented counts for *I. anisatum* (also as *I. religiosum*) and *I. floridanum.*]

SCHISANDRACEAE (SCHISANDRA FAMILY)

A family of two undoubtedly closely related genera of climbing vines, *Schisandra* Michx. (ca. 25 species) and *Kadsura* Kaempf. ex Juss. (ca. 22 species), all of eastern and southeastern Asia and Malaysia, with the exception of a single species of *Schisandra* in the southeastern United States. The two genera have numerous features in common with *Illicium* (q.v.) but differ in the scandent habit, unisexual flowers, enlargement of the torus after anthesis, arrangement of the carpels, absence of a vascularized style, indehiscent drupe-like carpels, unilacunar nodes with three traces, typically eu-stelic arrangement of the primary vascular tissues, relatively primitive type of secondary xylem and presence of crystal-bearing sclerenchyma. Although the group is of great phylogenetic and phytogeographic interest, its economic importance is restricted to the few Asiatic species which occasionally are cultivated as ornamentals.

1. **Schisandra** Michx. Fl. Bor.-Am. 2: 218. 1803, nom. cons.

Monoecious or dioecious (?) woody climbing vines, the leaves simple, petiolate, exstipulate, alternate on long-shoots or congested on short-shoots, the blade oblong-elliptic to ovate or lanceolate, pinnate veined, entire to sinuate or remotely undulate-denticulate. Flowers pedicellate, unisexual, solitary in the axils of caducous bracts or foliage leaves near the base of the annual shoots, sometimes subtended by 2 or 3 minute secondary bracts. ♂ flowers: tepals 9–12 [5–20], free, 2- or 3-seriate, all similar, the largest elliptic to obovate, 5–8 mm. long; androecium a sessile flattened fleshy 5-cleft pentagonal shield, consisting of 5 radiating stamens with the connectives fused into the shield, the anther-sacs borne on the lower margins of the anthers; opening longitudinally; [in other species stamens 4–60, variously aggregated; pollen 3- or 6-colpate.] ♀ flowers: tepals similar to ♂; gynoecium consisting of a receptacle distinctly longer than broad (1.5–3 mm. long), and numerous (12–)20–30 [–120], 3–5-seriate carpels; ovary ellipsoid to obovoid, the wall fleshy, with stigmatic crests produced distally into an acute, unvascularized pseudostyle and proximally into an irregularly oblong appendage; ovules 2(–3) superposed or obliquely superposed, attached to the adaxial wall of the carpel above the base. Fruit with a greatly elongated receptacle (2–3 cm. long, 2–3 mm. diameter), the pedicel remaining slender, the receptacle bearing 7–12 carpels spaced on its surface; carpels becoming berries, usually ellipsoid or subglobose, the pericarp red, fleshy; seeds 2, ellipsoid-reniform, more or less rugulose; endosperm copious, oily; embryo small, near the hilum. (*Stellandria* Brickell, 1803, nom. rejic.) TYPE SPECIES: *S. coccinea* Michx. = S. glabra (Brickell) Rehder. (The name from Greek *schisis*, a cleaving, and *andros*, of a man, in reference to the "fissures" between the anthers.)

About 25 species of eastern Asia (Manchuria southward to northern Indo-China and the Himalayas, Java and Sumatra), a single species, *S. glabra* in southeastern United States, entirely endemic to our area. *Schisandra glabra* apparently is a very rare plant, being rather poorly known from few and widely scattered localities mostly on the coastal plain in southeastern South Carolina, Georgia, western Florida, Alabama, Mississippi, eastern Louisiana, eastern Arkansas and western Tennessee. The outer perianth segments of the flowers, which are produced in May or June, are greenish, the inner ones increasingly bright red, the androecium red, and the anther-sacs yellow. The greatly elongated receptacle which bears the red or scarlet fruits (July–August) is especially noteworthy.

The genus has been divided by A. C. Smith into four sections based primarily on various modifications of the androecium, which in the most primitive section (*Pleiostema*) may be composed of relatively numerous (–60) and essentially free stamens. Our species belongs to section *Schisandra* in which the androecium is highly modified, flattened and shield-like, composed of five united stamens, and presumably representing one of the end-products of the genus. In addition to *S. glabra*, the section includes *S. repanda* (Sieb. & Zucc.) A. C. Smith, of southern Japan and southern Korea, and *S. bicolor* Cheng, of northwestern Chekiang, China. All three are strikingly similar in characters of perianth-segments, androecium and gynoecium and furnish still another example of the now-familiar pattern of disjunction between eastern Asia and eastern North America.

The chromosome numbers of *S.* (§ *Maximowiczia*) *chinensis* (Turcz.) Baill., *S.* (§ *Pleiostema*) *sphenanthera* Rehder & Wilson, and *Kadsura japonica* (L.) Dunal have all been reported as $2n = 28$.

REFERENCES:

BAILEY, I. W. AND G. NAST. Morphology and relationships of *Illicium, Schisandra* and *Kadsura.* I. Stem and leaf. Jour. Arnold Arb. **29:** 77–89. 1948.

GRAY, A. Ord. Magnoliaceae. Genera Pl. U. S. **1:** 52–64. *pls. 21–25.* 1848. [*Schisandra*, 57–58, *pl. 22.*]

KOZO-POLJANSKI, B. M. The floral mechanism of Woo-we-dzy, *Schizandra chinensis* (Turcz.) Baill. Compt. Rend. Acad. URSS. II. **53:** 749–751. 1946.*

LEMESLE, R. Les ponctuations aréolées des fibres des genres *Schizandra* L., *Kadsura* J., *Illicium* L. et leur rapports avec la phylogenie. Compt. Rend. Acad. Sci. Paris **221:** 113–115. 1945.

OZENDA, P. Sur l'anatomie libéroligneuse des Schizandracées. Compt. Rend. Acad. Sci. Paris **223:** 207–209. 1946.

REHDER, A. *Schisandra* Michaux, nomen genericum conservandum. Jour. Arnold Arb. **25:** 129–131. 1944.

SMITH, A. C. The families Illiciaceae and Schisandraceae. Sargentia **7:** 1–224. 1947. [A comprehensive monograph.]

WHITAKER, T. W. Chromosome number and relationship in the Magnoliales. Jour. Arnold Arb. **14:** 376–385. 1933. [Includes *Schisandra.*]

ZAKORDONETS', A. I. Propagation of *Schisandra chinensis* with green cuttings. (In Ukrainian; Russian summary.) Bot. Zhur. Kyiv **12:** 44–50. 1955.*

CANELLACEAE (WILD CINNAMON FAMILY)

A small family of disjunct distribution with five genera of the West Indies, Venezuela, Brazil, East Africa, and Madagascar. The family is notable for the combination of alternate, exstipulate leaves vascularized by 3 traces from 3 gaps, ethereal oil cells throughout the plant, wood with a number of primitive anatomical features, 3 sepals, 4–12 petals in one or more whorls, a monadelphous androecium forming a tube around the ovary with the anthers extrorse, a single pistil with 2–6 parietal placentae, and monocolpate pollen. Although placed in the Parietales in the Englerian system, the relationships to the woody Ranales have been pointed out a number of times. Within that group an affinity to Myristicaceae has been suggested by several investigators. The family has also been placed by itself in the order Canellales near the Laurales (here included in the woody Ranales).

REFERENCES:

BONNET, E. Essai d'une monographie des Canellées. Paris. 64 pp. 1876. [Treats Canellaceae as a tribe of Magnoliaceae.]

CRONQUIST, A. Outline of a new system of families and orders of dicotyledons. Bull. Jard. Bot. Bruxelles **27**: 13–40. 1957. [Canellales.]

GARRATT, G. A. Bearing of wood anatomy on the relationships of the Myristicaceae. Trop. Woods **36**: 20–44. 1933. [Includes Canellaceae.]

LEMESLE, R. Nouvelles remarques histologiques, microchimiques et phylogénétiques sur la famille des Canellacées. Revue Gén. Bot. **58**: 193–201. 1951.

MIERS, J. On the Canellaceae. Ann. Nat. Hist. III. **1**: 349. 1858. [Notes similarities of Canellaceae to *Drimys* and to *Illicium*!]

OCCHIONI, P. Nota sôbre a biologia das Canelaceas brasileiras. Arq. Jard. Bot. Rio de Janeiro **8**: 275–279. 1948. [Density and abundance of *Cinnamodendron* regulated by the simultaneous action of a seed-attacking fly and a fruit-eating bird.]

PRITZEL, E. Der systematische Wert der Samenanatomie, insbesondere des Endosperms, bei den Parietales. Bot. Jahrb. **24**: 348–394. 1898. [Canellaceae, 371.]

SOLEREDER, H. Systematische Anatomie der Dicotyledonen. 97–99. Stuttgart, 1899.

TIEGHEM, P. VAN. Sur les Canellacées. Jour. Bot. (Morot) **13**: 266–276. 1899.

VANDER WYK, R., AND J. E. CANRIGHT. The anatomy and relationships of the Annonaceae. Trop. Woods **104**: 1–24. 1956. [Includes stem and wood anatomy of Canellaceae.]

VESTAL, P. A. The significance of comparative anatamy in establishing the relationship of the Hypericaceae to the Guttiferae and their allies. Philipp. Jour. Sci. **64**: 199–256. 1937. [Canellaceae, 224, 225, 241, 242.]

WARBURG, O. Winteranaceae (Canellaceae). Nat. Pflanzenfam. III(6): 314–319. Nachträge 251, 252. 1895–1897.

1. **Canella** P. Br. Hist. Jamaica 275. *pl. 27. fig. 3.* 1756; Swartz, Trans. Linn. Soc. **1**: 96. 1791, nom. cons.[1]

Small tree, to 8–10 m. with gray bark and obovate to oblanceolate, rounded or emarginate, deep green, lustrous, evergreen leaves. Flowers small, perfect, regular, in terminal and axillary cymose inflorescences. Sepals 3, imbricate, persistent, the petals 5, deep red, connate at the base. Stamens 10, completely united in a tube with the 10 linear extrorse anthers on its outer surface below the summit. Ovary superior, 1-locular with 2 parietal placentae and about 4 semi-anatropous ovules, the stigma 2–3 lobed. Fruit berry-like, red, with 2–4 shining black seeds. Embryo small with a large amount of endosperm. Pollen monocolpate. (*Winterana* L., 1759, nom. rejic.) TYPE SPECIES: *Canella alba* Murr. (= *C. Winterana* (L.) Gaertn.). (Name from Low Latin, *canella*, cinnamon, from Latin,

[1] Conservation unnecessary.

canna, a cane or reed, applied to the bark which assumed the form of a roll or quill in drying, the name given by Browne to the West Indian plant "the *Canella alba* of the shops.") — WILD CINNAMON, CINNAMON-BARK.

Probably a single species wide-ranging in the West Indies and with outlying stations in northern South America and in the region of Cape Sable and the Florida Keys, in subtropical Florida, where the plant occurs in hammocks with other tropical genera, generally in the shade of larger trees.

Oil cells are conspicuous in most parts of the plant and the pale inner bark has a cinnamon-like odor. It has been used as a spice, stimulant and tonic. The wood is hard and very dense. The maroon flowers, glaucous on the outside, are borne primarily in June and July (January?) and the crimson fruit matures from March to April. The ripe fruit is eaten by birds which probably disperse the plant. It is cultivated as an ornamental to a limited degree.

The stamens are so closely united that the 10 anthers appear to be a ring of 20 close-packed anther-sacs, each splitting longitudinally. However, ten vascular bundles are present in the tube composed of the filaments.

The genus stands apart in the family by the 10 stamens and the 5 petals coherent only at the base.

REFERENCES:

GREENISH, H. G. Canella bark, a study of its structure. Pharm. Jour. III. **24**: 793–797. 1894.*

PLANCHON, G. Note sur la structure des écorces qui portent dans le commerce le nom de Canelles. Bull. Soc. Bot. France **20**(Session extraord.): xlvi–xlvii. 1873.

SARGENT, C. S. *Canella*. Silva N. Am. **1**: 35–38. 1891; **14**: 97. 1902.

SUDWORTH, G. B. On legitimate authorship of certain binomials with other notes on nomenclature. Bull. Torrey Bot. Club **20**: 40–46. 1893. [*Canella Winterana* vs. *C. alba*]

SWARTZ, O. The botanical history of the *Canella alba*. Trans. Linn. Soc. **1**: 96–102. 1791.

CALYCANTHACEAE (CALYCANTHUS FAMILY).

Shrubs with opposite, entire, exstipulate leaves, numerous strap-shaped tepals spirally arranged on a cup-shaped receptacle, the stamens at its apex and extrorse and the carpels numerous, free, on the inner surface of the receptacle, the mature receptacle resembling a large, dry rose-hip; embryo large, the cotyledons convolute, endosperm lacking.

A small family of disjunct distribution including only two very similar genera (sometimes combined): *Calycanthus* L. (about 4 species of the eastern and western U. S.) and *Chimonanthus* Lindl. (2 or 3 species of China).

The group is notable not only for its odd floral structure (highly modified receptacle and numerous free tepals, stamens and carpels) but for a number of anatomical features, including ethereal oil cells, dicolpate pollen (a modification of the monocolpate type), unilacunar nodes with a fundamentally double trace from a single gap, and 4 cortical vascular bundles (with inverted orientation of xylem and phloem) which extend throughout the stems of mature plants and which have branches entering the leaves at the nodes.

Although some authors have placed the family in the Rosales, the total evidence available clearly indicates that its relationships are with the Ranales, especially that group of families characterized by monocolpate and derived types of pollen and double-trace unilacunar nodes (or unilacunar modifications): Austrobaileyaceae, Amborellaceae, Trimeniaceae, Monimiaceae, Gomortegaceae, Lauraceae, Hernandiaceae, Chloranthaceae, and Lactoridaceae. Its closest relationships are probably with the Monimiaceae, a tropical group, chiefly of the southern hemisphere.

1. **Calycanthus** L. Syst. Nat. ed. 10. 2: 1066. 1759, nom. cons.

Deciduous shrubs with opposite, entire, exstipulate leaves and red-brown, purple-brown or greenish solitary flowers terminal on short, leafy axillary branches of the season. Receptacle cup-shaped, bearing on its outer surface and apex bracts and numerous undifferentiated strap-shaped, free, rather fleshy tepals. Stamens numerous, on the edge of the receptacle, with stout filaments, the apex of the connective prolonged, succulent, the anthers extrorse; inner stamens reduced to staminodia; pollen 2-colpate. Gynoecium of numerous free carpels within the receptacle; style filiform, stigma terminal, the ovary 1-celled with 2 anatropous, 2-integumented ovules. Fruit an indehiscent pseudocarp from the accrescent receptacle and tepal-bases, somewhat resembling a large dry rose-hip, bearing within it the numerous large achenes with tough exocarp. Seed solitary, large, lacking endosperm, the embryo large, with convolute cotyledons. $2n = 22$. (*Butneria* Duham., 1755, nom. rejic.) TYPE SPECIES: *C. floridus* L. (The name from Greek, *calyx*, a cup, and *anthos*, flower.) — STRAWBERRY BUSH, SWEET-SHRUB, BUBBY BLOSSOM, SWEET BUBBY, SWEET BETTIE, SPICEBUSH.

Perhaps three species of the eastern United States and a single well marked, less closely related species, *C. occidentalis* Hook. & Arn., of the North Coast Ranges and Sierra Nevada foothills of California. The 2 or 3 species of the Asiatic *Chimonanthus,* in which the number of stamens is reduced to five, are sometimes included in *Calycanthus* as a separate section. *Calycanthus fertilis* Walt., *C. floridus* L., and *C. Mohrii* (Small) Pollard are generally recognized in our area, but the range of variation and the true limits of the species are not well understood. Fruit characteristics have been little used but may provide good taxonomic characters.

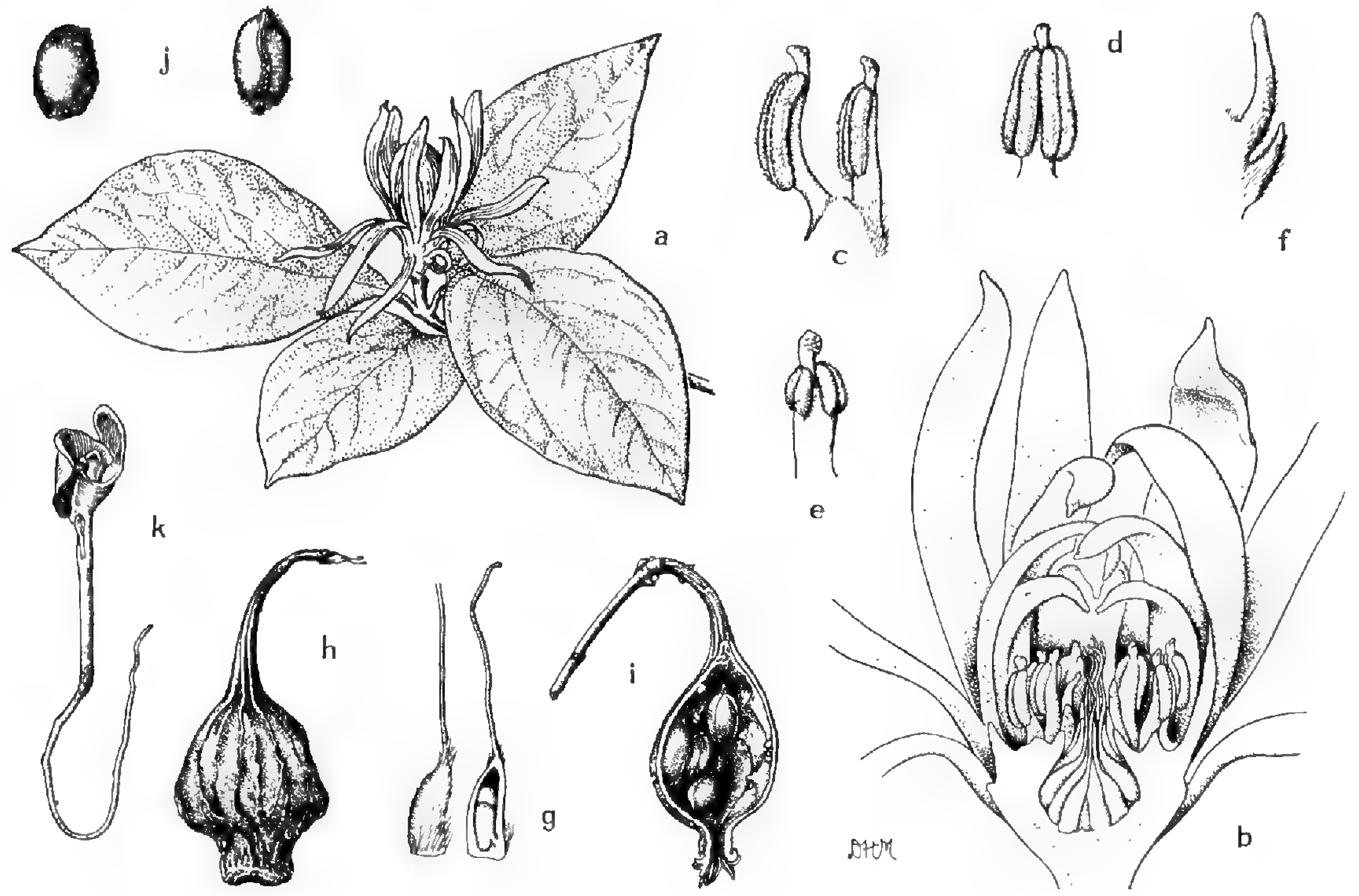


FIG. 3. **Calycanthus.** a–h, *C. floridus*: a, flowering branchlet, × 1/2; b, flower, vertical section, to show carpels, stamens, staminodia, and cup-shaped "receptacle," × 2; c, two stamens, lateral view, × 5; d, stamen, abaxial view, × 5; e, inner, reduced stamen, abaxial view, × 5; f, two staminodia from edge of cup, lateral view, × 5; g, carpels, × 5; h, mature dry pendulous pseudocarp, × 1/2; b, g, semi-diagrammatic. i–k, *C. fertilis*: i, pseudocarp, vertical section, with mature carpels, some removed, × 1/2; j, mature carpels, lateral and abaxial views, × 1; k, seedling with unfurling cotyledons, × 1/2.

Agamospermy (which may account for some of the taxonomic difficulties) has been reported in *Calycanthus fertilis, C. floridus, C. occidentalis* and *Chimonanthus praecox.* Embryos seem to be of nucellar origin, although parthenogenesis has been claimed for the same species. Pseudogamy appears to be the rule, pollination being necessary for the development of the endosperm, without which the embryo does not grow. *Calycanthus floridus* var. *ovatus* (Ait.) DC., presumably of garden origin, has been reported to be a triploid ($2n = 33$), with about 50 per cent sterile pollen.

The flowers are proterogynous. Pollination in *Calycanthus occidentalis* has been shown to occur through the agency of *Colopterus truncatus* (Randall), a small nitidulid beetle.

Ethereal oil cells occur especially in bark, leaves, and tepals. The flowers are quite variable in fragrance but some forms have an extremely pleasant spicy, strawberry-like odor when crushed. The seeds contain an alkaloid, calycanthine, with a physiological action similar to strychnine; poisoning of cattle and sheep eating the fruits has been reported in Tennessee.

References:

Brofferio, I. Osservazioni sulla sviluppo delle Calycanthaceae. Ann. Bot. Roma **18:** 387–394. 1930. [Pseudogamy, nucellar embryos.]

Boureau, E. L'evolution vasculaire du *Calycanthus floridus* L. (actuel: Calycanthacées) et l'explication du système vasculaire du *Zygopteris lacatti* B. R. (filicale palaeozoique; zygopteridées). Bull. Mus. Hist. Nat. Paris II. **18:** 440–447. 1946.

Cheadle, V. I., and K. Esau. Secondary phloem of Calycanthaceae. Univ. Calif. Publ. Bot. **29:** 397–510. 1958. [*C. floridus, C. occidentalis, Chimonanthus praecox.*]

Daumann, E. Das Blütennektarium von *Magnolia* und die Fütterkorper in der Blüte von *Calycanthus.* Planta **11:** 108–116. 1930. [*C. floridus.*]

Diels, L. Käferblumen bei den Ranales und ihre Bedeutung für die Phylogenie der Angiospermen. Ber. Deutsch. Bot. Ges. **34:** 758–774. 1916. [Beetle pollination in *Eupomatia* and *C. occidentalis.*]

Fahn, A., and I. W. Bailey. The nodal anatomy and the primary vascular cylinder of the Calycanthaceae. Jour. Arnold Arb. **38:** 107–117. 1957.

Grant, V. The pollination of *Calycanthus occidentalis.* Am. Jour. Bot. **37:** 294–297. 1950.

Kearney, T. H., Jr. The nomenclature of the genus *Büttneria* Duham. Bull. Torrey Bot. Club. **21:** 173–175. 1894.

Lignier, O. Recherches sur les massifs libéro-ligneux de la tige des Calycanthées. Bull. Soc. Bot. France **31:** 128–132. 1884.

———. Sur la valeur morphologique des massifs libéro-ligneux corticaux des tiges des Calycanthées. Compt. Rend. Acad. Sci. Paris **98:** 700–702. 1884.

———. Recherches sur l'anatomie comparée des Calycanthées, des Melastomacées et des Myrtacées. Arch. Bot. Nord France **3:** 1–455. 1886–1887.

Plouvier, V. Contribution à l'étude biochimique de quelques Calycanthacées, Magnoliacées et Rosacées. (Summary.) Ann. Sci. Nat. XI. **7:** 237–238. 1947.

Pollard, C. L. Calycanthaceae. N. Am. Fl. **22:** 237–238. 1908.

Quinlan, C. E. Contributions toward a knowledge of the anatomy of the lower dicotyledons. III. The anatomy of the stem of the Calycanthaceae. Trans. Roy. Soc. Edinb. **52:** 517–530. 1920.

Ramaley, F. Seedlings of certain woody plants. Minn. Bot. Stud. **2:** 69–86. 1899. [*C. floridus,* 72–73.]

———. Comparative anatomy of hypocotyl and epicotyl in woody plants. Loc. cit. **2:** 87–136. [*C. floridus,* 100–102.]

Sax, K. Chromosome behavior in *Calycanthus.* Jour. Arnold Arb. **14:** 279–281. 1933. [Undocumented counts of *C. fertilis, C. floridus, C. floridus* var. *ovatus.*]

Schaeppi, H. Morphologische Untersuchungen an den Karpellen der Calycanthaceae. Phytomorphology **3:** 112–118. 1953. [Carpel conduplicate, 3-veined; *C. floridus, Chimonanthus praecox.*]

Schürhoff, P. N. Zur Apogamie von *Calycanthus.* Flora **116:** 73–84. 1923. [Parthenogenesis.]

Smith, G. H. Vascular anatomy of Ranalian flowers, — II. Ranunculaceae (continued), Menispermaceae, Calycanthaceae, Annonaceae. Bot. Gaz. **85:** 152–177. 1928. [*Calycanthus floridus.*]

Sterns, E. E. The fruit of *Calycanthus,* L. Bull. Torrey Bot. Club **15:** 205–209. 1888. [*C. fertilis,* eastern Tenn.]

WILLIAMS, J. L. The sieve-tubes of *Calycanthus occidentalis*. Ann. Bot. 8: 367–370. 1894.

LAURACEAE (LAUREL FAMILY)

Evergreen (mostly) or deciduous trees or shrubs with alternate [or sometimes opposite or subopposite], exstipulate, entire or rarely lobed, pinnately veined, subtripli-veined [tripli-veined or 3-veined] leaves, (except *Cassytha*, a greatly reduced parasite resembling *Cuscuta*); wood and leaves usually with ethereal oil cells and often with mucilage cells. Inflorescences usually axillary, basically cymose, paniculate or reduced and sub-umbellate, racemose, spicate [or capitate]. Flowers bisexual or unisexual (the plants then dioecious or polygamo-dioecious), small, regular, generally whitish or yellowish, often hairy. Perianth regular, of 6 tepals in 2 whorls of 3, similar or the outer smaller, free nearly to the base or ± united to form a perianth tube on which the stamens are inserted. Stamens basically 12, in 4 series of 3, the outermost (series I) opposite the outer whorl of tepals, the succeeding series alternating; any one or more series (in all our genera) reduced to staminodia or altogether lacking and the filaments of one (series III) or more series of fertile stamens flanked by stalked or sessile "glands." Anthers 4- or 2-locular, introrse or extrorse, upwardly dehiscent by 4 or 2 flap-like valves; pollen sticky, the contents of each locule raised upward by the valve, grains non-aperturate, single. Pistil 1, with a single stigma and style and a 1-locular ovary with a single pendulous, anatropous, 2-integumented ovule; ovary free from the perianth tube, although sometimes ± surrounded by it. Fruit a berry or drupe; perianth lobes persistent [often accrescent] or deciduous in fruit, the perianth tube and pedicel often greatly enlarged to form a cupule subtending the fruit, in a few (e.g., *Cassytha*) the perianth tube completely surrounding the fruit but free from it. Seed lacking endosperm, the embryo large with fleshy plano-convex cotyledons, a small plumule and radicle; germination usually hypogeal. (Including Cassythaceae.)

A family of perhaps 30–40 genera and about 2500 species, mostly evergreen and primarily of the tropics and warm-temperate areas of both hemispheres, especially Central and South America and southern Asia. Represented with us by about 11 native and 2 more or less naturalized species in 8 genera.

The family is easily recognized by the small, regular, usually 3-merous flowers with their curious 4- or 2-locular stamens dehiscent by as many flap-like valves, the 1-locular ovary with a single pendulous anatropous ovule, the baccate fruit often subtended by a cupule derived from the accrescent perianth tube, and the large embryo without endosperm. Equally well characterized by a unique combination of anatomical characters, the Lauraceae seem to form a well-marked and natural family.

The relationships of the Lauraceae seem to be with that group of the woody Ranales (sensu lato) which have secretory cells, unilacunar nodes and monocolpate, dicolpate or derived (in this case non-aperturate) pollen grains. The relationships are particularly with Monimiaceae (cf. subfam. Hortonoideae, Atherospermoideae), Hernandiaceae, and Gomortegaceae (note woody habit, non-aperturate pollen grains, stamens with associated staminodes, valvular anthers, unilacunar nodes, simple and exstipulate leaves, related alkaloids).

Although the family is a natural one, the generic (and specific) lines are very difficult in some groups of Lauraceae and may be artificial in many instances. Convergent tendencies may be noted again and again. Strong emphasis has been placed upon the various permutations and combinations possible within the 4 series of stamens and staminodes and upon the 4- vs. 2-locular condition of the anthers (although both of the latter are known to occur within some undoubtedly related groups, e.g., *Cinnamomum, Sassafras*). Other important characteristics include inflorescence-type and the development of the perianth tube and lobes and their condition in fruit (persistent, deciduous, cupules, etc.). Patterns of leaf-venation and cuticle may be useful at the specific level but may vary widely within related groups and similar patterns may occur in completely unrelated species. (As a result, generic determinations of fossil materials based on vegetative characteristics are, at best, dubious.)

The four trimerous whorls of stamens in the basic lauraceous flower are designated here as series I–IV (cf. Mez), beginning with the outermost whorl which is opposite the outer tepals. The stamens of series III are usually flanked by nectaries (most often stalked and vascularized) which seem to be staminodial in origin. Series IV, if present at all, is usually staminodial.

Perfect flowers throughout the family probably are proterogynous, although observations from living plants seem to have been made only on two species of *Persea*, in which proterogyny is carried to an extreme (dianthesis). Stamens appear to elongate between the time the stigma is receptive and that at which the pollen is shed. The anther valves open from the base upward, recurving and carrying with them the entire contents of the locules.

Only a few species have been examined cytologically, but in these 12 is the basic chromosome number.

REFERENCES:

ALLEN, C. K. Studies in the Lauraceae, VI. Preliminary survey of the Mexican and Central American species. Jour. Arnold Arb. **26**: 280–364, 365–434. 1945. [Much information pertaining to our genera. See also loc. cit. **20, 22, 23**: 1939, 1941, 1942 for II–V dealing with Asiatic genera.]

———. Lauraceae *in* Woodson & Schery, Flora of Panama. Ann. Missouri Bot. Gard. **35**. 1–68. 1948.

BANDULSKA, H. On the cuticles of some fossil and recent Lauraceae. Jour. Linn. Soc. **47**: 383–425. 1925.

JANSSONIUS, H. H. Mucilage cells and oil cells in the woods of the Lauraceae. Trop. Woods **6**: 3–4. 1926.

———. De Slijm- en Oliecellen in het hout der Lauraceae in verband met de zienswijze van Tschirch. Pharm. Weekbl. **39:** 1053–1055. 1927.*

KOSTERMANS, A. J. G. H. Studies in South American Malpighiaceae, Lauraceae and Hernandiaceae, especially of Surinam. Meded. Bot. Mus. Utrecht **25:** 1–70. 1936.

———. Revision of the Lauraceae I. Rec. Trav. Bot. Néerl. **33:** 719–757. 1936. [*Acrodiclidium.*] II. **34:** 500–609. 1937. [Includes *Endlicheria, Cryptocarya* (American spp.), *Licaria.*] III. **35:** 56–129. 1938. [*Aiouea, Systemonodaphne, Urbanodendron, Mezilaurus*; notes on *Licaria, Cryptocarya.*] V. **35:** 834–931. 1938. [*Anaueria, Beilschmiedia* (American spp.), *Aniba.*] (Reprinted as Meded. Bot. Mus. Utrecht **37, 42, 46, 48** [1937–1938], respectively.)

———. Las Lauraceas Chilenas. Revista Univ. [Chile] **24:** 201–232. 1939. [Apparently Rev. Lauraceae IV.]

———. A historical survey of the Lauraceae. Jour. Sci. Indus. Res. Indonesia **1:** 83–95, 113–127, 141–159. 1952. [Chronological account including taxonomic notes.]

———. Lauraceae. Inst. Paranaense Bot. Cat. Est. Gen. Bôt. Fan. **34:** 1–4. 1957. [List of genera and synonyms, estimate of no. of spp.]

———. Lauraceae. Reinwardtia **4:** 193–256. 1957. (First publ. as Comm. Forest Res. Inst. Indonesia **57:** 22 Mar. 1957.*) [Review of family, incl. stem, leaf, wood, inflorescences, flower, fruit, pollen, pollination, myrmecophily, chromosomes, palaeontology, relationships, distribution, size of genera, classification, key to genera, brief descriptions of genera and synonymy.]

MEZ, C. Morphologische Studien über die Familie der Lauraceen. Thesis, 32 pp. Berlin, 1888.

———. Lauraceae Americanae. Jahrb. Königl. Bot. Gart. Berlin **5:** 1–556. 1889. [The basic framework for American studies; attention focused on inflorescence.]

———. Spicilegium Laureanum. I. Versuch einer pflanzengeographischen Anordnung der tropisch-amerikanischen Lauraceen. [Survey of distribution of American Lauraceae, pp. 71–105.] II. Zusätze zu meiner Monographie der amerikanischen Lauraceen im Jahrbuch des Berliner Gartens Vol. V. Arbeit. Königl. Bot. Gart. **1:** 71–166. 1892.

MIRANDE, M. Sur l'origine pluricarpellaire du pistil des Lauracées. Compt. Rend. Acad. Sci. Paris **145:** 570–572. 1907. [*Cassytha* and others; pistil basically 3-carpellate.]

MONEY, L. L., I. W. BAILEY, AND B. G. L. SWAMY. The morphology and relationships of the Monimiaceae. Jour. Arnold Arb. **31:** 372–404. 1950.

NEES VON ESENBECK, C. G. Systema Laurinum. 704 pp. Berlin, 1836. [The basic monograph.]

OHTANI, F. Über den Bau des Blattrandes bei Myrtaceen, Hamamelidaceen, Lauraceen, und Monimiaceen. Festschr. A. Tschirch. 299. 1926.* [See JUST, Bot. Jahresb. **54**(2): 456. 1926.]

PAX, F. Lauraceae. Nat. Pflanzenfam. III(2): 106–126. 1891. [Artificial classification.]

PETZOLD, V. Systematische-anatomische Untersuchungen über die Laubblätter der amerikanischen Lauraceen. Bot. Jahrb. **38:** 445–474. 1907.

RECORD, S. J. AND R. W. HESS. American timbers of the family Lauraceae. Trop. Woods **69**: 7–33. 1942.

SASTRI, R. L. N. Studies in Lauraceae. II. Proc. Indian Sci. Congr. Assoc. **42**(3, abs.): 225–226. 1925.* [Morphology.]

STERN, W. L. Comparative anatomy of xylem and phylogeny of Lauraceae. Trop. Woods **100**: 1–72. 1954. [Includes a general review of position of family; extensive bibliography.]

TUPPER, W. W. A comparative study of the lauraceous woods. Am. Jour. Bot. **14**: 520–525. 1927.

KEY TO THE GENERA OF LAURACEAE

A. Foliose trees and shrubs; not parasitic. Subfam. LAUROIDEAE.
  B. Plants evergreen; inflorescences variously cymose-paniculate, with no involucre at the base; flowers bisexual; anthers of at least one series of stamens (III) extrorse. Tribe PERSEEAE.
    C. Anthers 4-loculed; fertile stamens 9, the 2 outer series introrse; fruits without cupules or the cupules without evident double margins.
      D. Staminodia of series IV large, cordate-stipitate; locules of anthers of 2 outer series in 2 planes, one above the other.
        E. Fruit without a cupule at the base, the not greatly enlarged perianth persistent (or sometimes completely deciduous); leaves pinnately veined, lacking glands in the axils of the main veins beneath; perianth lobes unequal to subequal. . . 1. *Persea.*
        E. Fruit with a shallow cupule at the base, the perianth lobes deciduous from the enlarged tube; leaves pinnately or subtripliveined, with conspicuous glands in the axils of the main veins beneath; perianth lobes equal. . . . . 2. *Cinnamomum.*
      D. Staminodia of series IV small, inconspicuous, stipiform; locules of anthers of 2 outer series arranged in an arc. . . . . 3. *Nectandra.*
    C. Anthers 2-loculed; fertile stamens only 3, extrorse; fruits subtended by thick cupules with evident double margins. . . . . 4. *Licaria.*
  B. Plants deciduous, the small yellow flowers produced before or with the unfolding leaves; inflorescences racemose or sub-umbellate in the axils of enlarged bud-scales (*Sassafras*) or with an evident involucre of scales at the base; flowers usually unisexual; fertile stamens 9, the anthers of all series introrse. Tribe LITSEEAE.
    F. Inflorescences racemose, at the tips of branches, subtended by the enlarged, involucre-like bud-scales; leaves unlobed or with 2 or 3 lobes; fruit a dark blue drupe on a swollen red cupule; anthers 4-loculed; shrubs or trees. . . . . 5. *Sassafras.*
    F. Inflorescences sub-umbellate, involucrate with 4 or 5 decussate scales; fruits bright red on unswollen or slightly swollen pedicels; shrubs.
      G. Anthers 2-loculed; inflorescences nearly sessile; branchlets not evidently zig-zag. . . . . 6. *Lindera*
      G. Anthers 4-loculed; inflorescences clearly pedicellate; branchlets zig-zag. . . . . 7. *Litsea.*
A. Parasitic orange to green twining herbs of tropical Florida; leaves reduced to scales; anthers 2-loculed; fruit surrounded by the persistent fleshy perianth tube. Subfam. CASSYTHOIDEAE. . . . . 8. *Cassytha.*

Subfam. LAUROIDEAE Kosterm.

Tribe PERSEEAE Mez

1. **Persea** Miller, Gard. Dict. Abr. ed. 4. 1754, nom. cons.[1]

Evergreen trees and shrubs with chartaceous to coriaceous pinnately veined (usually more or less pubescent) leaves. Inflorescences axillary, peduncled, cymose or rarely sub-umbellate (usually described as paniculate but in ours small, with the exception of *P. americana*). Flowers bisexual, small. Perianth lobes 6, free nearly to the base, the 3 outer ones usually shorter than the inner ones, hairy and persistent in fruit. Fertile stamens 9, staminodia 3; stamen filaments slender, hairy, the anthers 4-loculed, the bases of the 2 upper locules laterally tangential to the apices of the 2 lower; stamens of series I & II introrse; stamens of series III extrorse (or the 2 upper locules lateral and the lower extrorse), the filaments flanked by 2 glands near the base; series IV sterile, the staminodia stipitate with cordate-sagittate tips. Ovary subglobose, the style slender, usually pubescent. Fruit baccate, small and globose or [in *P. americana* and relatives] large and fleshy and obovoid to pyriform (often obliquely so), borne on the spreading perianth-lobes and scarcely enlarged pedicel; [perianth lobes occasionally deciduous in fruit in some forms of *P. americana*]. (*Farnesia* Heist., 1763, nom. rejic.; incl. *Tamala* Raf.) TYPE SPECIES: *Laurus Persea* L. = *P. americana* Miller. (The name an ancient one used by Theophrastus, transferred by Plumier to one of the tropical American species of *Nectandra* and afterward adopted by Linnaeus.)

As usually delimited, a genus primarily of tropical America but reaching south to Chile and northward in our area to Delaware and Arkansas and with a single species *P. indica* (L.) Spreng., in the Canary Islands. Two or three native species occur in our area; *P. americana,* in general cultivation throughout tropical America and an important crop in southern Florida, persists after cultivation and has escaped to hammocks. Kostermans has extended the limits of *Persea* to include a number of Asiatic genera.

Persea Borbonia (L.) Spreng., the red bay, is a handsome tree of the borders of streams and swamps and "bayheads," ranging from Florida to Texas, northward to southern Arkansas and Delaware. A variant, *Persea palustris* (Raf.) Sarg., distinguished primarily on the basis of pubescence is currently treated as f. *pubescens* (Pursh) Fern. ($2n = 24$). A third plant, *P. littoralis* Small, of coastal dunes of Florida, is a small tree with small leaves mostly obtuse at the apex and smooth beneath. The variation in this group is in need of further study. *Persea humilis* Nash, scrub bay, is a distinctive shrub or small tree of the *Pinus clausa–Ceratiola* "scrub" of central Florida. Its habit and habitat, reduced inflorescences, somewhat larger fruits, and small leaves silky with shining golden hairs beneath, are characteristic.

---

[1] Conservation unnecessary.

The avocado, *Persea americana* ($2n = 24$) introduced into Florida at an early date by the Spaniards and long casually cultivated there, has become an increasingly important fruit crop in southern Florida in the last 40 years. Commercial plantations are concentrated especially in Dade County (about 4/5 of the total crop) but extend about as far north as Cape Canaveral, on the east coast, and Tampa, on the west. Scattered trees of the hardier cultivars may be found considerably farther north, however. A large technical and horticultural literature including much of the information available on the genus has accumulated in connection with the cultivation of this species.

Persea americana is a complex species of very wide distribution in cultivation in tropical America. Its origin presumably lies in Central America and involves the group composed of *P. americana,* its var. *drymifolia* (Schlecht. & Cham.) Blake, *P. Schiedeana* Nees, *P. floccosa* Mez, *P. nubigena* L. O. Williams, and others, all of the uplands of this region. At the present time three general groups of cultivars are recognized: West Indian (originally introduced there from Central America by the Spaniards), Guatemalan, and Mexican. The three groups differ in characters of foliage, fruit, time of flowering and ripening of fruits, and hardiness. *Persea americana* var. *drymifolia,* of the Mexican uplands, is most intimately involved in the Mexican cultivars which are the important commercial types in California but which are not well adapted to the conditions of tropical Florida, where Guatemalan and West Indian forms grow best. In recent years hybrids between members of the three groups have been made and some of these are quite successful (e.g., the 'BOOTH' cultivars, 'HICKSON,' and 'LULA').

The flowers of avocados are proterogynous and have two periods of opening on successive days (dianthesis), the flowers closing in between. "A" and "B" types are recognized. In the former the stigmas are receptive in the morning; the flowers close by early afternoon to re-open the following afternoon when the pollen is shed. In type "B" cultivars, the first (pistillate) opening occurs in the afternoon and the second the following morning. All of the flowers open on a tree at a given time will be in the same stage: thus self-pollination is virtually impossible and both "A" and "B" cultivars are necessary for cross-pollination, an important consideration in the planting of commercial groves. In a sub-type of the "B" form the first period opening is mostly suppressed, with only a few flowers open in the afternoon and most having only a single fairly long period of opening in the morning when the stigmas appear to be receptive and the pollen is shed. Such trees set very few fruit. Beyond this species, observations on pollination appear to have been made only on *P. Skutchii* C. Allen, of Costa Rica and Panama, which also shows dianthesis with equal numbers of "A" and "B" plants but with the two periods of anthesis between dawn and late-morning (10–11 A.M.) and late-morning and early afternoon (2–3 P.M.) on successive days.[2]

---

[2] Since the above was written, it has been possible through the kind hospitality of Mr. and Mrs. George R. Cooley for Dr. K. A. Wilson and the author to make some

Persea is generally considered to be most closely related to *Phoebe* Nees, a large genus of the tropics of both hemispheres. These genera are conventionally differentiated on the basis of position of anther-locules and nature of the perianth in fruit. Kostermans would reject the former as a generic criterion and would restrict Asiatic *Phoebe* to those species with an appressed and indurated perianth. The New World species might be retained partly in *Phoebe* or assigned to *Persea* and perhaps *Cinnamomum*. The same author greatly extends the limits of *Persea* to include the Asiatic genera *Machilus* Nees, *Nothaphoebe* Blume, *Alseodaphne* Nees, *Stemmatodaphne* Gamble, and *Caryodaphnopsis* Airy-Shaw, the first three of which would be retained as subgenera.

REFERENCES:

ABRAMSKY, M., AND J. B. BIALE. The pyruvate oxidation system in avocado fruit particles. (Abs.) Pl. Physiol. **30** (sup.): xxviii–xxix. 1955.

ANDERSON, E. Variation in avocados at the Rodiles Plantation. Ceiba **1**: 50–55. 1950. [Near Atlixco, Puebla, Mexico; scatter diagram of variation in leaf-characters in 132 trees.]

BLAKE, S. F. A preliminary revision of the North American and West Indian avocados (*Persea* spp.). Jour. Wash. Acad. **10**: 9–21. 1920.

BRINGHURST, R. S. Sexual reproduction problems of the avocado. Citrus Leaves 32(11): 26–28. 1952.*

———. Breeding tetraploid avocados. Proc. Am. Soc. Hort. Sci. **67**: 251–257. 1956.* [Colchicine; see also Genetics **41**: 646. 1956.]

BURGIS, D. S. AND H. S. WOLFE. Do avocado roots develop root-hairs? Proc. Fla. State Hort. Soc. (1945) **58**: 197–198. 1946.*

COLLINS, G. N. The avocado, a salad fruit from the tropics. U. S. Dept. Agr. Pl. Ind. Bull. **77**: 1–52. 1905.

CUMMINGS, K., AND C. A. SCHROEDER. Anatomy of the avocado fruit. Calif. Avocado Soc. Yearb. **27**: 56–64. 1942.*

FAIRCHILD, D. Two relatives of the avocado and their reintroduction into Florida. Proc. Fla. State Hort. Soc. (1945) **58**: 170–175. 1946. [*P. Schiedeana* and *Hufelandia Anay*.]

FERNALD, M. L. Botanical specialties of the Seward Forest and adjacent areas

---

preliminary observations on dianthesis in *Persea Borbonia* and f. *pubescens* near Brooksville, Hernando County, Florida. Four plants (one the glabrous form and three the pubescent) which began to flower in late April were observed on several days then and in early May 1958. As in *Persea americana* and *P. Skutchii*, dianthesis occurred, with both "A" and "B" types being represented (two of each), but, in contrast to these species, the two periods of anthesis occur in the afternoon. Each of the four plants held to a slightly different schedule, but the first afternoon period commenced about noon and ended between 3 and 4:30 P.M. (Eastern Standard Time). The other period of opening occurred between about 3:30 and 4:45, these flowers remaining open until dark (about 7:30) or after, but those of three plants closing before 8 and those of the fourth before 8:30. Flowers in the staminate (second) anthesis are noticeably less rapid in their final closing response, and a few on "B" plants may overlap the opening of new flowers in the pistillate (first) anthesis. Several large wasps and flies were observed visiting the flowers, along with minute flies, small beetles and ants, all apparently collecting nectar. Plants of *Persea humilis* seen at 3 P.M. in Highlands County, Florida, on May 4, 1958, showed only closed flowers, but branches of one of these (of the "B" type) placed in a polyethylene bag showed later that afternoon and the following day periods of anthesis which appeared to correspond roughly to those of *P. Borbonia*.

of southeastern Virginia. Rhodora **47**: 93–142, 149–182, 191–204. 1945. [Discussion of status of *P. Borbonia* and f. *pubescens*, 149–151.]

HAAS, A. R. C. Growth and water relations of the avocado fruit. Pl. Physiol. **11**: 383–400. 1936.

———. Chemical composition of avocado fruits. Jour. Agr. Res. **54**: 669–687. 1937.

HARRIS, J. A., AND W. POPENOE. Freezing-point lowering of the leaf sap of the horticultural types of *Persea americana*. Jour. Agr. Res. **7**: 261–268. 1916.

HOLM, T. The seedlings of *Jatropha multifida* L. and *Persea gratissima* Gärtn. Bot. Gaz. **28**: 60–64. 1899. [*P. americana*.]

HOUSE, H. D. Nomenclatorial notes on certain American plants — II. Am. Midl. Nat. **8**: 61–64. 1922. [Transfers our native species to *Borbonia* Mill. 1754.]

KROME, W. H. Avocado growing in Dade County [Florida]. Ceiba **4**: 339–350. 1956.

LEEMANN, A. Das Problem der Sekretzellen. Planta **6**: 216–233. 1928. [Development of secretory cells in *P. indica*.]

LESLEY, J. W., AND R. S. BRINGHURST. Environmental conditions affecting pollination of avocados. Calif. Avocado Soc. Yearb. **36**: 169–173. 1951.*

LYNCH, S. J., AND R. O. NELSON. Current methods of vegetative propagation of avocado, mango, lychee and guava in Florida. Ceiba **4**: 315–337. 1956.

POPENOE, W. The avocado in Guatemala. U. S. Dept. Agr. Bull. **743**: 1–69. 1919. See also, Avocados as food in Guatemala. Jour. Hered. **9**: 98–107. 1918.

———. Central American fruit culture. Ceiba **1**: 269–367. 1952. [*Persea*, 304–310.] In Spanish, Ceiba **3**: 225–338. 1953 [*Persea*, 267–274.]

PRATT, H. K., R. E. YOUNG AND J. B. BIALE. The identification of ethylene as a volatile product of ripening avocados. Pl. Physiol. **23**: 526–531. 1948.

RABAK, F. Wild volatile-oil plants and their economic importance: I. Black sage; II. Wild sage; III. Swamp bay. U. S. Dept. Agr. Pl. Ind. Bull. **235**: 5–37. 1912. [*P. Borbonia*.]

REECE, P. C. The floral anatomy of the avocado. Am. Jour. Bot. **26**: 429–433. 1939.

———. Differentiation of avocado blossom buds in Florida. Bot. Gaz. **104**: 323–328. 1943.

ROBINSON, T. R. Pollen sterility in the Collinson avocado. Jour. Hered. **21**: 35–38. 1930.

ROLFS, P. H. The avocado in Florida; its propagation, cultivation, and marketing. U. S. Dept. Agr. Bur. Pl. Ind. Bull. **61**: 1–33. 1904.

RYERSON, K. Avocado culture in California. Part I. History, culture, varieties, and marketing. Univ. Calif. Agr. Exp. Sta. Bull. **365**: 1–61. 1924.

SARGENT, C. S. *Persea*. Silva N. Am. **7**: 3–8. *pls. 301, 302*. 1905.

SCHROEDER, C. A. Pollen germination in the avocado. Proc. Am. Soc. Hort. Sci. **41**: 181, 182. 1942.

———. Multiple embryos in the avocado. Jour. Hered. **35**: 209, 210. 1944.

———. The structure of the skin or rind of the avocado. Calif. Avocado Soc. Yearb. **35**: 169–176. 1950.*

———. Flower bud development in the avocado. Calif. Avocado Soc. Yearb. **36**: 159–163. 1951.*

———. Floral development, sporogenesis, and embryology in the development of the avocado, *Persea americana*. Bot. Gaz. **113**: 270–278. 1952.

———. Abnormal fruit types in the avocado. Calif. Avocado Soc. Yearb. **38:** 121–124. 1953/1954.*

———. Proliferation of mature fruit pericarp tissue slices in vitro. Science **122:** 601. 1955. [*P. americana.*]

———. Pollen production in avocado. Calif. Avocado Soc. Yearb. **39:** 184–186. 1955.*

——— AND P. A. WIELAND. Diurnal fluctuation in size in various parts of the avocado tree and fruit. Proc. Am. Soc. Hort. Sci. **68:** 253–258. 1956.

SKUTCH, A. F. Observations on the flower behavior of the avocado in Panama. Torreya **32:** 85–94. 1932. [A, B, and modified B types in a dooryard planting.]

———. The behavior of the flowers of the aguacatillo (*Persea caerulea*). Torreya **45:** 110–116. 1945. [= *P. Skutchii* C. Allen, Costa Rica.]

SMALL, J. K. *Tamala littoralis.* Addisonia **17:** 45–46. *pl. 567.* 1932.

STONEBACK, W. J., AND B. CALVERT. Histology and chemistry of the avocado. Am. Jour. Pharm. **95:** 598–612. 1923.*

STOUT, A. B. The flower mechanism of avocados with reference to pollination and the production of fruit. Jour. N. Y. Bot. Gard. **25:** 1–7. 1924.

———. The pollination of avocados. Florida Agr. Exp. Sta. Bull. **257:** 1–44. 1933.

STURROCK, D. Tropical fruits for southern Florida and Cuba and their uses. Publ. Atkins Inst. Arnold Arb. Harvard Univ. **1:** 1–131. 1940. [*Persea,* 67–71.]

TORRES, J. P. Some notes on avocado flower. Philipp. Jour. Agr. **7:** 207–227. 1936.*

WALLACE, J. M., AND R. J. DRAKE. Albinism and abnormal development of avocado seedlings. Calif. Avocado Soc. Yearb. **40:** 156–164. 1956.*

WOLFE, H. S., L. R. TOY, AND A. L. STAHL. Avocado production in Florida. Florida Agr. Exp. Sta. Bull. **272:** 1–96. 1934.

WOLFE, H. S. Avocado varieties in Florida. Fruit Varieties & Hort. Digest 2(1): 14–17. 1947.*

ZENTMYER, G. A. Diseases of the avocado. U. S. Dept. Agr. Yearb. **1953:** 875–881. 1953.

2. **Cinnamomum** Trew, Herb. Blackwell. Cent. 4, signature M. *t. 354.* 1760; Blume, Bijdr. Fl. Nederl. Indië 568. 1825 [1826].

Evergreen trees with [or without] conspicuous buds with imbricate scales, the alternate [or opposite] leaves pinnately veined, subtripli-veined, [tripli-veined, or 3-veined], with [or without] glands in the axils of the veins beneath. Inflorescences paniculate, axillary, with deciduous bracts, produced on the growth of the season. Flowers small, inconspicuous, bisexual [rarely polygamous]. Tepals equal, [persistent or] deciduous from the perianth tube. Fertile stamens 9, the anthers 4 [rarely 2]-loculed; staminodia 3: stamens of series I & II introrse, glandless; stamens of series III flanked by glands at the base of the filament, the anthers [extrorse or] the 2 upper locules laterally extrorse, the lower extrorse; series IV of conspicuous stipitate cordate-tipped glandless staminodes. Stigma discoid or peltate. Perianth tube accrescent in fruit, growing out into a thin cup surrounding the base of the fruit; perianth lobes deciduous from the tube [or the basal part of the entire lobes persistent on the rim]. Fruit in ours a black, globose drupe. (Including *Camphora* Trew, loc. cit. signature L. *t. 347*; Nees in Wall. Pl. As. Rar. **2**: 61, 72. 1831.) TYPE SPECIES: *Laurus Cinnamomum* L. = *C. zeylanicum* [Garc.] Blume. (The name the Latin transcription of Greek *kinnamomon*, derived, in turn, through Hebrew from the ancient name for cinnamon.) — CINNAMON.

A large genus (100–275 species) of eastern Asia, with the largest number in India, Indo-China, China, and Japan, but also in the Philippines, Indonesia, New Guinea, Polynesia and Australia. No species are currently recognized from the western hemisphere, although Kostermans has suggested that some of the American species currently assigned to *Phoebe* Nees may well belong to *Cinnamomum*.

Section CAMPHORA (Trew) Meissn., characterized by completely deciduous perianth lobes, conspicuous perulate vegetative buds, and alternate leaves with pinnate venation (rarely 3-veined or tripli-veined) and with glands in the axils of the veins, is represented with us by *C. Camphora* (L.) Nees and Ebermaier ($2n = 24$). The wood of this species, native to the warm-temperate and subtropical rain-forest zone of eastern Asia from southern Japan to northern Indo-China but now widely planted in the tropics throughout the world, is the source of camphor, which is removed by distillation. The plant was introduced into Florida as early as 1875 as a shade tree and was later established in large plantations in a not very successful attempt to promote a camphor industry in competition with that of Formosa and Japan. At the present time this handsome evergreen with conspicuous scaly buds, very small glaucous flowers (March–April) and black, globose drupes is cultivated in our area as an ornamental tree and for windbreaks from southern Georgia and Florida to southern Louisiana (also s. Texas and Calif.). It is hardy wherever the temperature does not fall below 15°F and has become naturalized to varying degrees throughout this region.

Section CINNAMOMUM (*Malabathrum* Meissn.), in which the perianth lobes are persistent or absciss above the base (leaving the tube crowned by the truncate lobes), the leaf-buds naked or with obsolete scales, and the leaves opposite or subopposite, 3- or tripli-veined and without glands, occurs only in cultivation in the warmer parts of Florida. *Cinnamomum zeylanicum* ($2n = 24$), the cinnamon of commerce, is a tender plant in sub-tropical Florida, while *C. Cassia* Blume, of China, is a more hardy species in that area.

The flowers of *Cinnamomum* are similar to those of *Persea* and *Phoebe* but the perianth tube usually is deeper and grows out to form a thin cup in which the fruit sits. Some species have the anther-locules arranged in an arc (*Neocinnamomum* Liou), a situation paralleled in *Phoebe* vs. *Persea* and *Nectandra* vs. *Ocotea*. Close relationships with *Aiouea* Aubl. and *Phoebe* and also with *Ocotea* have been postulated by Kostermans.

REFERENCES:

BERRY, E. W. Primary venation in *Cinnamomum*. Torreya **4**: 10, 11. 1904.

BROWN, E. G. Cinnamon and cassia: sources, production and trade. I. Cinnamon. Colonial Plant & Anim. Prod. London **5**: 257–280. 1955 [1956].*

CHOUDHURY, J. K., AND J. N. MITRA. Abnormal tricotyledonous embryo and the morphological structure of normal fruit and seed of *Cinnamomum Camphora* F. Nees. Sci. & Cult. **19**: 159–160. 1953.*

DARLINGTON, R. C., AND B. V. CHRISTENSEN. A preliminary study of oils of cassia. Jour. Am. Pharm. Assoc. (Sci. Ed.) **32**: 118–120. 1943.* [Physical properties of extracted oils from *C. Cassia*, *C. zeylanicum*, "C. saigonicum."]

DEWEY, L. H. The camphor tree (*Cinnamomum Camphorum* Nees & Eberm.). U. S. Dep. Agr. Div. Bot. Circ. **12**: 1–8. 1897.

FUJITA, Y. *Cinnamomum Camphora* Sieb. and its allied species. Their interrelationships considered from the view-points of species characteristics, chemical constituents, geographical distributions and evolution. Bot. Mag. Tokyo **65**: 245–250. 1952. (English and Japanese text.) [Includes *C. Camphora* and var. *linaloolifera*, *C. nominale* and var. *linalis*, *C. micranthum*, *C. Kanahirai*.]

——— AND R. KITAOKA. Biogenesis of the essential oils in camphor trees. XXIV–XXV. (In Japanese.) Jour. Chem. Soc. Japan, Pure Chem. Sect. **77**: 328–333. 1956.*

GRASMANN, E. Der Kampferbaum. Mitt. Deutsch. Ges. Natür- und Völkerkunde Ostasiens Tokio **6**(56): 277–315. 1895.

HIROTA, N. An examination of the camphor tree and its leaf oil. Perfum. & Essential Oil Rec. **44**: 4–10. 1953.*

HOOD, S. C. AND R. H. TRUE. Camphor cultivation in the United States. U. S. Dep. Agr. Yearb. **1910**: 449–460. 1911.

MARLIER-SPIRLET, M. L. Sur quelques épidermes de feuilles de *Cinnamomum* L. Bull. Jard. Bot. Bruxelles **17**: 266–305. 1945.

LEHMANN, C. Studien über den Bau und die Entwicklungsgeschichte von Ölzellen. Planta **1**: 343–373. 1925. [Lauraceae, 346–356: *C. Camphora*, *Laurus nobilis*.]

MERRILL, E. D. *Camphorina* vs. *Cinnamomum*. Bot. Gaz. **70**: 84–85. 1920.

SANTOS, J. K. Leaf and bark structure of some cinnamon trees with special reference to the Philippine species. Philipp. Jour. Sci. **43**: 305–365. 1930. [6 spp. incl. *C. zeylanicum* and *C. Cassia*.]

SASTRI, R. L. N. Studies in the Lauraceae — I. Floral anatomy of *Cinnamomum iners* Reinw. and *Cassytha filiformis* L. Jour. Indian Bot. Soc. **31**: 240–246. 1952.

WILSON, E. H. Camphor, *Cinnamomum Camphora* Nees & Ebermaier. Jour. Arnold Arb. **1**: 239–242. 1920. [An account of the plant and the camphor industry in Formosa.]

YOTHERS, W. W., AND A. C. MASON. The camphor thrips. U. S. Dep. Agr. Bull. **1225**: 1–29. 1924. [A serious insect pest in Florida.]

YOUNGMAN, B. J. Professor Naonori Hirota's work on camphor trees. Kew Bull. **1952**: 61–65. 1952. [Summary of extensive work on taxonomy, chemistry, and distribution in Japan, Formosa, China.] See Mem. Ehime Univ. Sect. 2. **1**(2). 1951.*

3. **Nectandra** Rolander ex Rottböll, Acta Lit. Univ. Hafn. **1**: 279. 1778, nom. cons.

Trees [and shrubs] with alternate coriaceous [to membranaceous] leaves usually pinnately veined, the reticulation conspicuous [or obscure].

Inflorescences usually paniculate, axillary or subterminal, the narrow bracts deciduous. Flowers bisexual, small, the 6 elliptic perianth lobes hairy, spreading or reflexed at anthesis, deciduous, the tube conspicuous or almost entirely lacking. Fertile stamens 9, the staminodia 3 [when present]: stamens of 2 outer series (I & II) with nearly sessile reniform anthers [or fleshy and petaloid], the anther-locules 4, arranged in an arc, introrse. Stamens of series III longer, the squarish anthers on filaments almost equal their length, with 2 large subreniform nearly sessile glands at the base of filaments, the 4 anther-locules in two horizontal planes, the 2 upper laterally extrorse, the 2 lower extrorse. Staminodia stipiform (in ours triquetrous, on slender pubescent filaments). Ovary glabrous; stigma capitate, conspicuous. Fruit a thin-walled drupe, ellipsoid, globose or oblong, with a shallow woody cupule (formed by the enlarged perianth tube) subtended by the enlarged pedicel; cupule margin simple. (Not *Nectandra* Berg., 1767.) TYPE SPECIES: *N. sanguinea* Rol. ex Rottb. (The name from Greek, *nektar*, nectar, and *andros*, of a man, in reference to the stamens and anther valves which were mistaken for nectaries and stamens, respectively.) — LANCEWOOD.

A large genus (about 175 sp.) of tropical America, the majority of the species in South America (especially the Andes), with about 35 in Central America, and a few in the West Indies. *Nectandra coriacea* (Sw.) Griseb. (*Ocotea coriacea* (Sw.) Britton), which occurs in the West Indies, the Yucatan Peninsula, British Honduras, and Guatemala, reaches southern Florida, where it extends as far north as Indian River County, on the east coast, and Cape Romano (Collier County), on the west.

This species, which may reach 30–40 feet in height, bears small panicles of small, white, very fragrant jasmine-scented flowers which are followed by the first green, then dark-blue, then black fruit with green, yellow or red cupule and enlarged fruiting pedicel. Flowering and fruiting are quite variable. The leaf-venation is its most outstanding characteristic: there are 6–8 pairs of lateral nerves which are rather obscured by a very conspicuous over-all elevated reticulum (at least in dried specimens). *Nectandra coriacea* is most closely related to *N. salicifolia* (HBK.) Nees (*N. sanguinea* sensu Nees, non Bol. ex Rottb.), of wide distribution in Mexico and Central America.

Nectandra is distinguished from *Ocotea* Aubl. (1775) by the arrangement of the anther-locules of the two outer series of stamens, these being in an arc in the former and in two planes in the latter, a distinction which does not entirely hold. Further studies in tropical America may well show that *Nectandra* should be regarded as a subgenus of *Ocotea*, a course recently advocated by Kostermans.

It has been suggested, on the basis of the illustration of *Ocotea Catesbyana* in Sargent, Silva 7: *pl. 303,* that both *Nectandra* and *Ocotea* occur in southern Florida. Although this illustration does show the anther-locule arrangement of *Ocotea*, rather than that of *Nectandra*, this would appear to be an error, for only *Nectandra coriacea* (also incorrectly drawn in Small's Manual) seems to be represented by herbarium specimens, including those studied by Sargent, from southern Florida. The disposition of *Ocotea Catesbyana* (at least *sensu* Sargent) as a synonym of *N. coriacea* would appear to be the correct one.

REFERENCES:

ALLEN, C. K. *Nectandra coriacea.* Addisonia **22**: 9, 10, 12. *pl. 709.* 1943 [1944].

———. Studies in the Lauraceae, VI. Preliminary survey of the Mexican and Central American species. Jour. Arnold Arb. **26**: 280–364, 365–434. 1945. [*Ocotea*, 330–364; *Nectandra*, incl. *N. coriacea*, 365–406.] See also Fl. Panama in Ann. Missouri Bot. Gard. **35**. 1948.

HUMPHREY, C. J. Tests on the durability of green-heart (*Nectandra Rodiaei* Schomb.). Mycologia **7**: 204–209. 1915.*

BERRY, E. W. The physical conditions and age indicated by the flora of the Alum Bluff formation. U. S. Dept. Interior Geol. Surv. Prof. Paper **93–E**: 41–59. 1916. [Includes "Nectandra apalachicolensis."]

KOSTERMANS, A. J. G. K. Lauraceae. Reinwardtia **4**: 193–256. 1957. [Relationship of *Ocotea* and *Nectandra*, 232.]

SARGENT, C. S. *Ocotea.* Silva N. Am. **7**: 9–12. *pl. 303.* 1905. [*N. coriacea*, as *O. Catesbyana*; details of stamens incorrect.]

4. **Licaria** Aubl. Hist. Pl. Guiane Franç. 1: 313. *pl. 121.* 1775.

Evergreen trees [or shrubs] with pinnately-veined leaves and small flowers in axillary or subterminal panicles near the tips of the branchlets [or flowers rarely solitary, subumbellate or capitate]. Flowers bisexual; tepals 6, in two whorls, [spreading or] erect, united below into a distinct perianth tube; (in ours, flowers obconical, ca. 2–2.5 mm. long, the perianth tube about half this length). Fertile stamens 3: stamens of series I & II [small and staminodial or] abortive; stamens of series III fertile, [entirely free, partly connate or] united into a staminal tube, their anthers 2-loculed, extrorse [or introrse], the filaments each with 2 glands (these in ours flattish, pressed against the staminal tube below the anthers, united in pairs, touching each other); stamens of series IV abortive [or rarely staminodial, minute]. Ovary included in perianth tube, free, the style thick [to slender], stigma inconspicuous. Berry ellipsoid, (in ours black, to 2 cm. long), smooth, the base partly covered by a thick, hemispherical double-margined cupule, the inner margin entire, erect, the outer one spreading, thicker, irregular, the pedicel thickened, merging into the tube. Cotyledons flat-convex, large, including the minute 2–4-leaved, glabrous plumule and minute conical radicle. (*Acrodiclidium* Nees & Mart. 1833; incl. *Misanteca* Schlecht. & Cham. 1831, *Chanekia* Lundell, 1937 and others.) TYPE SPECIES: *L. guianensis* Aubl. (The name derived from *licari kanali*, the native name of the type species.) — SWEETWOOD.

A genus of about 45 species of wide distribution in tropical South and Central America and the West Indies; a single species, *L. triandra,* of the West Indies from Martinque to Cuba, has been known from a single locality in our area.

The handsome *Licaria triandra* (Sw.) Kostermans (*Misanteca triandra* (Sw.) Mez) is one of the rarest plants in our flora, if it still persists at all. It was first recorded from two trees discovered in 1910 in Brickell Hammock, in Miami, but as many as 25 trees were counted there as recently as 1946 by the late W. M. Buswell (see Little, Checklist of Native and Naturalized Trees of U. S.). However, this unique hammock has been swallowed up and destroyed by the greedy real-estate development of metropolitan Miami and the species is presumably extinct at that locality. Apparently a few trees (planted) still survive on the campus of the University of Miami.

Licaria, as used here, includes, among others, *Acrodiclidium* (characterized by the presence of series I and II as staminodes, the stamens of series III free), *Misanteca* (in which staminodia are lacking and the stamens of series III united), and *Chanekia* (lacking staminodia and with stamens free). These genera merge with one another and share their "general facies, the shape of the cupule, ovary and stigma," characters which also separate them from *Mezilaurus* and *Endiandra,* their nearest allies (Kostermans).

Although there is agreement that the group as now constituted is a natural one, the proper name for it has been a matter of dispute. *Licaria* is based upon sterile material which Kostermans identifies positively with *Acrodiclidium*; Lundell, however, rejects *Licaria* in favor of *Misanteca* because the genus is based upon a sterile specimen.

Our species falls into subgenus MISANTECA (Schlecht. & Cham.) Kostermans. Apparently *L. triandra* [West Indies], *L. limbosa* (Ruiz & Pavon) Kosterm. [Venezuela to Peru and Bolivia], *L. Pittieri* (Mez) C. Allen [Costa Rica], *L. Cervantesii* (HBK) Kosterm. [southern Mexico, Guatemala], *L. caudata* (Lundell) Kosterm. [Br. Honduras, Guatemala], and *L. Cufodontisii* Kosterm. [Costa Rica] form a group of more or less closely related species.

REFERENCES:

ALLEN, C. K. Studies in the Lauraceae, VI. Preliminary survey of the Mexican and Central American species. Jour. Arnold Arb. **26:** 280–364, 365–434. 1945. [*Licaria*, incl. relatives of *L. triandra*, 424–432.]

KOSTERMANS, A. J. G. H. Revision of the Lauraceae I. Rec. Trav. Bot. Néerl. **33:** 719–757. 1936. [*Acrodiclidium*, 719–754]. II. **34:** 500–609. 1937. [*Licaria*, 575–604.]

———. Studies in South American Malpighiaceae, Lauraceae and Hernandiaceae, especially of Surinam. Meded. Bot. Mus. Utrecht **25:** 1–70. 1936. [*Acrodiclidium*, including typification of *Licaria*, 34–38.]

LUNDELL, C. W. Plants of Mexico and Central America — I. Wrightia **1:** 145–160. 1946. [Rejects *Licaria* in favor of *Misanteca*.]

SARGENT, C. S. *Misanteca.* Trees and Shrubs **2:** 133–135. *pl. 155.* 1911.

Tribe LITSEEAE Mez

5. **Sassafras** Trew, Herb. Blackwell. Cent. 3, signature P. *t. 267.* 1757; T. F. L. Nees & Ebermaier, Handb. Med.-Pharm. Bot. 2: 418. 1831.

Deciduous trees with elliptic leaves, entire, mitten-shaped or 3-lobed at the apex, narrowed at the base, involute in the bud; buds with few imbricate outer scales. Plants usually dioecious, the flowers usually unisexual [or apparently bisexual, but not often functionally so], in lax, drooping, few-flowered "racemes," the upper flowers of the lowest raceme opening first. Perianth of 6 yellowish tepals, in two whorls of 3. Staminate flowers with 9 fertile stamens on the margin of the short perianth tube; anthers 4[or 2]-loculed, introrse (but the lower locules of series III latrorse), opening by 4[or 2] valves; filaments flattened, elongated, those of series III with a pair of orange-colored short-stipitate glands at the base; staminodes and pistillode absent [or 3 staminodes and pistillode present in the Asiatic species]. Pistillate flowers with 6 rudimentary stamens, in 2 whorls [or 12 in 4 whorls, similar to stamens and staminodes in staminate flowers]; ovary ovoid, nearly sessile in the short perianth tube, the style slender, the stigma enlarged. Fruit a dark blue ovoid berry supported by the club-shaped enlarged and fleshy pedicel and perianth base. Seed oblong, pointed; testa thin; embryo subglobose, erect. (Including *Pseudosassafras* Lec., *Yushunia* Kamikoti.) TYPE SPECIES: *Laurus Sassafras* L. = *S. albidum* (Nutt.) C. G. Nees. (The popular name for the plant, used as early as 1569 by the French in Florida, adopted by Trew.)

As currently delimited, a genus of three species of eastern American-eastern Asiatic distribution: *Sassafras albidum* ($2n = 48$) (including var. *albidum* and the more southern var. *molle* (Raf.) Fern.), of wide distribution from s. Maine to se. Iowa, s. to Texas and Florida; *S. Tzumu* (Hemsl.) Hemsl., of central China (from Kwantung and Kweichow, to Szechuan, Hupeh, Anhwei, and Chekiang); and *S. randaiense* (Hayata) Rehd., of the central mountain range of Formosa.

The two Asiatic species constitute the subgenus PSEUDOSASSAFRAS (Lecomte) Keng. Both are less specialized than the American and differ from it in the pubescent tepals, in the presence of 3 staminodes and a pistillode in the staminate flowers, and in having in the pistillate flowers 12 staminodes similar in appearance to the stamens and staminodes of the staminate flower. The anthers of *S. Tzumu* are 4-loculed, those of *S. randaiense* 2-loculed. All three plants are similar, however, in habit, bark, winter buds, leaves, inflorescence and fruit and certainly constitute a natural genus (although each of the three has been assigned to a separate monotypic genus at one time or another). Rehder suggested that the nearest relative of *Sassafras* is *Lindera* (some of the deciduous species of which have lobed leaves very similar to those of *Sassafras*) which differs primarily in its 2-celled anthers and in the "umbellate" inflorescence. Kostermans, however, would ally *Sassafras* with the evergreen *Actinodaphne* Nees, a rather different group, more suggestive of *Litsea*.

Sassafras albidum is with us a very familiar plant, long reputed to have medicinal properties. It is at most a mild, aromatic stimulant. Gumbo filé, a powder used to give flavor and consistency to gumbo soup, owes its properties to the secretory and mucilage cells of the leaves from which it is prepared.

Although seldom planted, the species is one of our most handsome native plants, attractive at all seasons of the year. The tree occasionally reaches a height of 80–90 feet and a diameter of 6 feet. It is sometimes weedy, for it tends to sucker from the roots. The attractive small, yellow flowers are produced in early spring with the first unfolding of the leaves.

REFERENCES:

ANONYMOUS. Dye from sassafras. Sci. News Letter **42**(18): 279. 1942. [From the root bark.]

BASTIN, E. S. Structure of *Sassafras*. Am. Jour. Pharm. **67**: 312–318. 1895.*

BERRY, E. W. Notes on Sassafras. Bot. Gaz. **34**: 426–450. 1902. [In relation to fossil forms, many of which are referred to *Platanus*.]

BLAKE, S. F. Note on the proper name for the sassafras. Rhodora **20**: 98, 99. 1918. [*S. officinale*.]

COY, G. V. Morphology of *Sassafras* in relation to phylogeny of angiosperms. Bot. Gaz. **86**: 149–171. 1928. [Staminate, pistillate flower; development of embryo sac (Polygonum type) and embryo.]

FERNALD, M. L. Nuttall's white sassafras. Rhodora **15**: 14–18. 1913.

———. Contr. Gray Herb. Harvard Univ. — No. CXII. IV. The nomenclature of *Sassafras*. Rhodora **38**: 178, 179. 1936. [*S. albidum* the correct name.]

HIGGINBOTHAM, B. W. Sassafras shaped history. Nat. Hist. **56**: 159–164. 1947.

HOLM, T. Medicinal plants of North America. 23. *Sassafras officinale* Nees. Merck's Rep. **18**: 3–6. 1909.*

HUMPHREYS, E. W. Variation among non-lobed *Sassafras* leaves. Torreya **10**: 101–108. 1910.

———. An analogy between the development of the plates of crinoids and the leaves of *Sassafras*. Bull. Torrey Bot. Club **35**: 571–576. 1909. [Entire leaves at base of annual growth followed by 2- or 3-lobed leaves and again by entire.]

LLOYD, J. U. *Laurus Sassafras*. Pharm. Rev. **16**: 450–459. 1898.*

KENG, H. A taxonomic revision of *Sassafras* (Lauraceae). Quart. Jour. Taiwan Mus. **6**: 78–85. 1953.

MCMILLAN, F. W., G. E. MCKIBBEN AND W. R. BOGGESS. Controlling sassafras, persimmon, and elm with 2, 4, 5–T and mixtures of 2, 4, 5–T and 2, 4–D. Ill. Agr. Exp. Sta. Forestry Note **58**: 1–5. 1955.*

REHDER, A. The American and Asiatic species of *Sassafras*. Jour. Arnold Arb. **1**: 242–245. 1920.

ROBERTSON, C. Flowers and insects. XVII. Bot. Gaz. **22**: 154–165. 1896. [Includes *Sassafras*, visited mostly by flies and a few small bees; list of visitors.]

RUSSELL, G. W. Large trees of *Sassafras*. Gard. Month. **28**: 22. 1886. See also HALLOCK, N., Science **23**: 51. 1894.

SARGENT, C. S. *Sassafras*. Silva N. Am. **7**: 13–18. *pls. 304, 305.* 1905.

SCHAFFNER, J. H. The jacket layer in *Sassafras*. Ohio Nat. **4**: 192, 193. 1904. [Ovule.]

SPAULDING, P. Heart rot of *Sassafras Sassafras* caused by *Fomes ribis*. Science **26**: 479, 480. 1907.

WEISS, H. F. The structure and development of the bark in the sassafras. Bot. Gaz. **41**: 434–444. 1906.

6. **Lindera** Thunb. Nov. Gen. Pl. 3: 64. 1783; Blume, Mus. Bot. Lugd.-Bat. 1: 323. 1851, nom. cons.

Dioecious or polygamo-dioecious shrubs with entire [or 3-lobed] deciduous [or evergreen] leaves. Flowers small, yellow, short pedicelled, in almost sessile [in ours] umbel-like cymose clusters of 3–6, each cluster subtended by 2 pairs of decussate deciduous bracts, the clusters 1–4 above the axils of the preceding year's leaves on greatly reduced supra-axillary branches terminated by a vegetative bud which grows after anthesis. Tepals glabrous, the two whorls similar, thin, the perianth tube very short or none; perianth deciduous, only a small disc remaining beneath the fruit in ours. Staminate flowers with 9 stamens (series IV completely aborted), the 3 innermost (series III) each with a pair of conspicuous stalked glands at the base; anthers 2-loculate, all introrse; pistillodium present. Pistillate flowers with stamens variously developed, the innermost series usually reduced to filaments with two glands at the base; some staminate flowers sometimes present among the pistillate; ovary and style about equal. Fruit a bright red drupe on the short, hardly or slightly thickened pedicel topped by the disc-like somewhat accrescent perianth base. (*Benzoin* Fabr. 1763, non *Lindera* Adans. 1763, nomina rejicienda.) TYPE SPECIES: *L. umbellata* Thunb. (Named for John Linder, 1676–1723, early Swedish botanist.) — WILD ALLSPICE, SPICEBUSH.

A large genus, of about 100 species, both deciduous and evergreen, primarily of eastern Asia, with only two in the western hemisphere, both occurring in our area. *Lindera Benzoin* (L.) Blume, var. *Benzoin* is widespread along streams and in damp woods from southwestern Maine to southern Michigan and Illinois, south to North Carolina, Kentucky, Missouri and southeastern Kansas. Its var. *pubescens* (Palmer & Steyerm.) Rehd. is more southern in distribution, reaching Florida and Texas. *Lindera melissifolia* (Walt.) Blume is apparently exceedingly rare and local being known from widely scattered localities from Florida to Louisiana, northward to southern Missouri and to eastern North Carolina. The two species are quite distinct, differing in their ecology and in numerous morphological features. (See Steyermark.) Both are known to occur close together but in different habitats in southern Missouri.

Lindera Benzoin is a handsome shrub, worthy of cultivation, although, like most native plants, it is seldom grown. The flowers are among the very earliest to appear in spring. Staminate flowers are somewhat larger than pistillate and frequently occur in clusters of 3 or 4 umbels, in contrast to the less conspicuous pistillate inflorescences which are usually either single or paired. As a result, staminate plants are far more frequent than pistillate in the flowering condition in herbaria. This species and the Asiatic *L. praecox* and *L. glauca* have all been reported to have 24 somatic chromosomes.

Characters of flower and fruit in *Lindera* are very similar to those of *Litsea*, the two genera being distinguished primarily by the 2-loculed (or very rarely partly 4-loculed) anthers of *Lindera* vs. the 4-loculed anthers of *Litsea*.

REFERENCES:

ALLEN, C. K. Studies in the Lauraceae, III. Some critical and new species of Asiatic *Lindera*, with occasional notes on *Litsea*. Jour. Arnold Arb. **22:** 1–31. 1941.

FUJITA, Y. Phylogeny of *Lindera membranacea* Maxim., *L. umbellata* Thunb. and *L. citriodora* Hemsl. viewed from the constituents of the essential oils. (In Japanese; English summary.) Jour. Jap. Bot. **31:** 188–190. 1956 ["The chemical constituents show that *L. membranacea* is the precursor of the other two species."]

JENSEN, H. W. The abnormal meiosis of *Benzoin aestivale* in relation to the origin of sex chromosomes. Am. Nat. **76:** 109–112. 1942. [*L. Benzoin.*]

LLOYD, C. G. *Lindera Benzoin.* Drugs & Medicines N. Am. **2:** 117–119. 1887.

MELVIN L. Notes on some rare plants in North Carolina. Jour. Elisha Mitchell Soc. **70:** 312–314. 1954. [Includes *L. melissifolia* from Bladen Co., N. C.]

NASH, G. V. *Benzoin aestivale.* Addisonia **5:** 15, 16. *pl. 168.* 1920.

SCHROEDER, E. M. Dormancy in seeds of *Benzoin aestivale* L. Contr. Boyce Thompson Inst. **7:** 411–419. 1935. [Best germination following stratification at low temperatures.]

STEYERMARK, J. A. *Lindera melissaefolia.* Rhodora **51:** 153–162. 1949. [Discovery in Missouri; clear distinctions between this and *L. Benzoin*; excellent general notes.]

7. **Litsea** Lam. Encyc. Méthod. Bot. **3**: 574. 1791, nom. cons.

Dioecious, [evergreen or] deciduous shrubs with pinnately veined leaves and naked [or imbricate-scaled] buds. Flowers unisexual, in small pedunculate axillary sub-umbellate 3–5 flowered clusters, each with an involucre of 4 or 5 decussate deciduous scales, globose before anthesis; in our species borne singly above the scar of leaves of the preceding year near the tips of the branches, or 2 or 3 on very short axillary branches. Tepals yellow, 6 [or occasionally fewer or lacking], almost completely free [or united into an ovoid or campanulate tube], deciduous after anthesis. Staminate flowers with 9 [or 12] fertile stamens, those of series III [and IV] with 2 stipitate glands at the base; filaments well developed, in ours 2–3 times as long as the ovate emarginate anthers; anthers all 4-locular, all introrse; pistillode lacking [or small]; staminodia none in our species. Pistillate flowers with 9 [or 12] staminodia, those of series I and II usually without glands, those of III [and IV] flanked by 2 glands at the base of the filaments; ovary attenuate into the style, the stigma dilated. Fruit a more or less globular berry seated on a minute disc [or on a shallow cupule or disc on the enlarged pedicel]. (*Malapoenna* Adans. 1763, *Tomex* Thunb. 1783, *Sebifera* Lour. 1790; nomina rejicienda. *Glabraria* sensu Blume, 1851, not L. = *Boschia* Korthals [Bombacaceae]). TYPE SPECIES: *L. chinensis* Lam. = *L. sebifera* Pers. (according to list of nomina conservanda) or = *L. glutinosa* (Lour.) C. B. Robinson (according to Kostermans). (The name presumably from a local name of southern China, *litsé* *de Chine* being given as the common name for the type species.) — POND-SPICE.

A large genus of perhaps 400 species, mostly evergreen, and primarily of eastern and southeastern Asia from Japan to the Philippines, India, New Caledonia, tropical and subtropical Australia and New Zealand, with 5 species in North America. Of the American species, 3 are distinctive closely related plants of the eastern Sierra Madre of Mexico; the fourth, *L. glaucescens* HBK. is highly variable and widespread from northwestern Mexico east and south to Costa Rica; the fifth, *L. aestivalis* (L.) Fern. (*L. geniculata* (Walt.) B. & H.), is a rare plant of very spotty distribution on the coastal plain from Florida to Louisiana, north to eastern North Carolina, southeastern Virginia (at least formerly), and Tennessee, occurring around pond-margins and in swamps.

Litsea aestivalis is a shrub to 2 or 3 m. with characteristic zig-zag branchlets and narrowly oblong leaves. The pedunculate and involucrate umbel-like clusters of small yellow flowers are borne in early spring before the appearance of the leaves (this being the only deciduous American species). The bright-red globose fruit is borne in early summer.

Like *Lindera*, presumably a close relative (from which it differs primarily in the 4-loculed anthers), the genus is complex and taxonomically difficult in eastern and southeastern Asia, where the interrelationships of *Litsea*, *Lindera*, *Sassafras*, *Actinodaphne*, *Neolitsea* and others are to be sought.

REFERENCES:

See under Lauraceae, ALLEN (1945), MEZ (1889).

ALLEN, C. K. Studies in the Lauraceae, III. Some critical and new species of Asiatic *Lindera*, with occasional notes on *Litsea*. Jour. Arnold Arb. **22:** 1–31. 1941.

BARTLETT, H. H. A synopsis of the American species of *Litsea*. Proc. Am. Acad. **44:** 597–602. 1909.

FERNALD, M. L. Botanical specialties of the Seward Forest and adjacent areas of southeastern Virginia. Rhodora **47:** 93–142, 149–182, 191–204. 1945. [Typification of *Laurus aestivalis* L., *L. Benzoin* L., 140–141.]

MELVIN, L. Notes on some rare plants in North Carolina. Jour. Elisha Mitchell Soc. **70:** 312–314. 1954. [Includes *L. aestivalis* from Bladen Co., N. C.]

SARGENT, C. Rare American shrubs. *Litsea geniculata*. Gard. & Forest **8:** 374, 375. 1895. [Includes an excellent plate; see also Sims, Bot. Mag. *t. 1471.* 1812.]

Subfam. CASSYTHOIDEAE Kosterm.

8. **Cassytha** L. Sp. Pl. 1: 35. 1753; Gen. Pl. ed. 5. 22. 1754, "*Cassyta.*"

Parasitic green to orange twining plants with wiry chlorophyll-bearing stems and minute, spirally arranged scale-like leaves, the plants superficially resembling *Cuscuta* and attached to host plants by small haustoria. Inflorescences indefinite, spicate [or racemose or reduced to heads], the minute flowers borne singly at irregularly separated nodes, sessile [or pedicellate] in the axil of a minute bract, with 2 similar bracteoles close under the perianth, bisexual. Tepals 6, the outer whorl much smaller and resembling the bracts, united below to form a shallow tube to which the stamens are adnate, later accrescent and inclosing the fruit. Fertile stamens 9, 2-loculed, staminodia 3: stamens of series I sub-petaloid, series I & II introrse, without glands; stamens of series III flanked by nearly sessile glands, the anthers extrorse; series IV of distinct cordate sessile [or stipitate] staminodes. Ovary broadly fusiform, the style indistinct, the stigma capitate. Fruit drupaceous with a hard endocarp, completely inclosed by, but free from the enlarged and succulent cream-colored perianth tube which has a small opening at the apex surrounded by the persistent erect perianth lobes. Seed coat membranous or coriaceous; cotyledons thick, fleshy, often unequal, sometimes more or less consolidated at maturity. TYPE SPECIES: *C. filiformis* L. (The name from Greek, *kasytas* or *kadytas*, dodder [*Cuscuta*].) — WOE-VINE, LOVE-VINE.

A curious genus with perhaps 15–20 species, more or less maritime and mainly Australian but with a few in Africa and a single species, *C. filiformis,* of pantropical distribution and the only species in the Americas. *Cassytha filiformis* occurs in the subtropical portions of our area, primarily in coastal areas as far north as Brevard and Pinellas counties, where it may easily be mistaken at first for *Cuscuta.* It is parasitic on a wide range of herbaceous and woody hosts and can be a destructive pest.

Although *Cassytha* is an obligate parasite, the plant is at least partly autotrophic, for chloroplasts with abundant starch are present in the cortical parenchyma throughout the stem. In addition, numerous stomata (oriented transversely on the stem), an extensive xylem system, and haustoria with many well-developed spiral tracheae running to their ends which curve directly into the wood area of the host, all suggest that the plant is primarily a water-parasite. This habit, the reduction in exposed surface, the extreme development of mucilage in the plant (reminiscent of the cacti), and the profuse development of the plant in the brilliant sunlight of coastal and white-sand scrubs suggest further a special adaptation to a xerophytic type of habitat unfavorable to most Lauraceae.

Seedlings germinate in nearly pure sand and elongate quickly with rather rapid nutating movements which bring about contact with a host plant. The primary root remains rudimentary and only four secondary roots (which lack root-caps) function during the period prior to attachment to the host.

Although the inflorescences of *Cassytha* are described as "indeterminate" racemes or spikes or (in a few species) heads, the "inflorescences" would not seem to be radical departures from the usual determinate, basically cymose inflorescences of other Lauraceae, but would merely reflect the reduction to "simplicity" in this highly modified plant. Each of the solitary axillary flowers with its two minute bracteoles would appear to be the product (by reduction) of an entire cymose lauraceous inflorescence.

Thus the short "racemes" or "spikes" of *Cassytha* would represent a stem with inflorescences (each reduced to one flower) produced at successive nodes, just as in many Lauraceae a succession of axillary inflorescences is produced as the growth of the season proceeds. The even more highly modified capitate inflorescences of some species of *Cassytha* would be derived through shortening of the internodes of "spicate" inflorescence.

Cassytha is sometimes separated from the Lauraceae on account of its great reduction and parasitic habit but in all anatomical features (including rubiaceous stomata, ethereal oil cells and mucilage cells) and in all floral characters it is very clearly a member of that family. In flower and fruit it approaches *Cryptocarya* R. Br., a large pantropical genus, in which the fruit is completely inclosed in the enlarged perianth tube.

REFERENCES:

BENTHAM, G., AND F. MUELLER. *Cassytha.* Flora Austral. **5**: 308–313. 1870.

BOEWIG, H. The histology and development of *Cassytha filiformis*, L. Contr. Bot. Lab. Univ. Pa. **2**: 399–416. 1904. [Includes germination of seedling; material from Florida.]

HART, T. S. The Victorian species of *Cassytha.* Victorian Nat. **42**: 79–83. 1925.

———. Notes on the identification and growth of certain dodder-laurels (*Cassytha*). Victorian Nat. **63**: 12–16. 1946. [Includes notes on germination and early growth.]

KEINHOLZ, R. An ecological and anatomical study of beach vegetation in the Philippines. Proc. Am. Philos. Soc. **65**(Suppl.): 58–100. 1926. [*Cassytha*, 81, 82.]

METCALFE, C. R., AND L. CHALK. Anat. Dicotyl. **2**: 1152, 1153. 1950. [Summary of anatomical details of *Cassytha*; mostly from Keinholz.]

MIRANDE, M. Recherches sur le développement et l'anatomie des Cassythacées. Ann. Sci. Nat. IX. **2**: 181–285. 1905. [Seedling and adult plant, *C. filiformis*; see also under Lauraceae.]

SASTRI, R. L. N. Embryo sac haustoria in *Cassytha filiformis* Linn. Cur. Sci. Bangalore **25**: 401, 402. 1956.*

———. Studies in the Lauraceae — I. Floral anatomy of *Cinnamomum iners* Reinw. and *Cassytha filiformis* L. Jour. Indian Bot. Soc. **31**: 240–246. 1952.

SCHMIDT, A. T. Zur Anatomie von *Cassytha filiformis* L. Oesterr. Bot. Zeitschr. **52**: 173–177. 1902.

STATISTICS OF COMPOSITAE IN RELATION TO THE FLORA OF CHINA

SHIU-YING HU

IN JULY 1953 a project for the preparation of a descriptive flora of China was initiated in the Arnold Arboretum under the auspices of the China International Foundation. The first undertaking of the project was the compilation of a comprehensive index to the species of Phanerogams of that country. A staff of five persons spent two and a half years in checking through the extensive botanical literature and in making reference cards of the species of the flowering plants of China. The complete index consists of one hundred and twenty thousand cards, each including name and synonyms of a species, the date and place of publication and the distribution of the taxon as indicated by the citation of various collections, with special emphasis on the type material. This index not only constitutes a comprehensive foundation for the floristic studies and taxonomic researches of the Flora of China Project, but it also reflects a much clearer picture of the vegetation of China than any information we have had before. In a concise and systematic way it tells both the kind of plants which can be found in China and the locations in which each species occurs.

The Compositae constitute the largest family of flowering plants in the world. This statement also holds true for China. The species of Compositae are represented in all parts of the country, from the extensive seashore, in the east, to the alpine tundra of Sinkiang and Tibet, in the west, and from tropical Hainan Island, in the south, to the Mongolian desert, in the north. With the information given on the above-mentioned index cards, I have made an enumeration of the Compositae of China, which gives a total of 219 genera and 3216 species described or recorded from this area. Due to certain nomenclatural changes some of these genera and many of the species have been reduced to synonymy. Meanwhile, because of the treaties made between China and Russia in 1860–64, certain monotypic and oligotypic genera, which were known only from the type localities or from small areas which are no longer within the boundary of China, have to be excluded. Consequently, only 167 genera and 2029 species are here recognized. The basis for choosing the valid binomials has been the recent treatments of various groups by competent taxonomists like Babcock, Chang, Chen, Good, Handel-Mazzetti, Kitamura, Ling, and Stebbins. There is no doubt that the numbers of the recognized taxa will be changed when careful studies of available material are made, the generic limits redefined, and the specific status better determined. Nevertheless, the changes of details probably will not have an appreciable effect on the general picture of the nature, distribution and origin of the vegetation, which an analytic study of the data on the principal elements of the family may reflect.

Up to the present there is no map which shows the phytogeography of China. In recent years students of economic geography as well as of plant geography have tried to prepare phytogeographic maps to illustrate vegetation types in China, but have failed to produce anything which can give a true picture of the vegetation. The difficulty has been that they have not had distributional data of the species that constitute the principal elements of the vegetation. The present paper is an attempt to analyze the distributional data for a large natural group and to utilize it to interpret some of the problems involved in the composition and phylogeny of the vegetation of China. When similar studies on the Gymnospermae, Gramineae, Cyperaceae, Liliaceae, Orchidaceae, Ranunculaceae, Fagaceae, Lauraceae, Rosaceae, Leguminosae and Ericaceae have been made, and with the aid of a few recently monographed families, such as the Magnoliaceae, Theaceae, and Araliaceae, we shall be in a much better position to present a truer phytogeographic map of China.

China is here defined so as to include all the territory covered by W. T. Ting's *Atlas* published in 1934. It has been a general practice among Chinese botanists to include every taxon published from "Manchuria," "Soongoria" and the "Tien-shan Range" in the flora of China. The reason for this practice is that in a standard map of China there is a Manchuria in the northeast (which includes Kirin, Liaoning and Heilungkiang), a Soongaria Basin in western Sinkiang and a Tien-shan in central Sinkiang. But when Maximowicz collected in Manchuria in 1856, and Regel made his Soongaria expedition in 1840 these areas covered much more territory than they do in the present map of China. Due to the 1860 treaty with Russia, the northern and eastern half of Manchuria became a part of the Russian Far East. Likewise, due to the 1864 treaty the western half of Soongaria and western Tien-shan no longer belong to China. For this reason, genera like *Symphyllocarpus* Maxim., from northeastern Manchuria (in the old sense), and *Plagiobasis* Schrenk and *Acanthocephalus* Karelin and Kirilov, from the region of Soongaria beyond the present Chinese border, are excluded from this study.

I. THE TRIBES OF COMPOSITAE

Cassini, in 1812–18, established eleven tribes for the Compositae. Hoffmann in 1889 arranged 806 genera in two subfamilies and thirteen tribes in Engler and Prantl's *Die Natürlichen Pflanzenfamilien* IV. **5**: 118. Dalla Torre and Harms in 1905 listed 899 known genera in their *Genera Siphonogamarum*. They placed 877 genera in two subfamilies and thirteen tribes following Hoffman's system and left twenty-two genera as *Genera incertae sedis* at the end. The latest record of the total number of genera of Compositae is found in Lemée's *Dictionaire Descriptif et Synonymique des Genres de Plantes Phanérogames* 7: 484. 1939, where 1014 genera are recognized. In this work the genera of Compositae are dispersed alphabetically among all the genera of the Phanerogams. It is of little use for our purpose of making comparative studies of the principal elements of the family. For a concise over-all picture of the Compositae and for systematic comparisons of its tribes and genera, the record in Dalla Torre and Harms still appears to be most useful, especially since many of the larger herbaria are arranged according to this scheme. In modern manuals and handbooks such as those of Fernald, Rehder, Bailey, etc., the names of these tribes appear repeatedly. Since both the system and the names are familiar to students of botany, they are adopted in this discussion.

When *Genera Siphonogamarum* was published, the flora of China was little known to the botanical world. It therefore contains rather inadequate information on the Chinese Compositae. The data on the number of genera in each tribe and the distributional notes of the genera as given in this work are here taken unchanged to give a general view of the tribes of the family. To insure clarity the figures on the tribes of Compositae in China as revealed by our studies are given separately.

1. The Tribes of Compositae in General

Dalla Torre and Harm's information on the sizes, ranges and centers of generic concentration of the tribes of Compositae are summarized in the following graph. Abbreviations commonly used in the literature are adopted for the area column with the following exceptions: Med. Reg. = Mediterranean Region; Aust. = Australia; Pac. Is. = Pacific Islands; and Mad. = Madagascar.

With respect to the number of genera most of the tribes are medium-sized, including forty to sixty-five genera. The large tribes are the Astereae, Inuleae and Heliantheae, each of which has over one hundred genera. The small tribes are the Calenduleae and Arctotieae, the former containing 8 genera and the latter 11. The distributional patterns of the tribes are worthy of notice. The small and medium-sized tribes all have definite areas of generic concentration. Even in the large tribes, although they occupy more extensive areas, the centers of the concentration of their genera are evident.

1. The tribe Vernonieae has about 49 genera, 19 of which are from South America, 16 from South Africa, 5 from tropical America, 3 pantropic, 2 in Madagascar, 2 in India, and 1 each in Australia and North America. This distributional record indicates that the Vernonieae is essentially a southern tribe with the centers of concentration in South America and South Africa. Only a few of its genera, such as *Elephantopus* and *Vernonia*, extend to the warm region of the north temperate zone.

2. The tribe Eupatorieae includes about 51 genera, 16 of which occur in South America, 16 in Mexico and Central America, 9 in North America, 3 in the West Indies. A few genera such as *Eupatorium*, *Mikania*, etc., are represented in all warm regions. Thus, this distributional record indicates that the Eupatorieae are essentially a New World tribe with the generic concentration in tropical America.

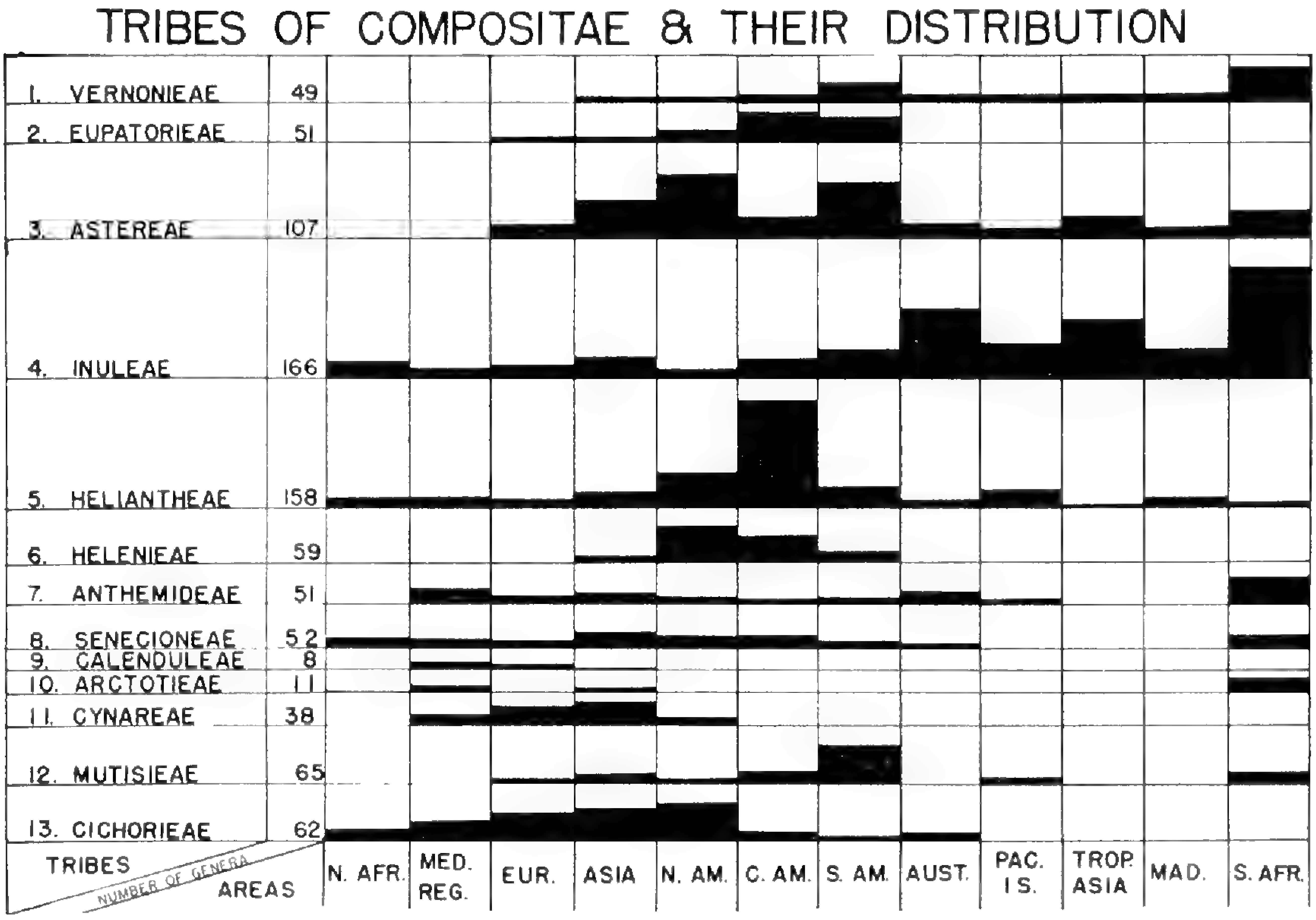


FIG. 1. The tribes of Compositae and their distribution in the world.

3. The tribe ASTEREAE includes about 107 genera, 27 of which are from North America, 19 from South America, 11 from Mexico and tropical America, 18 from Africa, 3 from Madagascar, 2 endemic to St. Helena, 2 in the Hawaiian Islands, 3 in Europe, 5 in Australia and New Zealand, and 4 from Asia. In addition, there are many genera that are widely distributed. For example, *Brachycome* is represented in Australia, Tasmania, New Zealand, eastern and tropical Africa; *Lagenophora* occurs in tropical and eastern Asia, New Zealand, Australia and the Pacific Islands; *Myriactis* is found in New Guinea, Java, India and Central Asia; *Podocoma* is represented in tropical America and Australia; *Vittadinia* occurs in New Guinea, Australia, New Zealand, New Caledonia and South America; and both *Aster* and *Erigeron* have large numbers of species in America, Asia, Europe and tropical Africa. This distributional record clearly indicates that the Astereae encompass both widespread and endemic genera. It has several centers of generic concentration, namely Asia, Africa, and North and South America. It is especially well-represented in the New World.

4. The tribe INULEAE is the largest tribe in the Compositae. Of its approximately 166 genera, 84 are from Africa (especially South Africa), 9 from Madagascar, 37 from Australia, 12 from South America, 4 from tropical America. In addition, 12 are common in the Old World tropics and 4 are pantropical genera. This distributional record indicates that the Inuleae is a southern tribe with the centers of generic concentration in South Africa, Australia and, to a lesser degree, tropical Asia. It is rather poorly represented in the northern temperate regions.

5. The tribe HELIANTHEAE includes about 158 genera, 80 of which are from Central America, 30 from the United States occurring chiefly in the southwestern states from Texas to California, 21 from South America, 6 from the Sandwich Islands, 5 from Madagascar and 3 from Africa. In addition, there are 6 pantropic and 4 cosmopolitan genera. This distributional record clearly indicates that the Heliantheae are a New World tribe and, with the exception of the introduced and adventive elements, one which is poorly represented in the Old World.

6. The tribe HELENIEAE includes 59 genera, 36 of which occur in the United States and Mexico, 17 in tropical America and 5 in South America. Tropical Africa has two genera, with *Welwitschiella* being endemic. This distributional record indicates that the tribe Helenieae is essentially a New World group. With the exception of the introduced taxa, it is almost absent in the Old World.

7. The tribe ANTHEMIDEAE includes 51 genera, 18 of which are from South Africa, 10 from the Mediterranean region and the Canary Islands, 4 from Australia, 6 from central and southern Asia, 5 pantropic or cosmopolitan, 1 from North America, 2 from South America and 1 from New Guinea. This record indicates that the Anthemideae are essentially Old World with the generic concentration in South Africa and, to a lesser degree, in the Mediterranean region. The tribe has a few widespread, as well as a few endemic, genera. It is very poorly represented in the New World.

8. The tribe SENECIONEAE includes 52 genera with 12 occurring in South Africa, 10 in western North America, 4 in Central America, 3 in South America, 2 in the Bourbon Islands, 2 in Australia, 2 in China, 1 endemic to Juan Fernandez Island, and 1 in the European Alps. In addition, three genera are represented in a range covering Africa, Persia and Afghanistan, four in a range covering North Africa, Europe, temperate Asia and North America, two in North Asia, North America, the West Indies and South America, and one, *Senecio*, including 1200 species, occurring throughout the world. At first sight these data do not seem to indicate any significant pattern of distribution for the tribe. But when the Afghanistan-Persia-Africa, the Europe-North Africa-temperate Asia-North America, and the North America-West Indies-South America patterns of distribution are correlated with the continuous chains of high mountains that tie together the continental masses, a very interesting pattern of distribution becomes apparent. Evidently the elements in this tribe are predominantly montane forms. Their distributions correspond with the direction of mountain axes which radiate from western China westward through central Asia to Europe and Africa, northward through northeastern Asia to the Americas and southward through the Malayan Peninsula, the Malayan Archipelago to Australia. The Senecioneae, unlike most other tribes which have obvious centers of generic concentration, are comparatively better represented in eastern Asia, western North America and South Africa.

9. The tribe CALENDULEAE is the smallest one of the family. It has eight genera, five of which occur in the south of Africa and the rest in the

Mediterranean region and western Asia. The Calenduleae are strictly Old World in distribution.

10. The tribe ARCTOTIEAE is the next smallest tribe in the family. It comprises eleven genera, ten of which occur in South Africa and one from Syria to Persia. It is strictly an Old World tribe.

11. The tribe CYNAREAE has 38 genera, 11 of which are confined to western Asia and Persia, 5 to the Mediterranean region, 12 to a wide range extending from southern Europe through Asia to Japan, 5 to Europe to central Asia, 2 common in the temperate and subtropical regions of the northern hemisphere, 1 endemic to China, 1 to India, and 1 to the Juan Fernandez Islands. The tribe Cynareae is essentially an Old World group.

12. The tribe MUTISIEAE has 65 genera, 36 of which are from South America, 4 from the West Indies, 3 from Central America, 8 from tropical and South Africa, 1 endemic to the Hawaiian Islands, 1 from North America, 1 from the European Alps, 2 to the Himalayan region, 2 to China, 2 to Japan and 1 from Afghanistan to Japan. The Mutisieae are predominantly southern with the centers of generic concentration in South America and, to a lesser degree, in South Africa. In the northern hemisphere the tribe is represented by a few endemic genera and one wide-spread genus.

13. The tribe CICHORIEAE includes 64 genera, of which 16 are confined to North America, especially the western United States, 13 to the Mediterranean region, 2 to Europe, 2 to North Africa, 2 to Australia, 5 to China, 1 to South America, 1 to the Society Islands, and 1 to Juan Fernandez Island. In addition, there are many genera with wide ranges. *Sonchus* and *Taraxacum* are cosmopolitan. *Launaea* ranges from South Africa to central Asia and temperate Europe. There are six other genera occurring from Europe to central Asia, six from Europe to temperate Asia and North America and four in western and central Asia. This distributional record seems to indicate that the Cichorieae are essentially an Old World group with an African-Eurasian-American distribution. There are nine genera, *Sonchus*, *Crepis*, *Lapsana*, *Hypochoeris*, *Mulgedium*, *Lactuca*, *Taraxacum*, *Prenanthes* and *Hieracium*, which occur on all these continents. It seems that along this African-Eurasian-American distribution-belt variation occurred particularly in the Mediterranean region, in China, and in the western United States.

2. THE TRIBES OF COMPOSITAE IN CHINA

All the 13 tribes of Compositae are represented in the flora of China by either native or introduced species. Their size, as represented by the recognized genera, their effect in the appearance of the general flora and their prominence in the natural flora, as illustrated by the species/genus ratio, may be summarized in the following table.

TABLE I. The Tribes of Compositae in China[2]

TRIBES	NO. OF GENERA	NO. OF SPECIES	SPECIES/GENUS RATIO	LARGE GENERA (10 OR MORE SPECIES)	SMALL GENERA (9 OR FEWER SPECIES)	NO. OF ENDEMIC GENERA
Vernonieae	6	40	7−	1	5	0
Eupatorieae	4	24	6	1	3	0
Astereae	22	203	9+	3	19	9
Inuleae	19	229	12+	6	13	2
Heliantheae	24	46	2−	0	24	1
Helenieae	3	5	2−	0	3	0
Anthemideae	17	271	16−	3	14	4
Senecioneae	17	358	23−	5	12	7
Calenduleae	1	2	2	0	1	0
Arctotieae	1	1	1	0	1	0
Cynareae	23	439	19+	6	17	7
Mutisieae	6	71	12−	3	3	2
Cichorieae	24	340	15	10	14	3
TOTAL	167	2029	12+ (average)	38	129	34

[2] No distinction is made here between native and introduced species. See text.

As indicated by the number of recognized genera the Heliantheae and the Cichorieae are the largest tribes of Compositae in China. However, their positions in the flora of China are very different. In the Heliantheae, with the exception of *Sheareria*, all the genera have been introduced through the intentional or accidental activities of man. Naturally, these introduced genera are small ones in the flora of China and their species/genus ratio for the tribe in China is less than two. Over two-thirds of these genera contain only one species each, and the others have two to six species. However, to a casual traveler who visits only the large cities or coastal areas of the country the members of this tribe may appear to be the most prominent feature in the general flora of the region. This is because the most commonly cultivated Compositae in the gardens of Chinese metropolises, (species of *Zinnia*, *Helianthus*, *Coreopsis*, *Dahlia* and *Cosmos*) are Heliantheae. Likewise, the most widespread weeds of the area, common in parks, gardens and school-yards (species of *Xanthium*, *Siegesbeckia*, *Eclipta*, *Bidens*, *Galinsoga* and *Wedelia*) also belong to this tribe. With the exception of these cultivated and weedy species, the other members of this tribe have a very limited distribution, being found chiefly in the warmer regions of the country. They occupy a very minor position as constituents of the natural vegetation in China.

Unlike the Heliantheae, the tribe Cichorieae is large both in the number and size of its included genera. The species/genus ratio for this tribe in China is fifteen. As illustrated in Table II, *Lactuca, Taraxacum, Crepis* and *Youngia* are the large genera in this tribe. Each of the first two genera has fifty-seven species in China, and each of the other two genera has over thirty species. Moreover, the Cichorieae include the largest number of large genera among all the tribes of the Chinese Compositae. Many of these large genera, such as *Taraxacum*, *Lactuca*, *Youngia* and *Ixeris* contain relatively widespread species, some of which have become more or less weedy. The region on the borders of Yunnan, Szechuan, and Sikang (the Meridional Ranges) seems to constitute the area of the species concentration of many genera of this tribe. Maps 22 and 23 indicate that a large number of the species in the genera *Lactuca*, *Crepis* and *Youngia* occur in this region. According to Stebbins, this area is also the point of origin and the center of distribution of three endemic genera, *Dubyaea*, *Soroseris* and *Faberia*. He also maintains that *Dubyaea* is the most primitive genus of the tribe. Because of its large number of genera, its rather high species/genus ratio and its unique endemism, the Cichorieae contribute important elements to the composition of the natural vegetation of the country.

The next largest tribes of Compositae in China are the Astereae, Cynareae, Inuleae, Anthemideae and Senecioneae. Like Cichorieae these tribes are comparatively large for the number of their included genera. Senecioneae and Cynareae both have high species/genus ratios, while Astereae, Senecioneae and Cynareae contain the largest number of endemic genera. They are important elements in the natural vegetation of the country. The most striking feature lies with the Senecioneae. This tribe has the highest species/genus ratio among all the tribes of Compositae in China, and this high ratio is due to the large number of species of only four genera, namely, *Senecio* 160, *Ligularia* 105, *Cacalia* 60, and *Cremanthodium* 47. The center of concentration of species of these closely related genera is the Meridional Ranges. This region is not only the home of many endemic species of these large genera, it is also the site of many monotypic and oligotypic endemic genera of this and related tribes. Good's statement (1929, p. 313) concerning *Cremanthodium* in this region, "the present point of highest species concentration happens also to be the generic point of origin," could be applied to many genera of the Astereae, Cynareae, Inuleae, Anthemideae and Senecioneae, including the genus *Senecio*.

The tribe Mutiseae is a relatively small one in China. Nevertheless, the tribe is fairly well represented in the natural vegetation of the country. With the exception of *Gerbera* which has a South Africa-Madagascar-tropical Asia distribution with the Chinese species marking the northern limit of its range, all the other genera of Mutiseae in China are essentially Chinese. Three of them (*Leucomeris*, *Myripnois* and *Nouellia*) are genera endemic to China. The other two have ranges extending either from India to Japan (*Ainsliaea*) or from Afghanistan to Japan (*Pertya*) with China being the center of their distribution. Forty-seven out of a total of fifty species of *Ainsliaea* occur in China, and ten of the twelve species of *Pertya* are Chinese.

Vernonieae and Eupatorieae are poorly represented in China and those genera which do occur are essentially widespread tropical taxa. As weedy species they may produce quite a prominent effect on the general flora in the warmer regions of China. With the exception of *Eupatorium* their distributions are very limited.

The Helenieae, Calenduleae and Arctotieae are represented in China only as cultigens.

II. THE GENERA OF COMPOSITAE IN CHINA

Two hundred and nineteen genera of Compositae have been recorded from China. Fifty-two of them belong to the doubtful and excluded category. The sizes and distributions of these genera within China and a comparison with the figures for the world are summarized in the following table. In this enumeration the genera are presented in the sequence of Dalla Torre and Harms. The numerals in the parentheses immediately following the names are those assigned by those authors. The names which do not have such numerals in parentheses are either invalid epithets or valid genera published after 1905. Most of the names in the latter group represent genera peculiar to the flora in China. The total number of species in each genus and the general area of distribution are chiefly adopted from Dalla Torre and Harms. A few of them are summarized from the *Index Kewensis.*

In presenting the distribution of the genera within China the following abbreviations are used. A = Anhwei, Cha = Chahar, Che = Chekiang, Chi = Chinghai, F = Fukien, H = Hainan, He = Heilungkiang, Hn = Honan, Hp = Hopei, Hun = Hunan, Hup = Hupei, J = Jehol, Kan = Kansu, Ki = Kiangsi, Kir = Kirin, Ks = Kwangsi, Kt = Kwangtung, Ku = Kiangsu, Kwe = Kweichow, L = Liaoning, M = Mongolia, N = Ninghsia, Sa = Shansi, Se = Shensi, Si = Sikang, Sin = Sinkiang, St = Shantung, Sy = Suiyuan, Sze = Szechuan, T = Taiwan, Tib = Tibet and Y = Yunnan.

In the remarks column the word "endemic" refers to the genus or species described from or limited to China.

Genera known only in cultivation or as adventives are in large and small capitals. Synonyms and other excluded names are in italics.

TABLE II. **An Enumeration of the Genera of Compositae in China**

TRIBES & GENERA	WORLD FIGURES		SPECIES IN CHINA		
	TOTAL NO. SPP.	GENERAL DISTRIBUTION	RECORDED & RECOGNIZED		DISTRIBUTION & REMARKS
Vernonieae					
ETHULIA (6)	3	Trop. As, Afr, Mad.	1	1	T; adventive.
Vernonia (23)	450	Am, Afr, Mad, trop. As.	55	34	See map 1, 20 spp. endemic.
Camchaya	3	Indo-China, Siam	1	1	Y.
STOKESIA (35)	1	N. Am.	1	1	Cultivated.
ELEPHANTOPUS (47)	16	Pantrop; Am, espec.	5	2	T, Kt, H, Sze; adventive.
PSEUDOELEPHANTOPUS	1	Pantrop.	1	1	T; adventive.

* * * * *

TABLE II. (*Continued*)

TRIBES & GENERA	WORLD FIGURES		SPECIES IN CHINA		
	TOTAL NO. SPP.	GENERAL DISTRIBUTION	RECORDED &	RECOGNIZED	DISTRIBUTION & REMARKS
Eupatorieae					
Adenostemma (57)	6	Pantrop.	4	2	T, Kt, H, Che, Hup, Kwe, Y, Sze, Hp.
AGERATUM (67)	30	Trop. N. Am.	3	2	T, F, Kt, H, Che, Y, Sze; cultivated, naturalized.
Eupatorium (88)	400	Am, Eur, As, Afr.	28	17	See map 2.
Mikania (90)	150	Pantrop; Am, espec.	4	3	Kt, H, T.
		* * * * *			
Astereae					
Solidago (121)	80	N. Am.	6	5	Kt, Hun, Kwe, Y, T, Kir, Ku, Mong, Sin.
Pteronia (134)	50	S. Afr.	1	0	Chinese sp. transferred to *Vernonia*
Dichrocephala (138)	5	Afr, trop. As.	8	3	T, F, Kt, H, Y, Kwe, Sze, Tib.
Cyathocline (139)	2	India to s. China.	1	1	Kt, Kwe, Y.
Grangea (137)	3	Trop. As, Afr.	3	2	T, Kt, H.
Lagenophora (146)	12	Trop. As, to Austr.	3	1	T, Kt.
Rhynchospermum (147)	1	India, Malaya.	2	1	T, Y; monotypic.
Myriactis (148)	10	E. Himal. reg.	9	5	Y, Sze, T, Kwe; natural distribution.
BELLIS (151)	10	Medit. reg.	1	1	Cultivated.
CALOTIS (157)	16	Austr.	1	1	H; adventive.
Asteromoea (165)	11	E. Asia.	11	10	Kt, Hun, Y, Sze, Sa, Se, St, Hp, Ku, F, Che, Ki, Hup.
Kalimeris	7	E. Asia.	7	0	Transferred to *Asteromoea*.
Martinia	1	E. Asia.	1	0	Transferred to *Asteromoea*.
Callistephus (170)	2	E. Asia.	2	1	Cha, Tib, Hp, Sa, Kir, He; endemic.
Callistemma	2	E. Asia.	2	0	= *Callistephus*.
Boltonia (164)	5	N. Am.	6	0	Misidentified; Chinese material = *Asteromoea*.
Heteropappus (168)	6	E. Asia.	10	5	St, He, M, Che, T, Kir, Kw.
Arctogeron	1	Mongolia.	1	1	M; endemic.
Wardaster	1	W. China.	1	1	Si; endemic.
Aster (172)	200	Am, As, Eur, S. Afr.	204	137	See map 3.
Calimeris			9	0	= *Aster*.
Diplopappus			4	0	= *Aster*.
Rhinactina			2	0	= *Aster*.
Turczaninovia			1	0	= *Aster*.
Asterothamnus	7	NW. China.	7	7	
Pseudolinosyris	2	Centr. Asia.	2	0	Not in Chinese territory now.

TABLE II. (*Continued*)

TRIBES & GENERA	WORLD FIGURES		SPECIES IN CHINA		
	TOTAL NO. SPP.	GENERAL DISTRIBUTION	RECORDED & RECOGNIZED		DISTRIBUTION & REMARKS
Galatella	25	Centr. Asia.	17	7	Si, M.
Brachyactis	13	Centr. Asia.	3	3	Hp, Se, Kan, Sin, J, Sy, Si, Tib.
Heteroplexis	1	S. China.	1	1	Ks; endemic.
Erigeron (173)	150	Am, As, Eur, Austr.	40	25	See map 4.
Microglossa (193)	10	Trop. As, Afr, Mad.	3	3	Kwe, Y, Sze
Vierhapperia	1	Monotypic.	1	1	Y; endemic.
Conyza (198)	50	Pantrop.	36	7	T, F, Y, Sze, Che, Kwe; indicates extent of tropical elements.
Thespis (199)	1	Himal. reg.	1	1	Y.
		* * * * *			
Inuleae					
Cava	1	W. China.	1	1	Tib, Sze; monotypic.
Blumea (211)	60	Trop. Afr, As, Austr.	59	30	See map 5; 10 endemics.
Bileveillea			3	0	= *Blumea.*
Leveillea			3	0	= *Blumea.*
Blumeopsis	2	Indo-China.	1	1	H, Y.
Laggera (212)	10	Afr, As, Austr.	6	2	T, Y, Sze, Hup.
Pluchea (213)	30	Pantrop.	7	3	T, Kt, H, Sze.
Epaltes (225)	10	Pantrop.	2	2	Kt, H.
Poilania	1	Indo-China.	1	0	= *Epaltes.*
Sphaeranthus (227)	17	Afr, As, Austr.	8	3	T, Kt, H, Y.
Pterocaulon (229)	12	Am, Austr, Maurit, Mad, India	1	1	H.
Evax (238)	15	Med. reg, As, N. Am.	1	1	Sin.
Filago (241)	12	Eur, N. Afr, As, Am.	3	3	Tib, Sin.
Leontopodium (254)	ca. 70	Eur, As, Am, S. Am, Japan.	63	57	See map 6.
Anaphalis (255)	70	Eur, As, N. Am.	67	51	See map 7.
Antennaria (250)	15	Eur, As, Austr, Am.	5	2	Sin, M, Sze.
Phagnalon (260)	20	Canary Is, Med. reg, Abyss, Himal. reg.	1	0	Not in Chinese territory now.
Gnaphalium (264)	120	Pantrop.	52	20	See map 8.
HELICHRYSUM (278)	300	Eur, Afr, Austr.	2	2	1 cult, 1 Sin; introduced
Tugarinovi	1	N. China.	1	1	Sy; endemic.
Inula (333)	90	Eur, As, Afr.	42	28	See map 9.
Duhaldea	1	S. China.	1	0	= *Inula.*
Vicoa	16	Centr. As. to trop. Afr.	1	1	Y.
Pulicaria (350)	30	Med. reg, Eur, As, S. Afr.	4	4	Sin, Tib, Kwe.
Carpesium (353)	30	Eur, As.	30	18	T, Kt, H, Che, Ku, Hun, Hup, Y, Sze, Kwe, Sa, Kan, Si, Hp, Se, St, Tib, Kir.
Adenocaulon (354)	4	Himal. Reg, Am, Chile.	4	2	St, Kir, Sa, Cha.

TABLE II. (*Continued*)

TRIBES & GENERA	WORLD FIGURES		SPECIES IN CHINA		
	TOTAL NO. SPP.	GENERAL DISTRIBUTION	RECORDED &	RECOGNIZED	DISTRIBUTION & REMARKS
Buphthalmum (364)	7	Eur, W. As.	1	0	Chinese material transferred to *Chrysanthemum*.
Anisopappus (368)	3	Trop. Afr.	2	1	Kt, H.
		* * * * *			
Heliantheae					
Sheareria (389)	2	Centr. China.	2	2	Che, Kt, Ki, Hup, Hun; endemic.
AMBROSIA (417)	15	Am, Med. reg, Afr.	1	1	Introduced.
Xanthium (419)	15?	Cosmopolitan.	7	2	Widespread.
ACANTHOSPERMUM (401)	3	Trop. Am.	1	1	Y; introduced.
PARTHENIUM (409)	9	N. & Centr. Am.	1	1	Kt; introduced.
ZINNIA (424)	12	N. & Centr. Am.	3	3	Cultivated.
SANVITALIA (427)	8	N. Am.	1	1	Kt; introduced.
HELIOPSIS (428)	7	N. & Centr. Am.	1	1	Cultivated.
Siegesbeckia (431)	10	Pantrop.	8	4	2 widespread, 2 ± localized.
ENHYDRA (435)	9	Centr. & S. Am, Austr.	1	1	H; introduced.
Eclipta (437)	4	S. Am, Austr; 1 sp. cosmopolitan.	1	1	Widespread; troublesome weed.
RUDBECKIA (449)	30	N. Am, Mex.	1	1	Cultivated.
Blainvillea (461)	9	Pantrop.	1	1	H.
Wedelia (463)	60	Pantrop.	6	5	T, Kt, Y, H, Sze.
Wollastonia			3	0	= *Wedelia*
TITHONIA (467)	10	Centr. Am.	1	1	Cultivated.
HELIANTHUS (471)	60	N. & Centr. Am.	6	4	Cultivated.
Spilanthes (478)	30	Am; 2 pantrop.	3	2	T, H, Y; 1 endemic.
SYNEDRELLA (495)	2	Trop. Am.	1	1	T, H, Kt
COREOPSIS (498)	70	Am, trop. Afr, Hawaian Is.	7	3	Cultivated.
DAHLIA (499)	9	Mexico.	1	1	Cultivated.
GLOSSOGYNE (505)	5	Trop. As, Austr.	2	1	T, F, Kt, H; introduced.
Bidens (508)	90	Cosmopolitan, espec. Am.	17	6	Widespread; many vars.
COSMOS (509)	20	Am.	1	1	Cultivated.
GALINSOGA (517)	4	Am.	1	1	Sze, Y, Kt; newly introduced weed.
TRIDAX (516)	20	Centr. Am.	1	1	T; newly introduced.
		* * * * *			
Helenieae					
HELENIUM (576)	30	Am.	1	1	Cultivated.
GAILLARDIA (577)	12	Am.	2	2	Cultivated.
TAGETES (582)	20	Am.	2	2	Cultivated.
		* * * * *			
Anthemideae					
ANTHEMIS (601)	100	Eur, Med. reg, Abyss, As, Am.	6	4	North China.

TABLE II. (*Continued*)

TRIBES & GENERA	WORLD FIGURES		SPECIES IN CHINA		
	TOTAL NO. SPP.	GENERAL DISTRIBUTION	RECORDED & RECOGNIZED		DISTRIBUTION & REMARKS
Handelia	1	Monotypic.	1	0	Not in Chinese territory.
Achillea (603)	100	N. hemisphere.	14	10	See map 10.
Ptarmica			6	0	= *Achillea.*
Matricaria (610)	50	Med. reg, S. Afr, Eur, As.	14	4	He, St, Hp, L.
Allardia (614)	2	Centr. As.	2	2	Tib, Sin; endemic.
Waldheimia	2		2	0	= *Allardia.*
Formania	1	China.	1	1	Y; endemic.
Filifolium	1	N. China.	1	1	Hp, to He; endemic.
Brachanthemum	5	Centr. As.	5	5	Sin, M, Kan; arid regions.
Chrysanthemum (612)	200	Eur, As, Afr, Canary Is.	96	73	See map 11.
Pyrethrum (612b)	50?	Centr. & W. As.	18	5	Sin.
Tanacetum	130	Centr. & W. As.	44	0	= *Chrysanthemum*
Cancrinia (633)	9	Centr. As.	4	3	Sin, Tib, Y, Kan.
Cotula (622)	50	Temp. & subtrop. reg.	4	2	T, Kt, Hup, Sze.
SOLIVA (623)	6	S. Am, Austr, N. Am.	1	1	T; adventive.
Centipeda (624)	5	Austr. trop. As. Mad, Chile.	1	1	T, Kt, H, Che, Ku, Hun, Sze, Hp, St; widespread weed.
Myriogyne	1		1	0	= *Centipeda.*
SPHAEROMORPHAEA	1	India, Siam.	1	1	T; adventive.
Crossostephium (630)	1	Luzon, E. As.	1	1	T, Kt; monotypic.
Stilpnolepis	1	Monotypic.	1	1	Sy; endemic.
Artemisia (629)	200	Cosmopolitan.	186	156	See map 12.
		* * * * *			
Senecioneae					
Stereosanthus (650)	4	China.	5	4	Y, Sze, Si; endemic.
Nannoglottis (649)	2	China.	2	2	Kan, Y; endemic.
Tussilago (651)	1	N. Afr, Eur, As, Am.	5	1	Y, Sze, Hp, Sy, Se, Kan, Sin.
Petasites (652)	14	N. hemisphere.	10	9	T, Ku, Hup, Sze, St, M, Y, Se, Si.
Nardosmia	19	N. hemisphere.	3	0	= *Petasites.*
Erechtites (660)	15	Trop. Am, Austr, N. Zeal.	2	2	T, H, Y, Ks, Kt.
Doronicum (671)	25	N. hemisphere.	6	3	Y, Sze, Si, Se, Kan, N, M, Sin, Tibet.
Gynura (676)	25	Trop. As, Austr, Afr.	26	16	T, H, Sze, Si, Kt, Y, Kwe, Hup, Che, Se, A.
Emilia (682a)	40	Trop. Afr, Mad, trop. As.	10	3	Kt, Che, westward to Y.
Cineraria (677)	25	S. Afr, Mad.	9	1	Largely transferred to *Senecio* or *Ligularia.*

TABLE II. (*Continued*)

TRIBES & GENERA	WORLD FIGURES		SPECIES IN CHINA		
	TOTAL NO. SPP.	GENERAL DISTRIBUTION	RECORDED & RECOGNIZED		DISTRIBUTION & REMARKS
Cacalia (680)	70	As, N. & Centr. Am.	67	60	Widespread; not in F, Kt, H; endemic sp.
Parasenecio	1		1	0	= *Cacalia.*
Syneilesis	4	China.	4	4	Kir, He, Che, A, T; see *Senecio.*
Chlamydites	1	Monotypic.	1	1	Tib; endemic.
Senecio (682)	1200	Cosmopolitan.	363	160	See map 14.
ARNICA (667)	20	N. Am, Eur.	3	1	Cultivated.
Ligularia (683)	150	Eur, As.	125	105	T, Y, Sze, Si, Kan, Kwe, Sa, M, Sin, Tib, L, Kir, Ki, St, Hn, Che, Hun, Hup, Hp, Chi, He, Sy, Cha, J.
Farfugium	3	E. As.	4	1	T, Kt, Che, Hup.
Senecillis	70	Centr. & E. As.	45	0	= *Ligularia.*
Cremanthodium (684)	60	Himal. reg.	57	47	See map 15.
Werneria (686)	30	S. Am, trop. Afr.	2	0	Transferred to *Cremanthodium.*
		* * * * *			
Calenduleae					
CALENDULA (694)	15	Med. reg. to Persia.	2	2	Cultivated.
		* * * * *			
Arctotieae					
ARCTOTIS (703)	60	S. Afr.	2	1	Cultivated, recent introduction.
Gorteria (704)	4	S. Afr.	1	0	Misidentified.
		* * * * *			
Cynareae					
Echinops (713)	60	E. As, S. Eur, Med. reg., S. Afr.	15	11	Lower Yellow River.
Xeranthemum (716)	6	Med. reg., W. As.	2	0	= *Helichrysum* or *Blumea.*
Atractylis (721)	15	Canary Is, Med. reg., N. Afr.	9	8	North of Yangtze, lower Yellow River.
Atractylodes			8	0	= *Atractylis.*
Giraldia			1	0	= *Atractylis.*
Arctium (723)	6	Eur, As, N. Am.	3	2	N. China to Sin.
Cousinia (724)	250	Centr. As.	2	2	Tib, Sin; arid regions.
Xanthopappus (726)	2	NW. China.	2	2	Chi, Si, Kan; endemic.
Takeikadzuchia	1	N. China.	1	1	Cha; endemic.
Olgaea	11	N. China.	11	9	M, Kan, N, Sa, Sin, Hp; endemic.
Alfredia	11	Centr. As.	3	0	Not in Chinese territory.
Carduus (732)	100	Eur, Afr, As.	19	11	See map 16.
ONOPORDON (738)	20	Afr, Eur, W. As.	1	1	Sink.

TABLE II. (*Continued*)

TRIBES & GENERA	WORLD FIGURES		SPECIES IN CHINA		
	TOTAL NO. SPP.	GENERAL DISTRIBUTION	RECORDED & RECOGNIZED		DISTRIBUTION & REMARKS
Cnicus (750)	1	Eur, As.	32	0	Transferred to *Cirsium*.
Cirsium (733)	150	N. Afr, Eur, As, N. & Centr. Am.	70	59	Widespread.
Cephalonoplos	4	E. As.	3	3	St, Sa, Se, Kir, He, L, J, Cha, Sy, Tib; a segregate from *Cirsium*.
CYNARA (734)	12	Med. reg.	2	2	Cultivated; recent introduction.
Hemistepta	1	E. As.	1	1	T, Kt, Ku, Y, Sze, St, Hn, Hp, Se; monotypic, a common weed.
Saussurea (728)	125	N. hemisphere, Austr.	338	270	See map 17; largest genus in China.
Bolocephalus	1	Monotypic.	1	1	Si; endemic.
Vladimiria	1	Monotypic.	1	1	Y; endemic.
Mazzettia	1		1	0	= *Vladimiria*.
Jurinea (730)	50	Centr. & S. Eur, N. Afr, W. & Centr. As.	18	18	Y, Sze, Tib, Sin.
Tricholepis (744)	12	Himal. reg.	1	1	Y, Tib.
Synurus	8	Temp. As.	4	3	Che, Ki, Hup, St, Hp, Se, Kir, He.
SILYBUM (735)	2	Canary Is, Med. reg. to Persia	1	1	Introduced.
Serratula (745)	40	Eur. to Japan	43	19	See map 18.
Leuzea			1	0	Transferred to *Rhaponticum*.
Rhaponticum			1	1	Hp, Se, Kir, He, Cha.
Centaurea (747)	500	Med. reg., Eur, As, N. & S. Am, Austr.	8	7	Sin, Ku, Hn, to M, Tib, Kan.
CARTHAMUS (748)	20	Med. reg. to Centr. As.	1	1	Cultivated in W. China.
		* * * * *			
Mutisieae					
Leucomeris (756)	2	E. Himal. Reg.	1	1	Y.
Pertya (775)	12	Afghan. to Japan	12	10	Y, S, Kan, to Che, Kt.
Myripnois (782)	2	China.	3	2	Hopei to Kansu, endemic.
Ainsliaea (783)	50	India to Japan.	58	47	Y, Sze, due east to Taiwan.
Nouelia (791)	1	Monotypic.	1	1	Y, Sze; endemic.
Gerbera (798)	40	S. Afr, Mad, trop. As, Tasmania.	18	10	Kt, Hun, Hup, Y, Kwe, Sze, St, Hp, Sa, Se, Kan, M, St, N, Kir, Cha; 2 widespread, the others endemic.

TABLE II. *(Continued)*

TRIBES & GENERA	WORLD FIGURES		SPECIES IN CHINA		
	TOTAL NO. SPP.	GENERAL DISTRIBUTION	RECORDED &	RECOGNIZED	DISTRIBUTION & REMARKS
Leibnitzia	5	E. As.	4	4	T, Kir, He, J, Y, Tib; segregate from *Gerbera*.
Anandria	6	E. As.	2	0	Misidentified; = *Gerbera*.
		* * * * *			
Cichorieae					
Cichorium (823)	8	Med. reg. to temp. As.	2	2	Ku, St, Hp, Sa, Se, Sin; cultivated or weeds.
Lapsana (825)	9	Eur, As, Am.	3	3	Kt, Che, Ku, Ki, Hup, Sze, Se; 1 widespread along Yangtze, 2 localized, coastal.
Koelpinia (832)	3	Med. reg., Afr, Centr. As.	1	1	Sink.
Acanthocephalus	2	Centr. As.	1	0	Not in Chinese territory now.
Rhagadiolus	8	Centr. As.	1	0	Not in Chinese territory now.
Hypochoeris (842)	50	Eur, Med. reg, N. As, N. Am.	4	3	Kir, He, Jehol, St, Hp, L.
Heteracea	1	Centr. As.	1	0	Not in China.
Tragopogon (849)	40	Eur, Med. reg, W. & centr. As.	10	10	See map 20; Centr. Asian element.
Scorzonera (851)	100	Eur, Med. reg, W. & Centr. As.	20	18	See map 20.
Picris (845)	40	Eur, Med. Reg, Abyss, temp. As.	9	8	Kir, He, Y, Sze, St, Sin, Kt, Kan; 1 widespread, 2 endemic.
Lagoseris	32	centr. & W. As.	1	0	Not in China.
Taraxacum (862)	1200?	Cosmopolitan	67	57	See map 21.
Leontodon	123	Eur, centr. & W. As.	8	0	Chinese spp. = *Taraxacum*
Chondrilla (860)	18	Eur, As.	3	3	Sin, Kan.
Sonchus (865)	45	Cosmopolitan	19	10	Widespread; weedy.
Launaea (863)	30	Med. Reg, S. Afr, trop. As, E. Indies	5	4	H, Y, Sze.
Lactuca (866)	150	Cosmopolitan.	112	81	See map 22.
Mycelis	5	E. As.	2	0	= *Lactuca*.
Cicerbita	60	Centr. As.	7	7	Y, Si, Sze.
Mulgedium	7	Centr. As.	2	0	= *Lactuca*.
Soroseris	9	W. China.	9	9	Y, Sze, Kan, Chi, Sin; endemic.
Prenanthes (876)	30	Eur, Med. reg, Canary Isl, As. Am.	25	19	Y, Sze, Si, Tib, Hup, Hun, Kan, Se, Sa, St, Hp, Cha, Kir.

TABLE II. (*Continued*)

TRIBES & GENERA	WORLD FIGURES		SPECIES IN CHINA		
	TOTAL NO. SPP.	GENERAL DISTRIBUTION	RECORDED &	RECOGNIZED	DISTRIBUTION & REMARKS
Faberia (872)	6	W. China.	7	6	Y, Sze, Kwe; endemic.
Crepis (875)	200	N. hemisphere.	83	31	See map 23.
Barkhausia			4	0	= *Crepis.*
Geblera			2	0	= *Youngia.*
Youngia	35	Himal. reg. to Japan.	39	30	See map 22.
Ixeris	20	Himal. reg. to Japan.	26	14	See map 23; common weed.
Crepidiastrum	7	E. As.	4	3	T, Che.
Dubyaea	**12**	E. Himal. reg.	12	7	Y, Sze.
Hololeion	3	Japan.	1	1	Ku.
Hieracium (877)	400	Eur, Am, Afr, As.	17	14	Ku, Ki, T, Sze, Kwe, Sin, Hp, M, Se, St, Kir, He, Cha, Sy; mostly isolated spp. known from one collection.
Crepidiastrixeris	3	Japan, E. China.	1	1	Che; a hybrid genus.

With the exclusion of the doubtful and invalid genera there are only 167 genera of Compositae in China. Most of these genera are small. Fifty-seven of them have only one species each, and 40 others have 2 or 3 species each. The largest of all is *Saussurea* with 279 species. The next in size are *Senecio* with 160 species, *Artemisia* with 156, *Aster* with 137 and *Ligularia* with 105 species. Some botanists, such as Franchet, interpret *Senecio* in a broader sense and place *Ligularia, Cacalia* and *Cremanthodium* in it as sections. In this broader sense, *Senecio* would have 372 species in China and thus become the largest genus of Compositae in that country, as it is also the largest genus of the Compositae in the world.

1. The Large Genera and Their Distributions

Only 38 genera of the Chinese Compositae contain ten or more species. For convenience of discussion, these are called the "large genera." They are scattered in the Vernonieae, Eupatorieae, Astereae, Inuleae, Anthemideae, Senecioneae, Cynareae, Mutisieae and Cichorieae (Table I). By plotting the occurrence of all the species of a large genus on an outline map of China, striking distributional patterns of these large genera are revealed. In these maps circles represent species occurring only in one province and the dots denote species recorded from two or more provinces. The combined number of circles and dots within the confines of a province gives the total number of species of the genus under discussion in that province. Thus a distribution map for a given genus tells both its range and its area of concentration of species. In a few cases two relatively small genera are plotted on one map. Triangles are used to represent the species of the second genus, with the white ones indicating local endemics and the solid ones species of wider range.

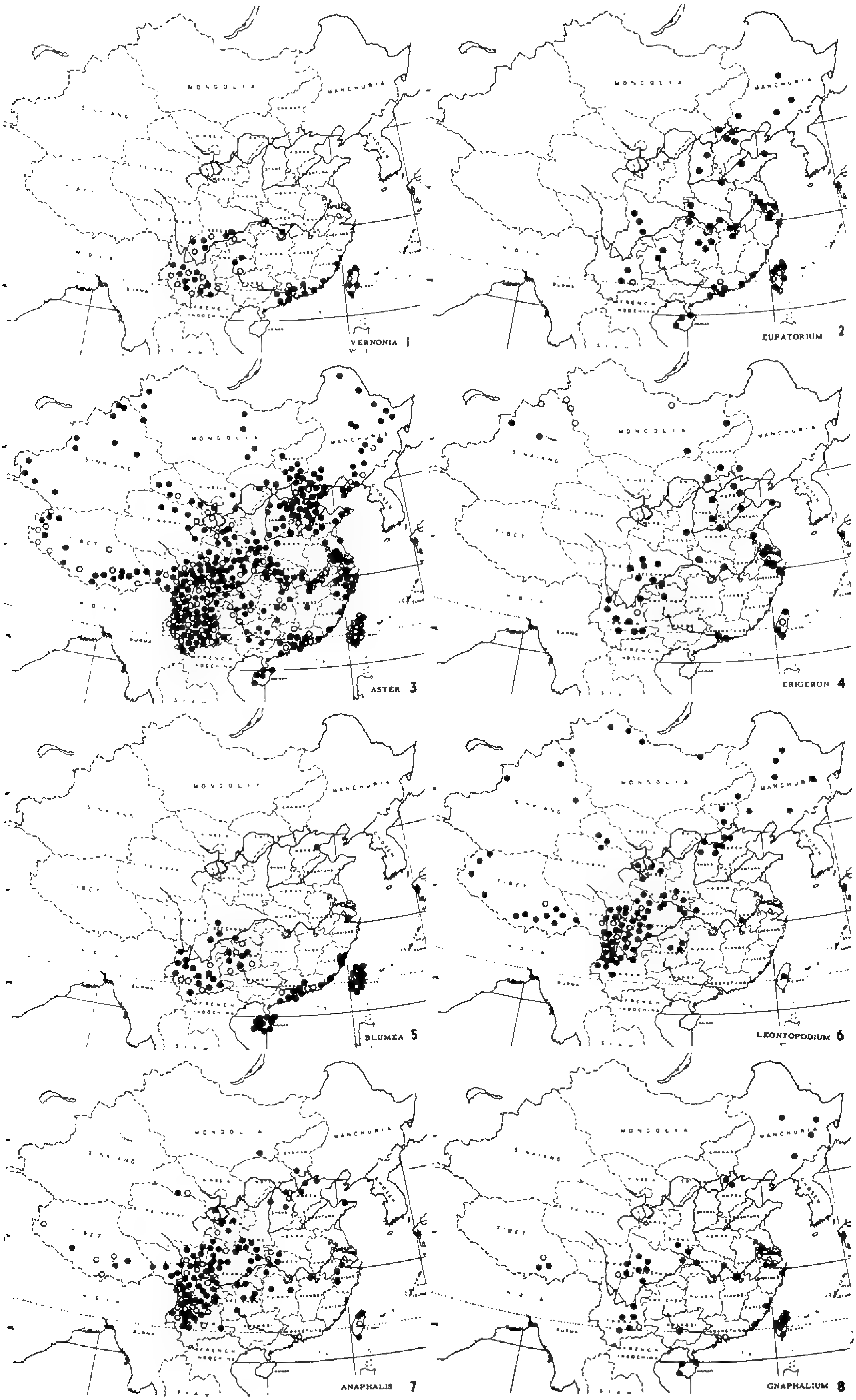
Vernonia is a genus of wide range with species in the Americas, Africa, Madagascar, and tropical Asia. In China there are thirty-four species, with a concentration in Taiwan, Kwangtung, Yunnan and Szechuan. Ten of these thirty-four have an Indo-Malaysian range, two of them extend to Java, and twenty of them are endemic to China. Six of these endemics occur in Yunnan (MAP 1). In general *Vernonia* is a southern genus and its range does not reach north of the Yangtze River.

Eupatorium is another widespread genus with many species, especially in Central and South America, Africa, Europe and Asia. In China there are seventeen species, and most of them are evenly distributed from Hainan to Heilungkiang (MAP 2). Endemism is relatively low. Taiwan seems to have the largest species concentration. It is interesting to note that this genus is absent in the northern and western half of the country.

Aster is the third largest genus of Compositae in China. It contains 137 species occurring in every province of the country. The centers of species concentration are Yunnan (51 species), Szechuan (48 species), Sikang (30 species), Kansu (20 species) and Hopei (20 species). Taiwan has 15 species. Considering the small size of the island, the genus is very well represented there. This genus has many widespread species in China. For example, *A. ageratoides* and its varieties occur in twenty-three provinces and *A. altaiacus* and its varieties occur in nineteen provinces. Many species share the Yunnan-Szechuan-Kansu range. Local endemism is high for the genus. Of the endemic species, Yunnan, with its 15 species, has the highest number, Szechuan has 13, Taiwan 10, Tibet 9, Kansu 6, Sikang 5. It is interesting to note that the species in Sinkiang are all widespread, while nearly half of the 21 species in its neighboring province, Tibet, are local endemics (MAP 3).

Erigeron is a widespread genus with species occurring in America, Australia, Asia and Europe. In China there are twenty-five which are fairly evenly distributed throughout the country. They are absent from Ninghsia, Kansu, Chinghai and Tibet (MAP 4). There are several weedy species which occur in extensive areas. For example, *E. acer* occurs in ten provinces from Hupei and Szechuan due north to Kirin and westward to Sinkiang. *E. canadensis* has an even wider range, occurring in fourteen provinces from Taiwan-Kwangtung northward to Kirin and thence due west to Sinkiang. This genus has very few endemic species. Half of the eight endemics are in the Altai region.

Blumea is a genus with an African-Asiatic-Australian range. In China there are thirty species which concentrate in Taiwan, Kwangtung, Hainan,



Maps 1–8. The geographical ranges in China of eight large genera of Compositae in the tribes Vernonieae, Eupatorieae, Astereae, and Inuleae.

Yunnan and Kweichow (MAP 5). Most of the species have an Indo-Malaysian distribution. In China they occur largely in the few border provinces where there are port cities. The large number of endemics in Kweichow (50%) is evidently due to the careless work of Léveillé and Vaniot who published too many species from fragmentary collections. *Blumea* serves as a good example of the route of migration and the area of extension of tropical elements in the flora of China.

Leontopodium is a discontinuous genus occurring in the high mountains or high latitudes of Europe, Asia and South America. In China there are 57 species which are concentrated in Yunnan, Szechuan, Sikang and Tibet, and thence northeastward through Kansu, Shansi, Chahar to Heilungkiang and Mongolia. In the mountains of the Meridional Ranges there are many endemics and hybrids (MAP 6). It is very likely that this region is both the center of concentration and the place of origin of the genus. For example, *L. kamtschaticum*, as is indicated by many recent collections, is concentrated in Sikang; thence it extends westward to Tibet, and northeastward to Szechuan, Kansu, Chahar, Mongolia, Heilungkiang, Far Eastern Russia and Kamchatka. It is evident that although the species was first described from Kamchatka, this peninsula is only on the periphery of its range. *Leontopodium japonicum* tells almost the same story. It is very likely that the species originated in the west, somewhere in the mountains on the Kansu-Shensi-Szechuan border, thence it extended eastward through Hupei and Anhwei to Japan or through Hopei and Korea to Japan. These are common routes for the migration of many Sino-Japanese species.

Anaphalis is another genus which has a discontinuous range and which has its concentration of species in the Meridional Ranges of China. It has been recorded from Europe, Asia and North America, but the bulk of the species are in China. There are 51 species, many of them local endemics, concentrated in Yunnan, Szechuan, Sikang and Kansu (MAP 7).

Gnaphalium is a genus of the warm regions throughout the world. In China there are twenty species, rather evenly distributed from Hainan to Heilungkiang. Although there are a few endemics in Yunnan, Sikang and Tibet, there is no region which can be considered as the center of concentration of species for this genus. There are a few widely spread species. For example, *G. affine* extends from Taiwan to Nepal, occurring in fifteen provinces in China. It is a very tough species and colonizes all sorts of waste places, even the perpendicular cracks of dry hard city walls. *G. hypoleucum* is another widespread species which extends from Taiwan to Nepal. It occurs in eight provinces. It is interesting to note that in China the species occurs only in areas where there are large centers of commercial or political activity (MAP 8).

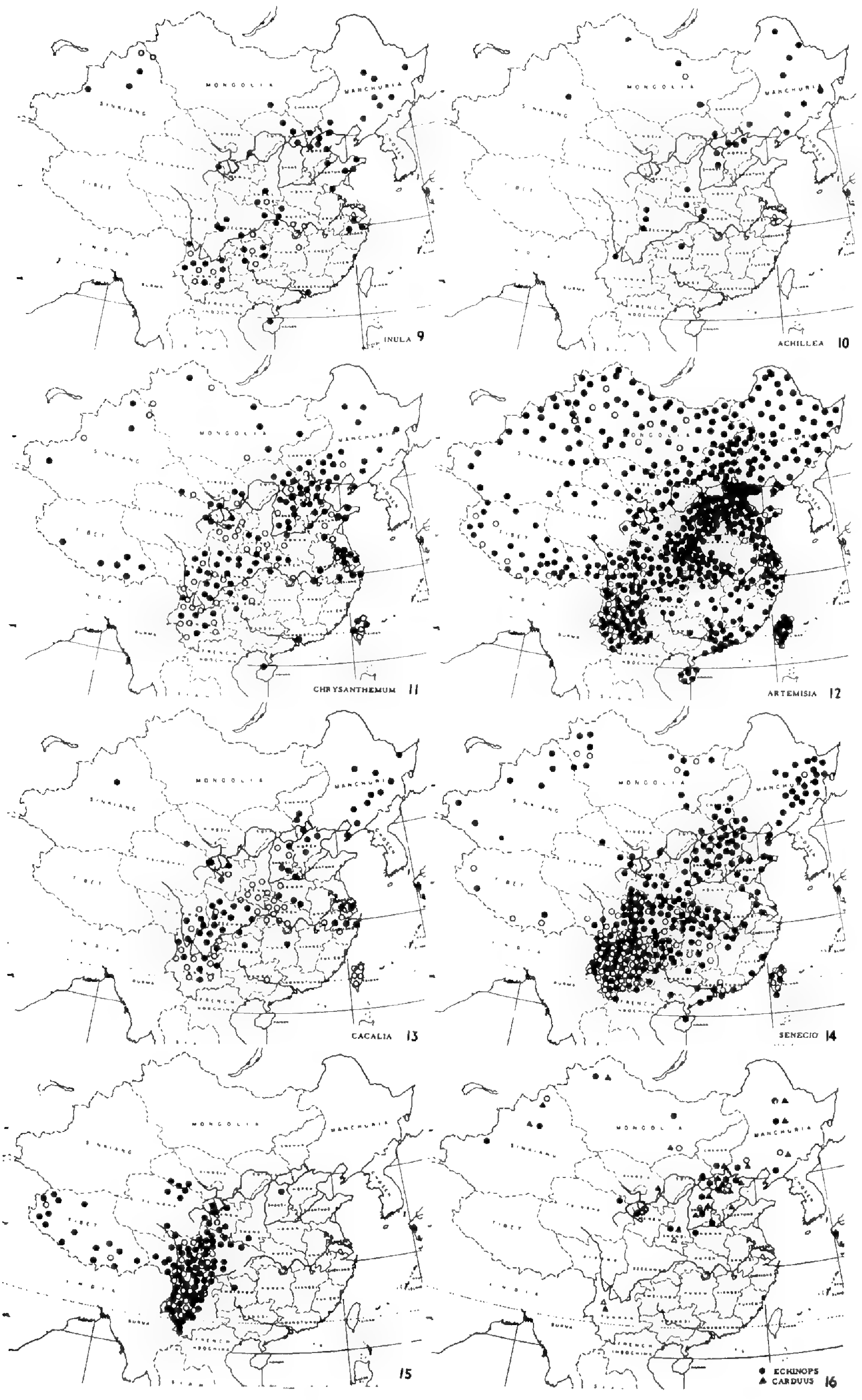
Inula is an Old World genus with species occurring in Africa, Europe and Asia. In China there are twenty-eight species which are evenly distributed in the temperate and the mid-high altitudes of the subtropical regions (MAP 9). It seems that Yunnan, Szechuan and Kweichow constitute the center of the species concentration. In Yunnan and Kweichow almost half of the species are endemics. There are a few widespread species. For example, *I. britannica* and its varieties occur in fifteen provinces north of the Yangtze River and *I. cappa* occurs in six provinces south of the same river. Several species of this genus are very good indicators of the types of vegetation in China. In addition to *I. britannica* and *I. cappa,* which have a northern or a southern distribution, *I. salsoloides* expresses a special floristic relationship between Hopei, Chahar, Suiyuan, Ninghsia, Shansi, Shensi, Kansu, Chinghai and Sinkiang, and *I. serrata* illustrates the floristic affinity between Sikang, Yunnan and Kweichow.

Carpesium is a genus of the north temperate or subtropical regions of the Old World. Its range extends from Europe through Asia to Japan. It has eighteen species in China. It seems to have two centers of concentration, the one being Yunnan, Szechuan, Sikang, Hupei, Shensi, Shansi and Hopei and the other being Taiwan and Kwangtung. There are several widespread species. *Carpesium abrotanoides* occurs in twelve provinces, from Taiwan-Kwangtung westward to Yunnan and Sikang and thence due north to Shensi and Hopei. *Carpesium cernuum* shares the same range, but extends even more northward to Kirin. There are relatively fewer local endemic species in this genus.

Achillea is a widely distributed genus of the northern hemisphere. There are 10 species in China. With the exception of a southern variety of *A. sibirica*, which occurs in Kweichow and Yunnan, and an Eurasian-American species, which was recorded from Chekiang, the genus is restricted to the north of the Yangtze River (MAP 10). Its distribution is a good illustration of the southern limit of the northern elements in the flora of China.

Chrysanthemum is a large genus with species occurring in Europe, Canary Islands, Africa, temperate Asia and America. In China there are seventy-three species, many of which are local endemics known only from the type collection. Most of the endemic species are in Sikang, Yunnan, Szechuan, Kansu, Shensi, Shansi, Mongolia and Sinkiang (MAP 11). The taxonomy of this group is in bad shape, and it is highly possible that many of the endemics described as species in this genus are merely local variants of a few species. It is interesting to note that the genus is poorly represented in low altitudes of South China. *Chrysanthemum indicum* is a widespread species recorded from thirteen provinces.

Artemisia is a cosmopolitan group which in China is the second largest genus of Compositae. Its 156 species represent every province of the country. As far as the number of species in each province is concerned, Hopei takes the lead with 59 species, 3 of which are local endemics. Yun-



MAPS 9–16. The geographical ranges in China of eight large genera of Compositae in the tribes Inuleae, Anthemideae, Senecioneae, and Cynareae.

nan has 50 species, 11 of which occur in that province alone. Szechuan has 41 species, 5 of which are local endemics. Taiwan has 25 species, 7 of which are endemics. Considering the small size of the island, the genus is very well represented there. In fact, *Artemisia* is the only genus of Compositae that has been recorded from every province (MAP 12). This genus needs revision; many local variants, apomictic or polyploid forms have been named as species and, consequently, many taxa show anomalous patterns of distribution. For example, *A. dubia* var. *septentrionalis* has been recorded from Hainan, Kweichow and Hopei, and *A. handel-mazzettii* has been recorded from Yunnan and Hopei only. Such disjunction is not known in any other species of flowering plants in China.

Gynura has an African-Asiatic-Australian distribution. There are 16 species in China. With the exception of *G. ovalis* var. *pinnatifida*, which extends into the southern part of Shensi, all the rest are distributed to the south of the 30°N. parallel. Thus the species of *Gynura* serve as good examples for showing the northern limit of the range of southern elements in the flora of China.

Cacalia is an Asiatic-American genus. Its species occur in Asia, North America, Central America and the West Indies. In China there are 60 species which are distributed in high altitudes and mid-latitudes. Yunnan, Szechuan, Sikang, Kansu, Shensi, Shansi, Hupei, Hopei and Honan seem to be the center for the concentration of the species. It has a high percentage of endemism (MAP 13). Forty per cent of the species in Yunnan are known only from the type material. All the species in Taiwan are endemics. *Cacalia* is morphologically closely related to *Senecio* and *Ligularia*. The distributional patterns of these three genera are also similar. It is worthy of note that this is the only genus that has 5 species in Honan, a province in which other genera of Compositae are relatively poorly represented.

Senecio is the largest genus of Compositae, and a very heterogenous one. Its species occur in all parts of the world. In China, because of the recognition of *Cacalia*, *Ligularia* and *Cremanthodium*, all of which are included in this genus by some authors, *Senecio* becomes the second largest genus. However, if Franchet or James Small's interpretation of the genus were adopted, *Senecio* would be the largest genus in China. The concentration of species of this genus is in Yunnan, Szechuan, Sikang, Kweichow and Hupei (MAP 14). In Yunnan alone there are 73 species, 41 of which are known only from that province. Szechuan has 51 species, 12 of which are local endemics. Sikang has 13 species, 6 of which are local endemics. Kweichow has 23 species, 7 of which are not known elsewhere.

Ligularia is a genus with European-Asiatic distribution. In China there are 105 species highly concentrated in Yunnan, Szechuan, Kansu and Hopei. In Yunnan alone there are 50 species, 27 of which are known only in that province. Szechuan has 49 species, 14 of which are local endemics.

Cremanthodium is an endemic genus of the Meridional Ranges. Its distribution extends to the Himalayan Region. In China there are 47 species concentrated in Yunnan, Sikang, Szechuan, Tibet and Kansu (MAP 15). There are 38 species in Yunnan, about one-fourth of which are endemic to that province. Within China this genus is strictly limited to the Southwest. Its closely related genera *Cacalia*, *Senecio* and *Ligularia* are all well represented in Taiwan, but the range of *Cremanthodium* extends hardly beyond the Long. 110° E.

Echinops is an Old World genus with species occurring in southern Europe, the Mediterranean region, tropical Africa and eastern Asia. There are 11 species in China distributed north of the 35° N. parallel (MAP 16). Judging from the specimens in the Gray Herbarium, the center of concentration of the species appears to be western and central Asia. China is only on the periphery of its range. Several species have a considerably wider range. For example, *E. latifolius* extends from Dahuria to Honan, and *E. gmelinii* covers almost the same area. There are four endemic species known only from their type collections.

Carduus is another European-African-Asiatic genus. There are eleven species in China, two of them with wide ranges. *Carduus acanthoides* occurs in six provinces from Yunnan-Kweichow northward to Kansu and Hopei. *Carduus crispus* has an even wider range, occurring in 16 provinces from Chekiang westward to Szechuan and northward to Heilungkiang and Mongolia. The other species are local endemics (MAP 16).

Cirsium is a widespread genus with species occurring in North Africa, Asia and North and Central America. There are 59 species in China. They are distributed throughout the country. Yunnan, Szechuan, Kweichow and Taiwan are areas of high endemism. Yunnan has 22 species, 13 of which are confined to that province. Taiwan has 12 species, 7 of which are endemics. There are several widespread species. For example, *C. arvense* (first recorded from the Canary Islands), and its various varieties occur in 11 provinces, from Kiangsu to Heilungkiang and thence due west to Sinkiang. *Cirsium chinense* is another widespread species. Its range extends from Taiwan to Yunnan and northward to Shensi and Hopei. In most places it is a very troublesome weed.

Saussurea is a genus widely distributed throughout the northern hemisphere and the mountains of Australia. In China it constitutes the largest genus of the Compositae. There are 279 species, especially well represented in Yunnan, Szechuan, Sikang, Tibet, Hupei, Kansu, Shensi, Shansi, Hopei, Jehol, Kirin, Mongolia and Sinkiang (MAP 17). Yunnan alone has 94 species, 53 (almost 57%) of which are confined to that province.

There are 82 species in Szechuan. Twenty-six (almost 32 per cent) of them are local endemics. Twenty-two (a little over 43 per cent) of the 51 species from Sikang are endemic to that province. It is interesting to note that the genus is poorly represented in eastern and southern China, and it has never been recorded from Kwangsi, Hainan and Honan. It is evident that the species of this genus prefer high altitudes or high latitudes.

Jurinea is an Old World genus with species occurring in central and southern Europe, North Africa, western and central Asia. In China there are 18 species, all of which are local endemics (MAP 18). They are known only from a few western provinces, and often only through the type collection.

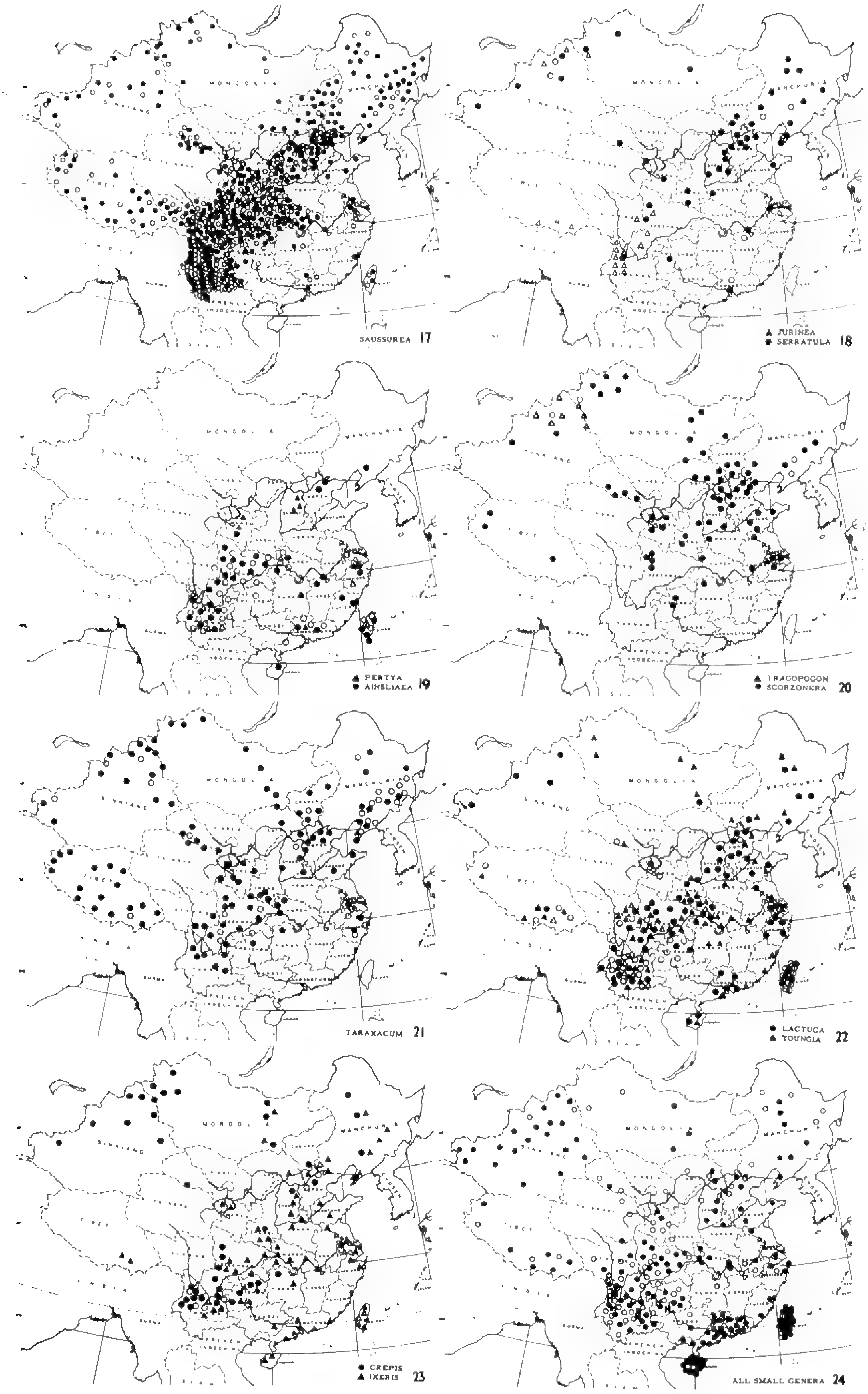
Serratula is another Old World genus occurring in Europe and North Africa, thence due east to Japan. In China there are nineteen species distributed chiefly north of the Yangtze River. Some species also occur in Kirin, Heilungkiang, Mongolia and Sinkiang (MAP 18).

Pertya is an Asiatic genus occurring from Afghanistan to Japan. There are ten species in China, all with very limited range (MAP 19). Almost half of them are known only through the type material.

Ainsliaea is another Asiatic genus. Yunnan, Szechuan and Hupei constitute its center of distribution, and northern India and Japan are on the periphery of its range. There are 47 species in China (MAP 19). Many of them are local endemics. For example, there are 22 species in Yunnan, 14 of which are endemic to that province. There are several species which indicate the relationship between the flora of Taiwan and the mainland of China. For example *A. fragrans* occurs in Taiwan, Kwangtung, Chekiang, Kiangsu, Kiangsi and Hopei. *Ainsliaea macroclinidioides* has the same range. In both cases the type localities are on the periphery of the range of the species. *Ainsliaea reflexa* and its varieties occur in Taiwan and also in Yunnan. This distributional pattern is common with many genera of woody plants.

Gerbera is a southern genus with species occurring in South Africa, Madagascar, tropical Asia and Tasmania. There are 10 species in China, and Yunnan and Szechuan again constitute the center of the species concentration. *Gerbera anandria* is a widespread species. It occurs in 15 provinces from Kwangtung northward to Kirin and Mongolia. A little over 45 per cent of the eleven species and varieties in Yunnan are endemic.

Tragopogon is an Old World genus with species occurring in Europe, the Mediterranean region, and western and central Asia. There are 10 species recorded from China. With the exception of three European species (one recorded from Nanking as a cultigen, and two from gardens in Peking) all the rest are localized in Sinkiang, especially the Tien-shan-Altai region



MAPS 17–23. The geographical ranges of seven large genera of Compositae in the tribes Cynareae, Mutisieae and Cichorieae. MAP 24. The distributions of small genera of Compositae in China. Dots = endemics, circles = adventives, and H = Himalayan genera.

(MAP 20). *Tragopogon* is a good example of the extent of Central Asiatic elements in the flora of China.

Scorzonera is another Old World genus with species occurring in Europe, the Mediterranean region, western and central Asia, and thence due east to China, Korea and Japan. In China, there are eighteen species distributed in the arid regions of mid-high latitudes and the arid regions of Szechuan and Tibet (MAP 20). The percentage of local endemics is low. Several species have wide ranges. For example, *S. albicaulis* occurs in twelve provinces from Chekiang westward through Hunan and Kweichow to Szechuan and thence due north through Honan, Shantung, Shensi and Hopei to Chahar, Liaoning and Kirin. *Scorzonera austriaca* occurs in eight provinces extending from Kiangsu northward through Honan, Shantung to Kansu and Mongolia. It is worthy of notice that in the distribution of *Senecio, Ligularia, Saussurea* and many other genera of Compositae, Yunnan and Szechuan are twin provinces in respect to high numbers of species, but this is not so with *Scorzonera*. Four species of *Scorzonera* have been recorded from Szechuan and none from Yunnan.

Taraxacum is a cosmopolitan genus of weedy species. The taxonomy of this genus is very difficult. When Handel-Mazzetti published his monograph of *Taraxacum* in 1907, he included 57 species. Index Kewensis lists in all over 1200 species, but binomials have been assigned to many apomictic forms. It is very hard to decide what is the approximate number of species of this genus in China. When Dahlstedt published H. Smith's collection in 1926 he added one-fourth more binomials to the Chinese *Taraxacum*. With the species added by Kitagawa in 1933–38, and Koroleva in 1940, 57 have been recognized from China. It seems that a large number of species are found in Yunnan, Szechuan, Tibet, Kansu, Sinkiang, Mongolia, Chahar, Liaoning and Kirin (MAP 21). It is interesting to note that this genus is poorly represented in the warmer regions of China. It has not been recorded from Fukien, Kwangtung, Kwangsi or Hainan.

Sonchus is another cosmopolitan and weedy genus. There are 10 species in China, several of them widespread. *Sonchus arvensis* and its varieties occur in twenty provinces, from Taiwan and Kwangtung northward to Sinkiang, Mongolia and Kirin and *S. oleraceus* occurs in fourteen provinces, from Hainan northward to Kirin and westward to Sinkiang. Four local endemics have been recorded from Yunnan, Szechuan, Kweichow and Tibet. There seems to be no center of species concentration in China.

Lactuca is a cosmopolitan genus. There are 57 species in China distributed from Kwangtung and Hainan northward to Kirin and Heilungkiang. It seems that Yunnan, Szechuan and Kweichow form a center of concentration of species on the mainland, and Taiwan furnishes an area of diversification off the coast. A high percentage of endemism occurs among species in both regions. In Yunnan there are 27 species, 17 (about 63 per cent) of which are endemics. In Taiwan there are 14 species, 11 (79 per cent) of which are endemics. There are a few widespread species: *L. indicus* and its varieties occur in 15 provinces, from Kwangtung northward to Kirin and *L. tatarica* occurs in 8 provinces, from Honan to Mongolia and westward to Sinkiang (MAP 22).

Prenanthes is a widespread genus with species occurring in South Africa, the Canary Islands, the Mediterranean Region, Europe, Asia, and America. The strongest development of this genus is in central and northern Europe. There are nineteen species in China. Yunnan, Szechuan and Kweichow again form the center of concentration of species. High ratios of endemism occur in Szechuan and Kweichow, where over 60 per cent of the species are known only from the type localities. There are a few widespread species. *Prenanthes brunoniana* and its varieties occur from northern India eastward through Yunnan, Kweichow to Hupei and Hainan. *Prenanthes tatarinowii* and its varieties occur in eight provinces from Hupei northward to Chahar and Kirin.

Crepis is a widespread genus with species occurring in the Canary and Madeira Islands, Europe, Africa, Asia, and North America. In China there are 31 species, concentrated in Yunnan, Szechuan, Kweichow, Sikang, Tibet, Sinkiang, and Mongolia (MAP 22). Yunnan seems to be the area of the highest species-diversification. It has not only the largest number of species but also the highest ratio of endemism (about 30 per cent). Most species have small ranges, usually limited to two or three provinces. For example, *C. rigescens* is limited to Yunnan and Szechuan, *C. tibetica* to Yunnan, Sikang and Tibet, *C. bodinieri* is confined to northern Yunnan and the adjacent area of Szechuan, and *C. chrysantha* to the Altai Region. As suggested by Babcock, *Crepis* is originally an Asiatic genus and the Altai region (northwestern Sinkiang and southwestern Mongolia) seems to be its center of origin. This region is still a part of the center of the concentration of species for the genus today. It is also worthy of note that *Crepis* is not represented in Taiwan, Fukien, Kwangtung, Hainan, Chekiang, Anhwei, Kiangsi, Shantung, Honan or Kirin.

Youngia is an Asiatic genus with species occurring from the Himalayan Region eastward to Japan. In China there are thirty species distributed from Hainan, Kwangtung and Taiwan, thence northward to Heilungkiang (MAP 22). Like *Crepis*, it has its center of species concentration in Yunnan and Szechuan, but it differs from *Crepis* in that it occurs also in the tropical regions. Again it differs from *Crepis* in that it has many widespread species. For example, *Y. japonica* and its varieties occur in thirteen provinces from Hainan, Kwangtung and Taiwan northward to Shantung, Hopei and Shensi. *Youngia sonchifolia* occurs in thirteen provinces from Chekiang to Szechuan and thence due north to Kirin and Heilungkiang.

Ixeris is another Asiatic genus with species distributed from the eastern Himalayan Region to Japan. In China there are fourteen species ranging from Hainan and Kwangtung northward to Heilungkiang (MAP 23). Most of them are widespread weeds. For example, *I. chinensis* occurs in twenty-one provinces. Actually it is very difficult to determine the approximate number of species of *Ixeris* in China, since contemporary authors do not agree on the status of some of the taxa. The criteria for distinguishing *Ixeris*, *Youngia*, *Crepis* and *Lactuca* are not sufficiently strong and many species have been changed back and forth among these genera. For example, *I. chinensis* has been named *Prenanthes chinensis*, *Youngia chinensis* and *Lactuca chinensis*. Likewise, *Ixeris chinensis* ssp. *graminifolia* has been named *Ixeris graminifolia*, *Crepis graminifolia* and *Lactuca chinensis* f. *graminea* by outstanding synantherologists of our time.

Hieracium is a widespread genus with species in Europe, North and South America, North and South Africa, and northern and eastern Asia. There are fourteen species in China, distributed from Kiangsu, Kiangsi, Kweichow and Szechuan northward to Kirin, Heilungkiang and Sinkiang. Most of them have small ranges. *Hieracium umbellatum* is the only widespread species. It occurs in twelve provinces from Kiangsi-Hupei-Szechuan northward to Kirin, Heilungkiang, Mongolia and Sinkiang. According to Stebbins most of the Asiatic species are apomictic (Babcock, 1947, p. 83).

In conclusion, we may point out that the larger genera of Chinese Compositae evidently have four types of distribution. The first type, which is the most frequent, includes widespread genera with definite centers of species concentration. Twenty-two of the thirty-eight large genera (almost 57 per cent) have this type of distribution. *Aster*(T), *Leontopodium*, *Anaphalis*, *Artemisia*(T), *Inula*, *Chrysanthemum*(T), *Cacalia*(T), *Senecio* (T), *Ligularia*(T), *Cremanthodium*, *Cirsium*(T), *Saussurea*(T), *Jurinea*, *Gerbera*, *Ainsliaea*(T), *Prenanthes*, *Taraxacum*, *Lactuca*(T), *Crepis*, *Youngia*, *Pertya* and *Ixeris*(T) all belong here. The center of species concentration of all these genera is the Meridional Ranges. The genera marked (T) also have secondary centers of concentration in Taiwan. The second type comprises the northern genera with ranges limited to the north of the Yangtze River. Seven of the thirty-eight large genera (about 20 per cent) have this type of distribution. *Achillea*, *Echinops*, *Tragopogon*, *Scorzonera*, *Carduus*, and possibly *Hieracium* and *Serratula* belong here. Most of these genera also occur in Europe, the Mediterranean Region and central or western Asia. The third type includes the southern genera, the ranges of which are limited to the south of the Yangtze River. Of the thirty-eight large genera only *Vernonia*, *Eupatorium*, *Blumea*, and *Gynura* have this type of distribution. The fourth type includes those widespread genera which have no definite centers of species concentration. *Erigeron*, *Gnaphalium*, *Carpesium* and *Sonchus* exemplify this type of distribution and all include some widespread weedy species.

2. The Small Genera and Their Distributions

The small genera are taxa comprising one to nine species. This arbitrary classification is made merely for the convenience of discussion. There are 128 such small genera of Compositae in China. Their distribution among the tribes is given in Tables I and II. Most of these genera include one to three species, but a few have four or more species. The sizes of these small genera as indicated by the number of the included species are shown in the following graph (Fig. 2).

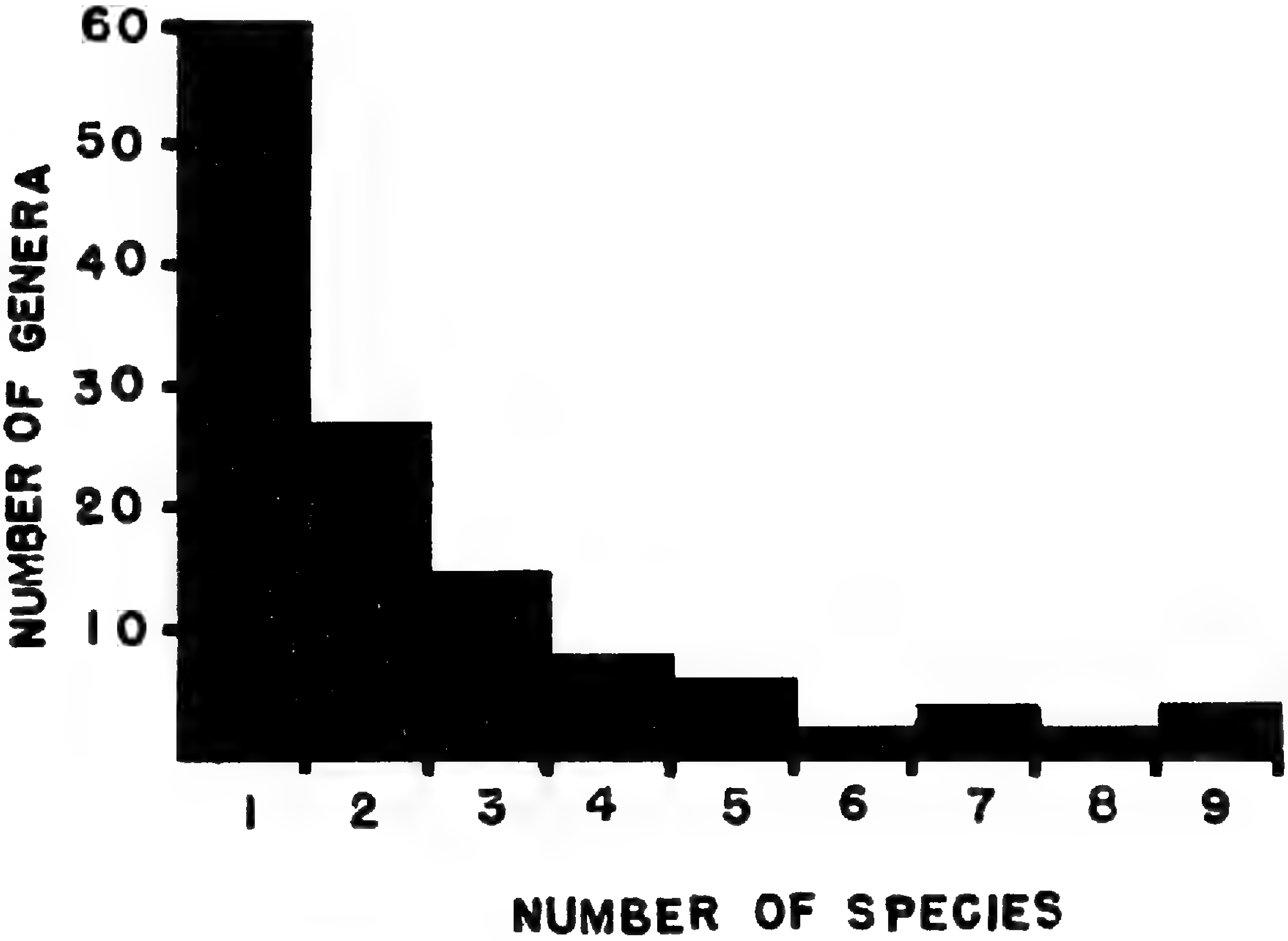


Fig. 2. The size and number of small genera of Compositae in China.

Map 24 illustrates the general pattern of distribution and the areas of concentration of the small genera of Compositae in China. An analysis of the distributional record of these genera reveals that they may be grouped into three types. These are the genera with species in China known only in cultivation, the genera containing only isolated endemics, and the genera with native species in China and also elsewhere in other floristic regions.

Endemics. Thirty-four of the 128 small genera are endemic to China. Their occurrence in various provinces is as follows: Yunnan 15, Szechuan 8, Kansu 6, Sikang and Hopei each 4, Heilungkiang, Kirin, Kweichow, Taiwan and Tibet each 3, Chekiang, Chinghai, Kwangtung, Mongolia, Shansi and Suiyuan each 2, and Hupei, Kiangsi, Ninghsia, Kwangsi and Shensi each 1.

A few of these endemic genera were first described from the Himalayan

Region. Recent collections extend their range to Yunnan, Szechuan, Kweichow, Kwangtung and Taiwan. It is evident that the high mountains bordering Yunnan, Szechuan, Sikang and Kansu (the Meridional Ranges) constitute a center of aggregation for the small genera.

Genera known in China only as cultivated plants. Twenty-one of the 128 small genera of Compositae are known in China only in cultivation. The commonest species belong to the genera *Zinnia*, *Helianthus*, *Coreopsis*, *Cosmos*, *Ageratum*, *Gaillardia* and *Calendula*. In the warmer part of the country, the escaped *Ageratum conyzoides* is naturalized and appears weedy in gardens, fields or along the roadside.

Genera with native species in China as well as in other floristic regions. Seventy-three of the 128 small genera of the Chinese Compositae occur also in central Asia, tropical Asia, Africa, the Pacific Islands, Australia or America. There is no record of their introduction from these regions to China or vice-versa. They were probably dispersed accidentally through man's activities. Five of them have widespread species which are usually considered as weeds. *Eclipta* has only one species in China, and this species has been recorded from thirteen provinces. It is a common weed in cotton or soybean fields and its occurrence in China can be traced back to the ancient historical period. Likewise, *Xanthium*, as represented by *X. strumarium*, occurs in seventeen provinces in China. *Bidens parviflora* occurs in thirteen provinces and *B. biternata* in ten provinces.

However, the majority of these small genera have limited distributions. MAP 24 indicates that they concentrate in Taiwan, Kwangtung, Hainan, Chekiang, Hupei, Szechuan, Yunnan, Hopei, Shansi, Sinkiang and, to a lesser extent, in Mongolia, Liaoning and Heilungkiang. A comparison of their distributions outside China and their concentration within the country presents evidence of a correlation between the occurrence of these small genera of Compositae and the courses of the ancient trade routes or the ports of the newer waterways. These correlations are shown by the following statistics:

(1) Within China the distributions of small genera with tropical Asian and African range are like this: Hainan 5, Kwangtung 4, Taiwan 4, Szechuan 3, Yunnan 2, Kweichow 2 and Fukien 1.

(2) Within China the distributions of small genera with pantropical or tropical American range are like this: Taiwan 18, Kwangtung 16, Hainan 14, Szechuan 10, Yunnan 9, Chekiang 3, Fukien 3, Hupei 2, Kiangsu, Kweichow, Hunan and Kwangsi 1 each.

(3) Within China the distributions of small genera with tropical Asian, Pacific Islands and Australian Range are like this: Taiwan 3, Hainan 3, Kwangtung 2, Yunnan, Szechuan and Hupei 1 each.

(4) Within China the distributions of small genera with Central Asian-Mediterranean-European-American Range are like this: Sinkiang 20, Tibet 6, Mongolia 5, Kansu, Shantung, Hopei, Szechuan, and Liaoning each 3, Kiangsu, Kweichow and Heilungkiang each 2, Honan and Anhwei 1 each.

It is interesting to point out that the largest number of the tropical Asiatic or African genera occur chiefly in Hainan, Kwangtung and Taiwan. Their absence from the coastal towns in Chekiang and Kiangsu or the metropolises along the Yangtze River, and their occurrence in Yunnan, Kweichow and Szechuan, indicate that these genera were probably introduced through the ancient trade routes connecting Rangoon (Burma) and Yunnan (MAP 31), or those connecting Hanoi (Indo-China) and Yunnan, thence due north through Kweichow and Szechuan to the ancient Chinese capital, Sian, in Shensi.

The pantropical genera are also concentrated in Taiwan, Kwangtung, Hainan, and, to a lesser degree, in Yunnan and Szechuan. Some of them also occur in Chekiang, Hupei and Kiangsu. It is evident that these genera were introduced to the interior provinces of Yunnan, Szechuan, Kweichow, etc., through the Yangtze waterway as well as through the Burma and Indo-China trade routes.

The most striking facts are centered about the genera with central Asiatic, Mediterranean and European distribution. Of these genera Sinkiang has the largest number, followed by Tibet and Mongolia. Liaoning and Heilungkiang also have some species. It is evident that the distributions of these genera follow the ancient trade routes. The most-used trade routes of ancient China passed through Sinkiang Province, and it is here that the largest number of genera common to China and Central Asia, the Mediterranean Region, and Europe are found.

Tibet is on the main ancient trade route that connected the upper Gangetic Plain, Central Asia and west China. Heilungkiang is on the eastern end of the great Northern Trade Route which connects Manchuria, Siberia, Central Asia and Europe. The occurrence of genera of Compositae which are predominantly central Asiatic, Mediterranean or European indicates that these small genera are adventives to the flora of China.

Regarding the small genera of Compositae in China we may observe that (1) most of the small genera are really small, about 70 per cent of them including only one or two species; (2) slightly over one-fourth of the small genera are endemics, many of them being aggregated in the Meridional Ranges; (3) about half of the small genera are probably adventives introduced to China either through the ancient trade routes or through the more recent waterways.

(To be concluded)

JOURNAL
OF THE
ARNOLD ARBORETUM

VOL. XXXIX OCTOBER 1958 NUMBER 4

STATISTICS OF COMPOSITAE IN RELATION TO THE FLORA OF CHINA *

SHIU-YING HU

III. A COMPARISON OF THE COMPOSITAE OF CHINA WITH THOSE OF NEIGHBORING COUNTRIES

The nature of the Compositae in the flora of China can be understood better and its significance more fully realized by a comparison of its components with those of its neighboring countries, namely, Korea, Japan, Indo-China, India, Central Asia (Pamir) and Siberia. The numbers of species in genera common to those areas are given in TABLE III.

TABLE III. A comparison of the genera of Compositae common to China and its neighboring countries

TRIBES & GENERA	CHINA	KOREA	JAPAN	INDO-CHINA	INDIA	PAMIR	SIBERIA
Vernonieae							
Vernonia	34	—	1	29	45	—	—
Ethulia	1	—	—	1	1	—	—
Elephantopus	2	—	—	3	1	—	—
Camchaya	1	—	—	1	—	—	—
Eupatorieae							
Adenostemma	2	—	1	1	1	—	—
Ageratum	2	—	—	1	1	—	—
Eupatorium	17	3	13	6	2	—	—
Mikania	3	—	—	1	1	—	—
Astereae							
Solidago	5	—	7	1	1	—	1
Dichrocephala	3	—	1	2	4	—	—
Cyathocline	1	—	—	1	2	—	—
Lagenophora	1	—	1	1	—	—	—
Grangea	2	—	—	1	1	—	—
Rhynchospermum	1	1	1	1	1	—	—
Myriactis	5	—	1	1	3	—	—

---

* Continued from Volume XXXIX, p. 378.

TABLE III. (*Continued*)

Tribes & Genera	China	Korea	Japan	Indo-China	India	Pamir	Siberia
Asteromoea (*Kalimeris* or *Boltonia*)	10	3	5	1	1	—	—
Heteropappus	5	2	6	—	—	—	—
Aster	137	9	35	1	14	2	9
Galatella	7	—	—	—	—	—	5
Erigeron	25	1	4	3	7	3	13
Microglossa	3	—	—	1	3	—	—
Conyza	9	—	1	3	8	—	—
Thespis	1	—	—	—	1	—	—
Inuleae							
Blumea	30	—	—	31	35	—	—
Blumeopsis	1	—	—	1	—	—	—
Laggera	2	—	—	3	4	—	—
Pluchea	3	—	—	4	7	—	—
Epaltes (*Poilania*)	2	—	—	1	2	—	—
Sphaeranthus	3	—	—	2	4	—	—
Pterocaulon	1	—	—	3	1	—	—
Filago	(?)	—	—	—	2	—	2
Leontopodium	57	3	6	1	1	1	2
Anaphalis	51	1	5	3	27	—	—
Antennaria	2	—	1	—	—	—	2
Phagnalon	(?)	—	—	—	1	—	—
Gnaphalium	20	4	3	3	7	—	4
Helichrysum	2	—	—	—	2	—	1
Inula	28	3	6	5	20	1	7
Vicoa	2	—	—	1	3	—	—
Pulicaria	4	—	—	1	10	—	1
Carpesium	18	5	10	2	3	—	—
Adenocaulon	2	1	1	—	1	—	—
Heliantheae							
Xanthium	2	1	1	1	1	—	2
Parthenium	1	—	—	1	—	—	—
Siegesbeckia	4	3	3	1	1	—	—
Eclipta	1	1	1	1	1	—	—
Enhydra	1	—	—	1	1	—	—
Blainvillea	1	—	—	1	1	—	—
Wedelia	5	1	1	4	4	—	—
Spilanthes	2	—	1	1	1	—	—
Synedrella	1	—	1	1	1	—	—
Glossogyne	1	—	1	3	1	—	—
Bidens	6	6	9	2	3	—	3
Cosmos	1	—	—	1	—	—	—
Galinsoga	1	—	—	—	1	—	—
Tridax	1	—	—	1	1	—	—
Helenieae							
Tagetes	2	—	—	2	—	—	—

TABLE III. (*Continued*)

TRIBES & GENERA	CHINA	KOREA	JAPAN	INDO-CHINA	INDIA	PAMIR	SIBERIA
Anthemideae							
Anthemis	4	—	—	—	—	—	1
Achillea	10	4	8	1	1	1	10
Matricaria	4	2	2	—	2	—	6
Allardia	2	—	—	—	5	1	2
Chrysanthemum	73	10	30	2	4	7	3
Pyrethrum	5	—	—	—	—	2	15
Brachanthemum	5	—	—	—	—	—	2
Centipeda	1	1	1	1	1	—	—
Crossostephium	1	—	1	1	—	—	—
Artemisia	156	37	40	4	27	20	58
Senecioneae							
Tussilago	1	—	—	—	1	—	1
Petasites	9	2	2	—	—	—	1
Doronicum	3	—	—	—	3	—	4
Nardosmia	(?)	—	—	—	—	—	4
Gynura	16	—	—	—	7	—	—
Emilia	3	—	1	4	5	—	—
Cacalia	60	7	25	—	—	—	1
Arnica	1	—	4	—	—	—	1
Syneilesis	4	2	2	—	—	—	—
Senecio	160	10	13	9	63	3	22
Ligularia	103	7	10	—	—	1	5
Farfugium	1	1	3	—	—	—	—
Cremanthodium	47	—	—	—	7	—	—
Cynareae							
Echinops	11	—	1	—	3	1	7
Atractylis	8	—	1	—	—	—	—
Arctium	2	—	1	—	1	—	2
Cousinia	2	—	—	—	5	5	1
Carduus	11	1	1	—	2	—	3
Cirsium	59	7	77	3	8	1	13
Cephalonoplos	3	—	1	—	—	—	—
Hemistepta	1	1	1	1	—	—	—
Saussurea	270	31	53	3	39	7	25
Jurinea	18	—	—	—	3	1	4
Tricholepis	2	—	—	1	10	—	—
Serratula	19	—	1	—	1	1	8
Centaurea	7	—	—	—	6	1	14
Carthamus	1	—	—	—	3	—	—
Mutisieae							
Pertya	10	—	2	1	—	—	—
Leucomeris	1	—	—	2	2	—	—
Ainsliaea	47	3	10	—	4	—	—
Gerbera	10	—	—	—	5	—	1
Cichorieae							
Cichorium	2	—	—	—	1	—	1

TABLE III. (*Continued*)

TRIBES & GENERA	CHINA	KOREA	JAPAN	INDO-CHINA	INDIA	PAMIR	SIBERIA
Lapsana	3	—	—	—	1	—	1
Koelpinia	1	—	—	—	1	1	1
Hypochoeris	3	1	1	—	1	—	—
Tragopogon	10	—	—	—	3	4	10
Scorzonera	18	2	2	—	3	1	11
Picris	8	1	5	1	1	—	2
Taraxacum	57	2	37	—	2	2	22
Chondrilla	3	—	—	—	2	—	11
Sonchus	10	1	2	2	4	—	5
Launaea	4	—	—	2	7	—	—
Lactuca	57	4	6	9	22	1	7
Cicerbita	7	—	—	—	—	—	2
Prenanthes	19	—	2	—	6	—	—
Crepis	31	—	2	6	14	3	14
Youngia	30	6	6	—	—	—	—
Ixeris	14	6	14	—	—	—	—
Crepidiastrum	2	2	6	—	—	—	—
Hololeion	1	—	2	—	—	—	—
Hieracium	14	—	3	—	5	—	26

1. CHINA, KOREA AND JAPAN

The close floristic affinity between Korea, Japan and China is well known, and for this reason plant geographers usually group the three countries in one phytogeographical province, the Eastern Asiatic Region. The Compositae of these countries confirm this relationship. Kitamura, in his monographic work *Compositae Japonicae*, and Hara, in his *Enumeratio Spermatophytarum Japonicarum*, both include Korea as well as Japan. The figures given in TABLE III for these countries are abstracted from these publications. It illustrates several interesting features which help us to understand the flora of China and eastern Asia.

(1) As indicated by the number of species in the genera which they have in common, China has the more complex Composite flora. China and Japan have 69 genera in common and in these there are a total of 1751 species in China and 514 species in Japan. The species/genus ratio for China is 25, and for Japan 7.4. There are 44 genera common to China and Korea and in these China has 1473 species and Korea has 203 species. The species/genus ratio is 35.9 for China and 4.6 for Korea. It is interesting to note that the differences of species/genus ratio are due chiefly to the large genera like *Vernonia*, *Aster*, *Leontopodium*, *Anaphalis*, *Senecio*, *Ligularia*, *Echinops*, *Saussurea*, *Prenanthes* and *Crepis*. Many small genera which may be regarded as adventives to the flora of China have the same, or nearly the same, number of species in China, Korea and Japan. *Solidago*, *Xanthium*, *Siegesbeckia*, *Eclipta*, *Centipeda*, *Hemistepta*, *Hypochoeris* and *Lapsana* are only a few examples.

(2) Thirty-one of the thirty-seven large genera of Chinese Compositae occur also in Japan. Twenty-five of these are also found in Korea. Numerous species of these large genera are common to all three countries. For example, *Anaphalis sinica* Hance, *Artemisia annua* Linn., *A. borealis* Pallas, *A. campestris* Linn., *A. japonica* Thunb., *Aster fastigiatus* Fischer, *A. indicus* Linn., *A. scaber* Thunb., *Carpesium abrotanoides* Linn., *Chrysanthemum indicum* Linn., *Cirsium pendulum* Fischer, *Gnaphalium affine* D. Don, *Lactuca sibirica* (Linn.) Benth. are only a few of them. In a way, Korea and Japan are merely additional areas to the continuous range of the large Chinese genera or of the widespread species. As observed by Kitamura, many of these genera extend from China to Japan through Korea and, in fact, this is an important route of plant migration between China and Japan.

(3) Geographically Japan is farther from China than is Korea but floristically there are over one-third more Composite genera which China shares with Japan than with Korea. This is probably due to the small size of Korea and the corresponding limitations in the climatic and edaphic factors that support a more varied vegetation. It is worthy of note that the genera which are common to China and Japan but absent from Korea are pantropical taxa (*Elephantopus*, *Adenostemma* and *Emilia*), tropical Asiatic or African elements (*Dichrocephala* and *Crossostephium*), Australian elements (*Lagenophora*), and Sino-Japanese elements with the range extending from the eastern Himalayan region to Japan but not reaching Korea (*Myriactis* and *Pertya*). The last named genera are especially interesting because they illustrate some southern routes of plant migration between China and Japan. These routes, as illustrated by *Pertya*, are evidently from eastern China, especially through Chekiang or Taiwan to Japan.

(4) It is interesting to consider the genera of Chinese Compositae that are absent from Korea and Japan. Among the large ones there are *Blumea*, *Gynura*, *Cremanthodium*, *Jurinea*, *Gerbera* and *Tragopogon*. Among the small ones, with the exclusion of the 34 which are Chinese endemics, there are still 38 that occur in China but not in Korea or Japan. These are (a) pantropical genera (*Mikania*, *Grangea*, *Pluchea*, *Epaltes*, *Pulicaria*), (b) tropical Asiatic or African genera (*Ethulia*, *Anisopappus*, *Sphaeranthus*), (c) the Australian genus, *Pterocaulon*, (d) American genera (*Acanthospermum*, *Tridax*, *Sanvitalia*), and (e) European-African-Central Asiatic genera (*Allardia*, *Centaurea*, *Cousinia*, *Filago*, *Tragopogon*). Species of groups (a–d) occur only in the tropical and subtropical areas of China (Taiwan, Hainan, Kwangtung, and Yunnan) while species of group (e) occur chiefly in Sinkiang and Tibet.

(5) It is interesting to point out the genera of Compositae that are represented better in Japan than in China or are absent from China. There are five genera which are common to China and Japan, but better represented in Japan. These are *Solidago*, *Heteropappus*, *Bidens*, *Cirsium*, and *Crepidiastrum*. There are 11 genera represented in the flora of Japan but absent from China. These are *Arnica*, *Dendrocacalia*, *Diaspanthus*, *Heterokalimeris*, *Ixyoungia*, *Macroclinidium*, *Macropertya*, *Miricacalia*, *Paraixeris*

and *Senecillicacalia*. Ten out of these 11 genera are segregates from Chinese groups (*Youngia*, *Ainsliaea*, *Pertya*, *Senecio* and *Cacalia*). *Arnica* is an American genus which, together with *Solidago*, another American genus which is better represented in Japan than in China, may be taken as an indication that in certain respects the Japanese flora contains more North American elements than the flora of China.

2. CHINA AND INDO-CHINA

Gagnepain in 1924 in the third volume of Lecomte, *Flore générale de l'Indo-Chine* treated 78 genera and 205 species of Compositae. Sixty-eight of these genera (87%) and 67 of these species (34%) are common to China and Indo-China (TABLE III). This large percentage of common genera and species indicates that there is a close floristic relationship between these two countries. A careful analysis of the data presented in TABLE III reveals that this statement is only partially true. First, many genera of Compositae important in the natural flora of China are absent from Indo-China. For example, 15 of the 38 large genera of Chinese Compositae, such as *Cacalia*, *Ligularia*, *Taraxacum*, *Ainsliaea* etc., do not occur in Indo-China. Secondly, the genera best developed in China, having hundreds of species there, such as *Leontopodium*, *Anaphalis*, *Chrysanthemum*, *Saussurea*, *Artemisia*, etc. are represented in Indo-China by only 1–4 species. In China they occur chiefly in Hainan, Taiwan, Kwangtung and some in Fukien and Yunnan. Thus we may conclude that there is a close affinity between the Composite flora of the warmer regions of China and Indo-China. There is no outstanding geographical barrier between these two countries and, as might be expected, they have many species in common.

The genera of Compositae of Indo-China are all small. Of the 69 occurring in both countries there are 1365 species in China and only 199 species in Indo-China. The species/genus ratio for these genera are 19.8 for China and 2.88 for Indo-China. If it were not for the two pantropical genera *Vernonia* and *Blumea*, this ratio would be even lower for Indo-China.

Indo-China is not suited to Compositae and its contribution to the Composite flora of China is almost nil. Gagnepain described several new genera for Indo-China. Two of these, *Blumeopsis* and *Camchaya*, have been recorded from Yunnan. As there is a great chance of mistaking a localized adventive for an indigenous genus, all of Gagnepain's Indo-Chinese genera of Compositae await verification through comparative study with material from other parts of the world.

3. CHINA AND INDIA

Hooker, in 1881, in the third volume of the *Flora of British India* (including Pakistan, Bhutan, Nepal and Burma) covered 127 genera and 591 species of Compositae. Ninety-four of these genera (74%) are common to China and India (TABLE III).

The Composite flora of India is richer than that of Indo-China. There are more genera in that country and some genera have as many as 60 species. Nevertheless, when the Composite flora of India is compared with that of China, it reveals that India is better represented at the generic level and rather poor in species. This is shown by the species/genus ratios of Compositae in the two countries. In China there are 2029 species for its 167 genera of Compositae, with an average of 12 species to each genus. In India there are only 591 species for its 127 genera, with an average of less than 5 species to each genus. The high generic number and the low species/genus ratio may be taken as an indication that India is a good meeting ground for the genera of Compositae characteristic of many of its neighboring countries, and a poor place for the generation of new entities in the evolution of the family. In regard to the Composite flora of China, there are more genera that migrate from China to India than in the opposite direction.

The high species/genus ratio of the Chinese Compositae is due to the occurrence of the 38 "large" genera (i.e., with ten or more species) in that country. With the exception of *Pertya*, these genera also occur in India, but only in *Vernonia* and *Blumea* are there more species in India than in China. In the rest of the 35 genera, India has far fewer species. In the following genera, for example, the numbers of species in China and India are respectively: *Aster* 137:14, *Leontopodium* 57:1, *Gnaphalium* 20:7, *Artemisia* 156:27, *Cremanthodium* 47:7, *Senecio* (including *Cacalia*) 220:63, *Saussurea* 279:39, *Cirsium* 59:8, *Ainsliaea* 47:4, and the *Crepis* complex 96:14. Moreover, in India, the number of species belonging to these genera is largest for the northern provinces, especially the southern slopes of the Himalayas, and becomes gradually less toward the central and southern provinces. Obviously, in the distribution of these genera, India is on the periphery of their range. In these large genera, there are many species common to China and India, e.g., *Aster altaicus*, *A. tibeticus*, *Anaphalis cuneifolia*, *A. triplinervis*, *Artemisia glauca*, *A. desertorum* and *Saussurea deltoides*. *Saussurea* is one of India's largest genera of Compositae. Twenty-nine of its thirty-nine species (almost two-thirds) also occur in China. Many of them are recorded only from the Himalayan region of India, but are widespread in China.

There are 15 other genera of the 94 common to the two countries which have more species in India than in China. These are: (1) *Blumea*, (2) *Cotula*, (3) *Dichrocephala*, (4) *Emilia*, (5) *Laggera*, (6) *Pluchea*, (7) *Sphaeranthus*, (8) *Vernonia*, (9) *Allardia*, (10) *Carthamus*, (11) *Cousinia*, (12) *Launaea*, (13) *Pulicaria*, (14) *Cyathocline*, and (15) *Tricholepis*. Genera 1–8 are pantropical elements, occurring in Africa, Asia, America and Australia. In the course of their migration, they may have reached China by way of India or Burma, or they may have been introduced from other tropical regions to tropical China independently. Genera 9–13 are central Asiatic or Mediterranean entities. There are many possible routes for their migration to China. Again, India, because of her more numerous chances for communication with the Arabic world, may have supplied routes for the migration of these genera to China, especially through the Gangetic plains. Thus genera 1–13 cannot be considered as Indian influences on the flora of China. Genera 14 and 15 (*Cyathocline* and *Tricholepis*) are native of India and are Indian contributions to the Composite flora of China. The number of their species is small, and their effect on the flora of China is slight, however.

Twenty-eight genera of Indian Compositae are absent from China. Twelve of these are genera endemic to India, occurring chiefly in the western peninsula (7 genera, e.g. *Centratherum*) but also in central India (2 genera, e.g. *Lagascea*), the western Himalayan region (2 genera, e.g. *Catamixis*), and northern India (the genus *Caesulia*). The remaining 16 genera have a wider distribution. Some of them extend from India westward through Africa to the Canary Islands (*Ifloga*), or to the Mediterranean region or Europe, (*Volaturelia*), or to western or central Asia (*Epilasia*). Others are tropical genera occurring also in America, Australia and Africa (e.g., *Sclerocarpus* and *Chrysogonum*).

4. China, Central Asia and Siberia

Fedtschenko, in 1903 in his *Flore du Pamir*, covered 25 genera and 61 species of Compositae. All of them, except *Kentrophyllum* and *Pterotheca*, are genera common to China and Pamir (TABLE III). Tribes Vernonieae, Eupatorieae, Mutisieae and Heliantheae are absent from Pamir. Senecioneae and Inuleae are very poorly represented, the former tribe with 4 species (3 in *Senecio* and 1 in *Ligularia*) and the latter tribe with only two species (1 each in *Leontopodium* and *Inula*). Cichorieae and Astereae are weakly represented in Pamir. The best developed tribes in this region appear to be the Cynareae and Anthemideae. The largest genus is *Artemisia*, which has 20 species. *Cousinia* is the only genus that has more species in Pamir than in China. For the comparable genera, the species/genus ratios are 63.5 for China and 2.5 for Pamir. The overwhelmingly large number of Chinese species in most of the common genera of these two regions seems to indicate that Pamir has had very slight influence in the development of the Composite flora of China.

Krylov, in 1949 in his *Florae Sibiriae Occidentalis*, treated 68 genera and 399 species of Compositae. Fifty-two of these genera are common to China and Siberia (TABLE III). Tribes Vernonieae and Eupatorieae are absent from western Siberia. Mutisieae are represented by only one species. Heliantheae are represented by only two genera, these famous for their weedy species. In fact, three out of the five Siberian species of this tribe are widespread taxa in China.

Twenty-five of the large genera in China also occur in western Siberia. All of them except *Hieracium* have much smaller numbers of species. For the comparable genera there are 1729 species in China, with an average of 33 species to a genus, and only 397 species in western Siberia, with an average of 7 species to a genus.

The only genera that have approximately the same number of species in the two regions, or slightly more species in Siberia, are *Pyrethrum*, *Doronicum*, *Centaurea*, *Tragopogon*, *Achillea*, *Chondrilla* and *Hieracium*. It is very likely that in these genera the Chinese Composite flora expresses the influence of the Siberian elements.

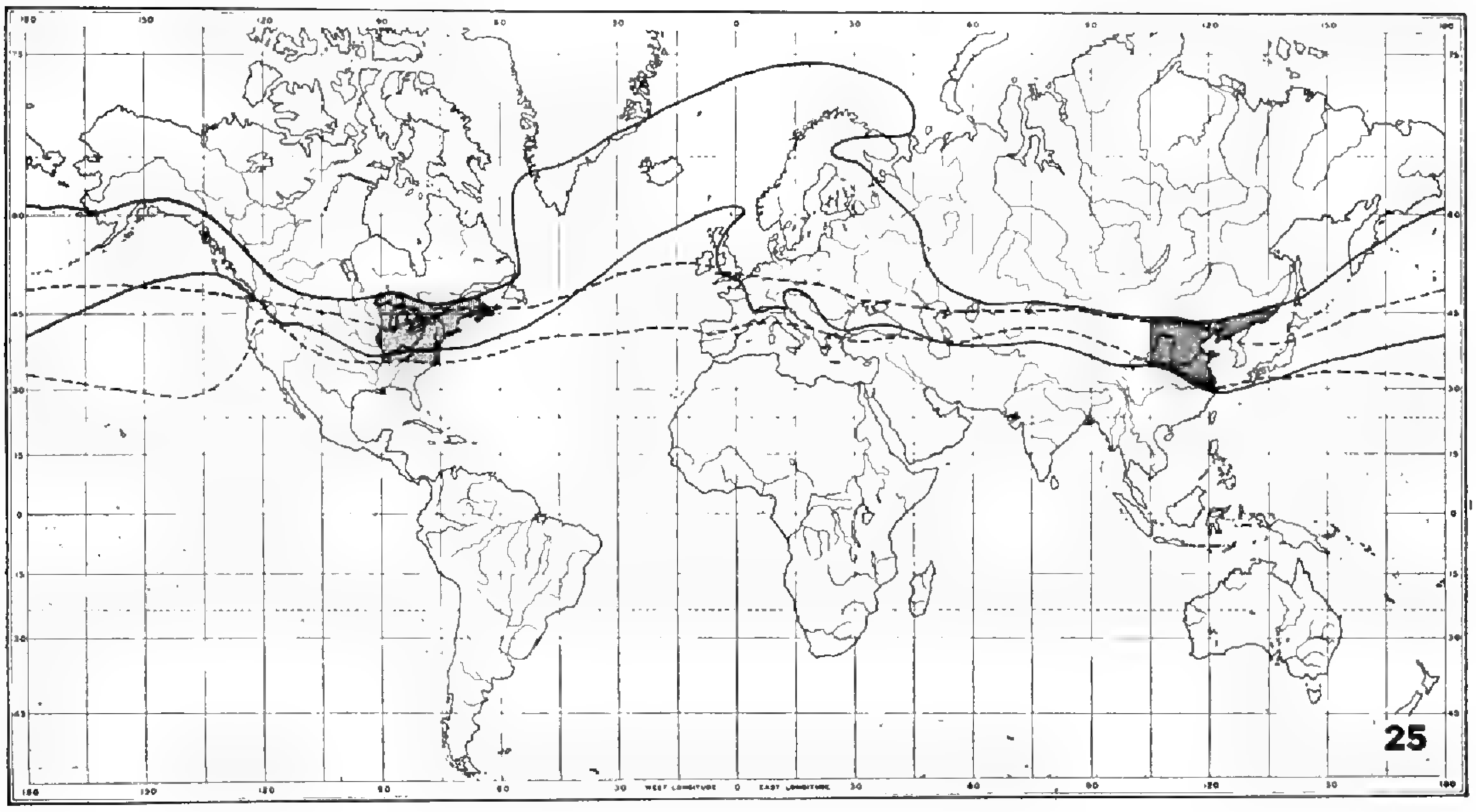
IV. A COMPARISON OF THE COMPOSITAE OF CHINA WITH THOSE OF NORTH AMERICA

The recognition of the identity or close similarity of angiospermous genera of eastern Asia and eastern North America is as old as the history of plant taxonomy. This relationship was known before the publication of Linnaeus' *Species Plantarum*. In a proposition prepared for the debate of a student, J. P. Halen, who was the respondent of the thesis entitled "*Plantae Camschatcenses Rariores*," Linnaeus in 1750 pointed out this affinity by listing 11 species which were supposed to be common to North America and Siberia (Linn. Amoen. Acad. 2: 336. 1752). About 1840 Asa Gray became keenly interested in the relationship of the flora of Japan to that of the temperate part of North America. In a book review on Siebold and Zuccarini, *Flora Japonica* (Am. Jour. Sci. Art. 39: 175–176. 1840), Gray selected 14 species of the ornamental or otherwise generally interesting plants of Japan and contrasted them with their closely related North American forms. His interest in discovering the relationship of the vegetation of the eastern sides of the two great continental masses in the northern hemisphere lasted for a long time. By 1856, in his *Statistics of the Flora of the Northern United States*, he concluded that there were more genera characteristic of eastern North America that it shared with an antipodal region, eastern temperate Asia, than with its neighboring district, western North America.

Among his examples of extra-European genera common to eastern North America and eastern Asia, Gray listed six genera of Compositae, namely, *Vernonia*, *Elephantopus*, *Diplopappus*, *Pluchea*, *Eclipta* and *Cacalia*. At that time the flora of China was practically unknown to the botanical world. Our knowledge of that rich flora did not commence to develop until some French missionaries, including David, Farges and Delavay, sent their collections from Szechuan and Yunnan to Paris. Our summary of the data scattered in publications on the Chinese flora yields 72 genera of Compositae which are common to China and North America. They belong to 10 tribes, namely Vernonieae, Eupatorieae, Astereae, Inuleae, Heliantheae, Helenieae, Anthemideae, Senecioneae, Cynareae, and Cichorieae.

An analysis of the numerous articles dealing with the floristic relationships of eastern Asia and eastern North America reveals that the authors have built up their evidence and accordingly drawn their conclusions from areas that are not comparable in size, climate, degree of rainfall or other factors which directly and indirectly affect the development and composition of vegetation. Actually, these authors were comparing a rather limited area of the eastern United States with the entire "China Proper," which includes all the regions commonly known as "North China," "South China," "East China," "Central China," "West China," "the Southwest" and "the Northwest." Some authors also included the Northeast, Korea and Japan. These names, to the people in China who use them daily, do not refer to regions with defined boundaries. Rather, they signify territories radiating from the better-known metropolises over a distance of one to three hundred miles. These centers are Peking and Tensin in the North, Nanking and Shanghai in the East, Canton and Foochow in the South, Wu-Han (Wuchang-Hanchow) in central China, Chengtu and Chungking in the West, Kunming in the Southwest, Sian and Lanchow in the Northwest, and Mukden and Harbin in the Northeast. Any general physical atlas (for example, Plate 3 of Bartholomew's *The Times Survey Atlas of the World*) would show that eastern Asia, as such, includes a much greater area, a more varied physiography, and more greatly diversified climate and related ecological conditions, than does eastern North America. For this reason, some of the conclusions drawn by eminent phytogeographers on the floristic interrelations of these regions are rather misleading. When the vegetation of comparable areas of eastern China and eastern United States is analyzed, and when the known cultigens and adventives are excluded, the corresponding area of eastern China does not have two or three times as many genera as that of eastern United States, as some authors have claimed. In the case of Compositae, for example, the contrary is true. There are far fewer genera and species in the corresponding part of China. Moreover, the same analysis of the genera and species of Compositae gives no evidence to confirm Gray's well-known conclusion that eastern North America shares more genera with its antipodal region in eastern Asia than with its neighboring district of western North America.

In outlining comparable areas of eastern China and eastern North America the extreme low temperature and the amount of annual rainfall are considered as the determining factors. For obvious reasons the area covered by Fernald's eighth edition of Gray's Manual is chosen as the basis for a comparison. MAP 25 shows that the January temperature of this area varies from 10°F. in the north to 40°F. in the south, and the annual mean temperature is approximately 60°F. The corresponding area in China has a more southerly limit in the coastal area which reaches the 30th parallel. Fernald's area on the North American mainland extends approximately over Long. 65°–96°W. and Lat. 26°–50°N. (shaded area of map). The area in China with the same annual isotherms and approximately the same length of growing season falls on Long. 104°–135°E. and Lat. 30°–47°N. (shaded). In China this area covers parts of Kirin and Heilungkiang, Liaoning, Jehol, Chahar, Suiyuan, Shensi, Shansi, Shantung, Hopei, Honan, Kansu, northern Chekiang, Anhwei, Hupei and eastern Szechuan. The physical features of the land-mass are of very ancient formation. The eastern portion of this area constitutes the alluvial plains of the Lower Yangtze River, the Yellow River, the Liao-ho and the Sungari River. The western portion of the area is an old plateau. The area includes many famous ranges where classical botanical collections were made in the last hundred years. Tsingling (including Tai-po Shan, 2000–4000 m.), Alashan (2000 m.), Lu-pan Shan, Taihang Shan, Ta-ching Shan, Wu-tai Shan (3040 m.), Chang-po Shan, Tai Shan and Tien-mu Shan are the well-known explored mountains. In rainfall and general climate this area is comparable with Fernald's area. Both of them have warm or hot summers and cold winters, and both have a mean annual rainfall of 20–40 inches.



MAP 25. World map showing comparable areas of eastern China and eastern North America (shaded). Solid lines mark the area with temperatures varying from 10° F. in the north to 40° F. in the south during January. The broken lines mark the area with an annual mean temperature of 60° F.

Regarding the Compositae, Fernald treated 115 genera, 82 of which are native and 33 introduced. In the comparable area of China there are 94 genera of Compositae, 27 of which are known to have been introduced as cultigens or weeds. A comparison of Fernald's 115 genera with the Compositae of China indicates that 47 of them occur in China at large, and only 37 of them occur in the corresponding area. Evidently of the genera of Compositae common to the two countries, only about four-fifths are shared by the corresponding area in China. A detailed comparison of these common genera is presented in TABLE IV. The total number of species for China at large and that for the northwestern United States, as included in Hitchcock's *Vascular Plants of the Pacific Northwest*, are also given for reference. The abbreviations in the column for Fernald's area are: E = naturalized from Europe, T Am = adventives of tropical America, A = naturalized from Asia. For the corresponding area in China, such an accurate record is lacking. The relatively short botanical history and the prolonged period of human activities in the area make it forever impossible to ascertain the origin of certain of its extra-Chinese elements of Compositae. These genera, the center of species concentration of which are known to be in the Americas, the Mediterranean region, or western or central Asia, are marked with (?).

TABLE IV. **A Comparison of Genera of Compositae Common to Limited Areas of China and North America**

GENUS	NO. OF SPP. IN CHINA AT LARGE	NO. OF SPP. IN COMPARABLE AREAS OF CHINA	NO. OF SPP. IN FERNALD'S RANGE	NO. OF SPP. IN HITCHCOCK'S AREA
Vernonia	34	4(?)	7	0
Elephantopus	2	0	3	0
Eupatorium	17	9	26	2
Mikania	3	0	1	0
Solidago	5	4(?)	75	10
Aster	137	43	68	34
Erigeron	25	7	17	62
Anaphalis	51	7	1(E)	1
Antennaria	2	0	32	25
Gnaphalium	20	7	10	8
Pulicaria	4	1	1(E)	0
Adenocaulon	2	2	1	1
Xanthium	2	1(?)	15	2
Acanthospermum	1	0	1(T Am)	0
Parthenium	1	0	3(T Am)	0
Eclipta	1	1(?)	1	0
Rudbeckia	1	0	19	3
Spilanthes	2	0	1	0
Bidens	6	6(?)	19	6
Galinsoga	1	0	4(T Am)	1
Achillea	10	5	5(E, A)	1
Chrysanthemum	37	33	4(E)	3
Cotula	2	0	1(A)	1
Matricaria	4	4(?)	3(E)	2
Artemisia	158	81	17	24
Tussilago	1	1	1(E)	1
Petasites	9	2	4(E)	2
Erechtites	2	0	2	3
Cacalia	60	23	4	0
Senecio	160	27	22(E, A)	33
Echinops	11	4	1(E)	1
Arctium	2	2(?)	4(E)	2
Carduus	11	5	3(E)	3
Cirsium	59	16	17(E)	16
Silybium	1	1(?)	1	1
Centaurea	7	6	12(11 E)	10
Hypochoeris	3	2(?)	1(E)	0
Cichorium	2	2(?)	2	1
Lapsana	3	3(?)	1	0

TABLE IV. (*Continued*)

Tragopogon	10	3	3(E)	5
Picris	8	2	2(E)	0
Taraxacum	57	22	11(some E)	5
Sonchus	10	4	4(E)	4
Lactuca	57	23	16	6
Prenanthes	19	5	10	2
Crepis	31	2	5(some E, A)	11
Hieracium	14	4	19	8

Several noteworthy points on the floristic relationship as expressed by the Compositae of the two areas can be drawn from the above data. First, in regard to the number of native genera, Fernald's area has 82, while the corresponding area in China has 67, which is one-fifth less than in Fernald's area.

Secondly, regarding the genera common to the two areas, in Fernald's area 22 out of the 47 genera which also occur in China are naturalized or adventive. The adventives of tropical American origin, such as *Parthenium*, *Galinsoga*, *Acanthospermum*, etc., occur in the warmer regions of China, but they are absent from the corresponding area under discussion. This phenomenon may indicate one of the two or both measures: that northeastern North America supports more elements of the warmer regions than the corresponding area in Asia, and that due to the longer distance and the shorter period of communications between this part of Asia and tropical America these elements have not yet been introduced or established.

Thirdly, among the common genera native to both areas there are nine genera which have far more species in Fernald's area (*Eupatorium*, *Solidago*, *Aster*, *Erigeron*, *Gnaphalium*, *Xanthium*, *Bidens*, *Prenanthes* and *Hieracium*), while there are only three which have more species in the corresponding area in China (*Artemisia*, *Lactuca* and *Taraxacum*).

Lastly, among the native genera, only *Cacalia* is common to the northeastern North America and the corresponding area of China while absent from the Pacific Northwest. Meanwhile, there are three genera, *Antennaria*, *Rudbeckia* and *Erechtites*, which are common to the areas of Fernald and of Hitchcock and are absent from the corresponding area of China. In the Composite flora, there is no evidence that the northeastern North America shares a larger number of genera with a comparable area of eastern Asia than with her neighboring area in western North America.

V. THE REFLECTION OF COMPOSITAE ON THE VEGETATION OF CHINA

In the foregoing analyses I have presented the general features of the Chinese Compositae. Special emphasis was given to the constituent genera of the family and their distribution. What light can the knowledge of this overall picture of the largest family of flowering plants of China cast on the understanding of the vegetation of that country? The following discussion will be centered around this subject.

The Compositae reflect the very uneven floristic composition of the vegetation of China. If the distributional maps of the Compositae (MAPS 1–24) were superimposed on a single map, the resulting picture would have various shades of darkness, with the darkest area, representing the region richest in Compositae, falling over Yunnan, Szechuan and parts of their neighboring provinces, and the lightest area, representing the poorest region, falling over Honan, Kiangsu, Shantung and parts of their neighboring provinces. What is true of Compositae is also true of the general vegetation. The region with the largest number of genera and species of Compositae is also the richest floristic region in China, and the region poorly represented with Compositae is also poor in natural vegetational coverage.

1. THE AREA RICHEST IN COMPOSITAE SUPPORTS THE RICHEST VEGETATION

The area of greatest floristic richness is very limited, being formed by the Meridional Ranges which extend from western Yunnan northward to eastern Sikang, western Szechuan and the adjacent territory in Kansu and Shensi. Here, in order to present the vertical distribution of the predominant genera of the Compositae in these mountains, a brief account of the complex physiography, which results in sharp changes of elevation and climatic differentiation, is also given. The consequent diversified types of vegetation are then described more fully.

This region consists of very ancient formations characterized by high mountains and deep gorges. The mountains are formed mainly from mud-shales and granitic rocks. Occasionally limestones have been forced up through the older rocks to form bold peaks and stupendous precipices. At the bottom of the deep gorges flow torrential tributaries of seven large rivers which are, from west to east, the Chiukiang, Salween, Mekong, Chinshakiang, Yalungkiang, Tatuho and Min Rivers. Most of the tributaries drain from mountains capped with perpetual snow. The principal courses of the seven rivers all run from north to south, parallel to the meridian and hence the mountains are known collectively as the Meridional Ranges.

At lower altitudes, the valleys of the large rivers are bordered by deeply eroded treeless mountains. The climate here is hotter and drier than the altitude warrants and barren areas and desert-like vegetation are common, with *Artemisia* and *Inula* predominant among the Compositae. As one ascends the mountains along the tributaries of the rivers, the change in topography and vegetation is sudden. Gentle slopes are inhabited by various tribes, such as the Lolo, Miao, Chiarung, Ch'iang, etc., and up to about 7500 ft. all the arable land is cultivated, the natural vegetation being greatly disturbed. The slopes which are too steep to reach, and the areas which are too far from human dwellings are covered with mesophytic forest. Trees, shrubs and herbaceous undergrowth flourish. The muchtravelled and experienced collector, E. H. Wilson, considered this zone to have one of the world's richest vegetations. Along the roads skirting the banks of the streams, on the edges of the forests, or on drier grassy slopes are many species of *Artemisia*, *Crepis*, *Aster*, *Eupatorium*, *Gnaphalium*, *Arctium*, *Carpesium*, *Erigeron* and *Tussilago*. The slopes from 7500–9000 ft. are covered by mixed forests of many species of deciduous trees and conifers. On the southern flanks of the mountains bamboo forests, mixed with some deciduous or evergreen trees are common. In the forests or on the flood plains species of *Senecio*, *Anaphalis*, *Cirsium*, *Ainsliaea* and *Gerbera* are common. From 9000 ft. to timber line the slopes are covered with virgin coniferous forests. The Composite family is rather poorly represented in this zone. Above timber line, in the alpine meadows, with the extraordinarily rich assemblage of herbaceous types, the family has its best development. Many species of *Artemisia*, *Saussurea*, *Dubyaea*, *Soroseris*, *Cremanthodium*, *Ligularia*, *Aster* and *Jurinea* form pure colonies. Many others growing mixed with grasses, sedges, *Aconitum*, *Saxifraga*, *Delphinium*, etc. are found. It is not an exaggeration to call the alpine meadows of the Meridional Ranges the Land of Compositae. On the razor-like ridges species of *Leontopodium* and *Anaphalis* form colonies. In fact, species of Compositae can be found in all kinds of habitats in the alpine region of the Meridional Ranges. In places where no other flowering plant thrives, species of Compositae grow. Thus, immediately below the perpetual snow line, in the rock cracks where there is a thin veneer of wind-blown soil, one may find different species of *Saussurea* and *Soroseris*.

In considering the floristic richness of this area it must be remembered that the seven rivers have hundreds of tributaries. Thus, in a very limited region, the complicated habitats and the diversified vegetation are repeated several hundred times. The proximity of subtropical swamps, semi-desert scrubs, mesophytic forests, grassy slopes, bamboo woods, coniferous forests, alpine meadows and high-altitude tundra provide unusual opportunities for the close contact of many species. This brings about unique chances for the hybridization of related forms. In many places these diversified habitats can be found within five miles of one another. The heterogeneity of external conditions induces mutation and accelerates speciation. Frequent landslides after the annual monsoon storms, or occasional earthquakes, provide new habitats for the colonization of new forms. All these conditions are contributing factors to the rich Composite populations of the Meridional Ranges.

As stated before, the region that is richest in Compositae is also the land with the richest vegetation in China. It is rich in gymnosperms and there is no comparable region in the world that has so many species of *Taxus*, *Cephalotaxus*, *Larix*, *Abies*, *Picea*, *Tsuga* and *Juniperus* as the Meridional Ranges in China. It is rich in broad-leaved trees and shrubs. In fact, this region is the homeland of many garden specialties, especially those in the genera *Acer*, *Akebia*, *Berberis*, *Camellia*, *Clematis*, *Cotoneaster*, *Deutzia*, *Euonymus*, *Hydrangea*, *Ilex*, *Jasminum*, *Kerria*, *Lonicera*, *Nandina*, *Paeonia*, *Rhododendron*, *Rosa*, *Syringa*, *Viburnum*, etc. It is particularly rich in herbaceous types. Species of *Aconitum*, *Allium*, *Anemone*, *Corydalis*, *Cypripedium*, *Delphinium*, *Dianthus*, *Fritillaria*, *Lilium*, *Polygonum*, *Potentilla*, *Rheum*, *Ranunculus*, *Saxifraga*, *Sedum*, *Thalictrum*, etc. are very numerous. There is no place in the world that can surpass this region in the number of species of *Primula*, *Gentiana*, *Meconopsis* and *Pedicularis*. It is also rich in monotypic or oligotypic families and genera. *Aucuba*, *Alangium*, *Coriaria*, *Delavayia*, *Dipteronia*, *Eucommia*, *Euptelea*, *Euscaphis*, *Helwingia*, *Stachyurus* and *Tetracentron* are only a few examples. They are important constituents of the mesophytic forests of the region. As the mountains of this region generally reach 12,000–16,000 ft., alpine vegetation reaches the peak of its development. Grasses and sedges are numerous both in kind and in individuals. The southern portion of the region reaches the subtropics. The north-south direction of the valleys of the main rivers favors the movement of tropical monsoon rainfall farther north than the latitudes warrant. Species characteristic of the warmer regions are well developed in the lower elevations. *Cycas*, *Podocarpus*, palms, bamboos, lauraceous trees and shrubs, and large woody leguminous vines characteristic of the tropical rain forests are abundant in the jungles at low elevations. The experienced explorer F. K. Ward, after visiting the southwestern corner of this region, called it the "Plant Hunter's Paradise." E. H. Wilson, after going through the northern portion of the region, commented upon it as being the richest area in vegetation on earth. The entire area is highly significant in the vegetation of China.

2. The Area Poorest in Compositae has the Poorest Vegetation

This area is called the Central Plain (Chung-yuan) in ancient Chinese literature. It is the plain on which the ancient history of China was built. Even in modern times it is still the focal point in the struggle for power among the war lords, for whatever party gets this area gets control of the national government. In modern geography and in current news this area is called the North China Plain. In size it is approximately equal to the region which has the richest vegetation, but in its physiography it is very different.

Geographically this plain is the alluvial fan formed by the Yellow River. It covers central and eastern Honan, southeastern Hopei, western Shantung, northern Kiangsu and northern Anhwei. Throughout the territory no elevation exceeds 200 ft. above sea level, excepting in northern Kiangsu, where there are a few low, barren hills up to 600 ft. high. On the Kiangsu-Anhwei border in the south there is a swampy lake, Hung-tse-hu, and on the Kiangsu-Shantung border there is a similar lake, the Wei-shan-hu. The changeable courses of the lower Yellow River radiate like the ribs of a fan with Loh-yuan at the pivot, Tiensin on a rib to the north, and Suchow on another rib to the south.

Geologically this area is a new land. It is so new that the configuration of the surface has undergone noticeable changes in the last fifty years. Around my home village (Kiangsu Province), the heavy deposits of the frequent floods, so frequent that thirteen floods occurred in the summer of 1924, have elevated the land up 3 ft., and the repeated erosions have converted a former road into a river.

Historically this area is one of the earliest inhabited spots of the world. The discovery of the Peking man, *Sinanthropus pekinensis*, in 1928, materially proves this proposition. The rich alluvial land, the temperate climate of this latitude and the timely rainfall, the maximum of which occurs in July, all favor the development of agriculture. For four thousand or even more years, the people in this area have been farmers. It is estimated that at present every square mile of the cultivated land in this region supports 1479 people. Ninety per cent of them are farmers, who obtain their entire livelihood from the products of the soil. For at least four thousand years men have reshaped every inch of the land in this area, and there is no spot with natural vegetation. All land surfaces that can possibly be cultivated are utilized. The small lots of farm land are carefully tilled. There are no farms in the world that have so few weeds as the farms in this area. Natural resources are utilized to the limit. After the planting of winter wheat, and the harvesting of sweet potatoes and carrots, for hundreds of miles at a stretch the land is of one brown color. The fields are turned over. The fallen leaves are collected for fuel. The herbs on the roadsides, or along the banks of canals are carefully scraped off with a thin veneer of the top soil. When dry, the mixture of plants and earth is collected and used for spreading over the floor of the animal house in winter. Eventually this becomes the fertilizer for the fields the next spring.

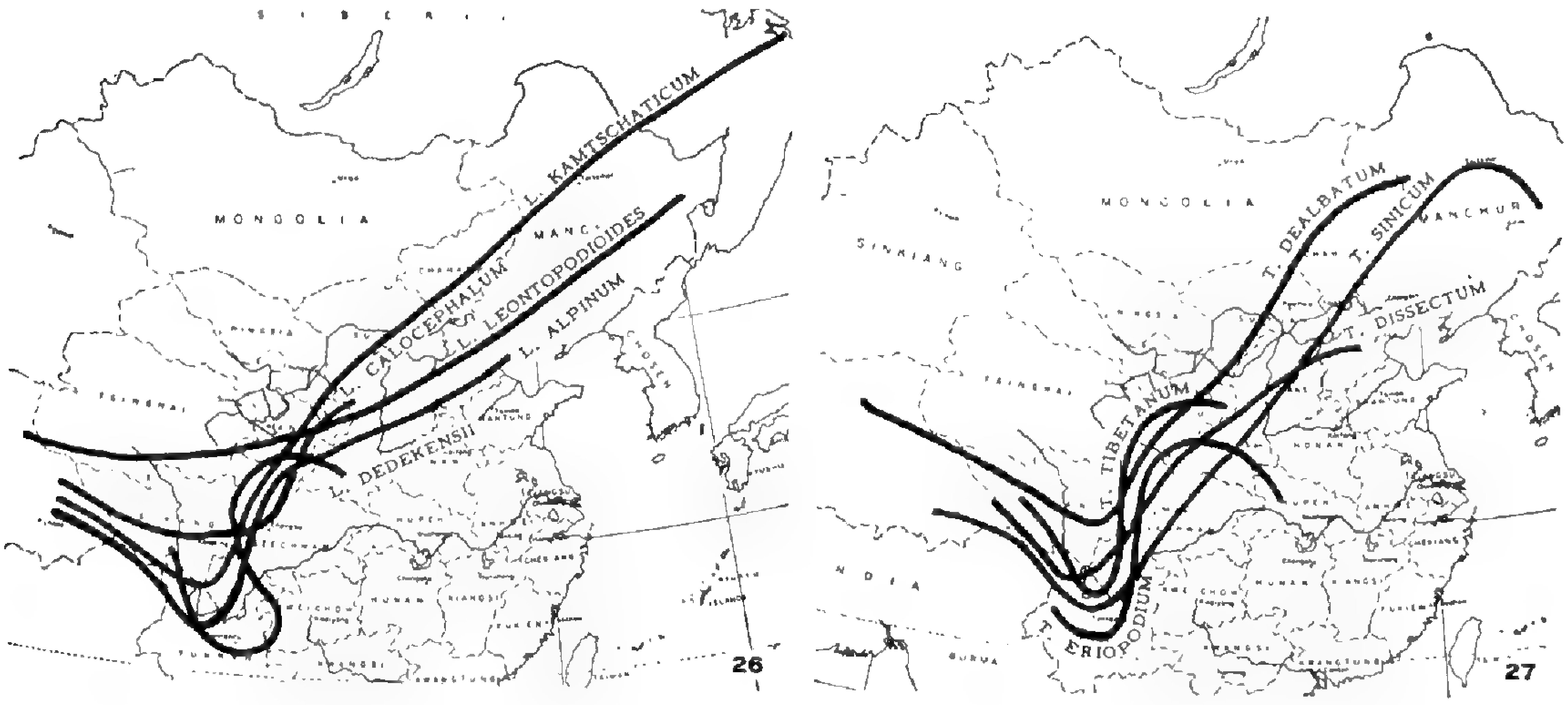
Under such intense utilization of land, the species of Compositae occurring in the area, with the exception of the cultivated forms, are no more than can be counted on the fingers of two hands. These are all widespread weeds. *Eclipta alba* is common in gardens and cotton or soybean fields. *Cirsium lineare* is common in kao-liang (*Sorghum*) fields. *Lactuca tartarica* and *Artemisia campestris* occur in alkaline soil. *Saussurea affinis* and *Ixeris chinensis* occur in gardens and graveyards. *Artemisia annua* and *Xanthium strumarium* occur on village commons. *Inula britannica* occurs in protected woods on the outskirts of villages. *Bidens chinensis* and *Taraxacum officinale* occur in graveyards. *Scorzonera albicaulis* is limited to the arid region of the barren hills. With the exception of *Eclipta* and *Cirsium*, the occurrence of all the above-mentioned species is occasional. Thus the Composite flora of this area is poor in the number of individuals as well as poor in kinds.

The region poor in Compositae is also poor in other vegetation in China. Forests are unknown to this area. Woods protected by temples or well-to-do families are rather rare. The component species are few. *Thuja orientalis, Salix babylonica, Populus alba, Juglans regia, Castanea mollissima, Ulmus pumila, Ulmus parvifolia, Morus alba, Sophora japonica, Ailanthus altissima, Melia azedarach* and *Euonymus bungeanus* are the common species. *Lycium chinensis* and *Tamarix chinensis* are often found in long stretches of sand which may mark the course of a former river. Herbaceous species are also few. *Cynodon dactylon, Eleusine indica, Im-*

perata cylindrica, *Miscanthus sacchariflorus*, *Eremochloa colonum*, *Digitaria sanguinalis*, *Chenopodium album*, *Amaranthus viridis*, *Celosia argentea*, *Acalypha australis*, *Apocynum sibiricum*, *Galium aparine* and *Mazus rugosus* are the common species.

3. THE CHARACTERISTIC RANGES OF SOME SUBGENERIC TAXA IN CHINA

MAPS 26 and 27 represent the linear distribution of several species of *Leontopodium* and *Taraxacum*. This is done by drawing a line through the provinces where the species under discussion has been recorded. It is interesting to note that the lines representing the distribution of each species form a more or less modified S-shape. Looking at these distributional lines by provinces they connect Tibet, Sikang, Yunnan, sometimes Kweichow, Szechuan, Kansu, Shansi, Shensi, Hopei or Suiyuan and Mongolia or Chahar, Heilungkiang, Kirin and Liaoning. Looking at them by topography, they link up the Tibetan Plateau, the Meridional Ranges, the Tsingling, the Taihang Shan or the Yin Shan, the Great Khingan, the Little Khingan and the Chang-po Shan. Although the length and the shape of the lines representing different species may vary, they all pass the Tsingling. Evidently, with regard to the distribution of these species, the Tsingling is a bridge for their northeastward extension and not a barrier to their dispersion.



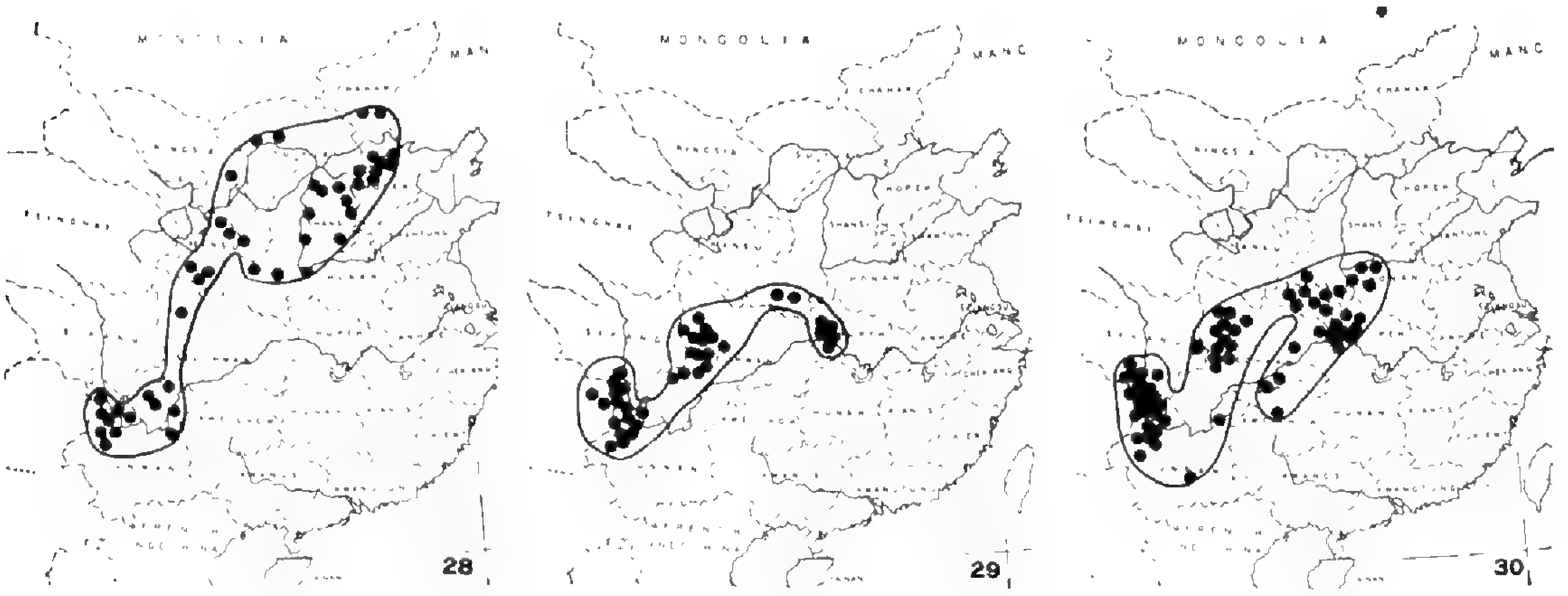
MAPS 26, 27. Linear ranges of some species of two genera showing S-shaped distributional patterns: 26, Species of *Leontopodium*; 27, species of *Taraxacum*.

Geographers in describing the physiognomy of China have emphasized the ill effect of the Tsingling on the unity of the country. They have also created a misleading impression that the Tsingling Range has been a barrier to the distribution of animals and plants. For example, one author (Cressey, 1934. p. 14–15) wrote, "Greatest of all the mountains of China is the eastward extension of the Kuen Lun, known in China collectively as the Tsingling Shan. . . . The mountains divide China into two major geographical regions, characterized by striking contrasts in climate, agriculture and human activities. . . . There are two Chinas, each with distinct characteristics in sharp contrast to those of the others. . . . One China is in the South, a land of abundant rainfall. . . . This is the land of . . . rice and bamboo . . . the people are shorter in stature. . . . The other China is in the North, a land of limited and uncertain rainfall. . . . The standard crops are millet and Kaoliang and beans. . . . The people are taller. . . . The South tends to be radical and revolutionary, while the north is stolid and conservative. . . . The boundary between the North and the South is transitional . . . it coincides with the crest of the Tsingling Shan." Another author (Lee, 1939, p. 2) in a more concise manner maintained, "The Tsingling Range forms the natural divide between northern China and the Yangtze Valley . . . these ranges that have naturally sharpened the climatic contrasts and regional differences in other geographical conditions, against which the Chinese have struggled for their unity during historical time."

Actually whether Tsingling does have such far-reaching influence on the physical conditions of the land, on the distribution of plants and animals, and on the life of the people is questionable. First, the mountains constituting the Tsingling Range are of unequal heights. As the range extends from the border of Kansu-Szechuan-Shensi eastward to Hupei, Honan and Anhwei, the elevation is gradually reduced. In the west the mountains are continuous and often snow-capped, but to the east they seldom reach 600–1200 ft. in altitude. Moreover, there are many broad gaps from Hupei eastward, and in Kiangsu Province there are only plains and hills. The differences in climatic conditions and human activities described in the foregoing quotations are found in the low land where the tail-end of Tsingling is not high enough to be a climatic barrier. Actually the people living to north and south in the mountains of the western end of Tsingling have much more in common than those living in the plains in the east where there are no mountain barriers. For example, the people in the mountains of Szechuan, south of Tsingling, and those of Labrang in southwestern Kansu, north of the Tsingling, have more in common than the people of Suchow and Shanghai, both in Kiangsu Province. Likewise in plant distribution the high mountains constituting the western portion of Tsingling are bridges over which the montane and alpine elements of the south extend to the higher latitudes of the north and the boreal elements migrate to the high altitudes of the south. To regard Tsingling as a bridge and not a barrier in the distribution of plants of the subgeneric level is essential in the understanding of the vegetation of China.

In the Compositae many species in the genera *Aster*, *Chrysanthemum*, *Artemisia*, *Senecio*, *Cacalia*, *Leontopodium*, *Taraxacum*, *Ligularia*, *Saussurea* and *Lactuca* extend from Tibet, Yunnan, Szechuan or Sikang in the south, over the Tsingling Range to Shensi, Shansi, Kansu and even Hopei, Manchuria and Korea in the north. Linear connections of these distributions reveal an S-shaped pattern with Tsingling falling at the northern half beyond the middle. MAPS 26 and 27 illustrate the S-shaped distribution of the species of *Leontopodium* and *Taraxacum* which may be taken as examples of this type of distribution.

This is a pattern of distribution not limited to the Compositae alone, but a general pattern of distribution of many taxa at the subgeneric level. There are numerous examples in the Coniferae. Ostenfeld and Syrach-Larsen in *The Species of the Genus Larix* (p. 18) give a perfect S-shaped distribution of *L. potaninii*. In fact this species is closely related to *L. griffithiana* and *L. mastersiana*. Morphologically there is no clear-cut division between them. Their status as species depends largely on the temperament of the taxonomist. They can certainly be regarded as geographical variants. *Larix griffithiana* occurs also in Yunnan. Looking at the distribution of the group as a whole, the S-shaped range can be extended to the southern Himalayas. *Abies delavayi, A. georgei, A. forrestii, A. faberi, A. faxoniana* and *A. chensiensis* (French spelling for Shensi) present the same taxonomic problem, and form the same S-shaped range. These species are fairly distinct, but there are some intermediate collections.



MAPS 28–30. Distribution of three monotypic genera showing S-shaped ranges: 28, *Ostryopsis davidiana*; 29, *Tetracentron sinense*; 30, *Euptelea pleiosperma*. Each dot represents a collection in the herbarium of the Arnold Arboretum.

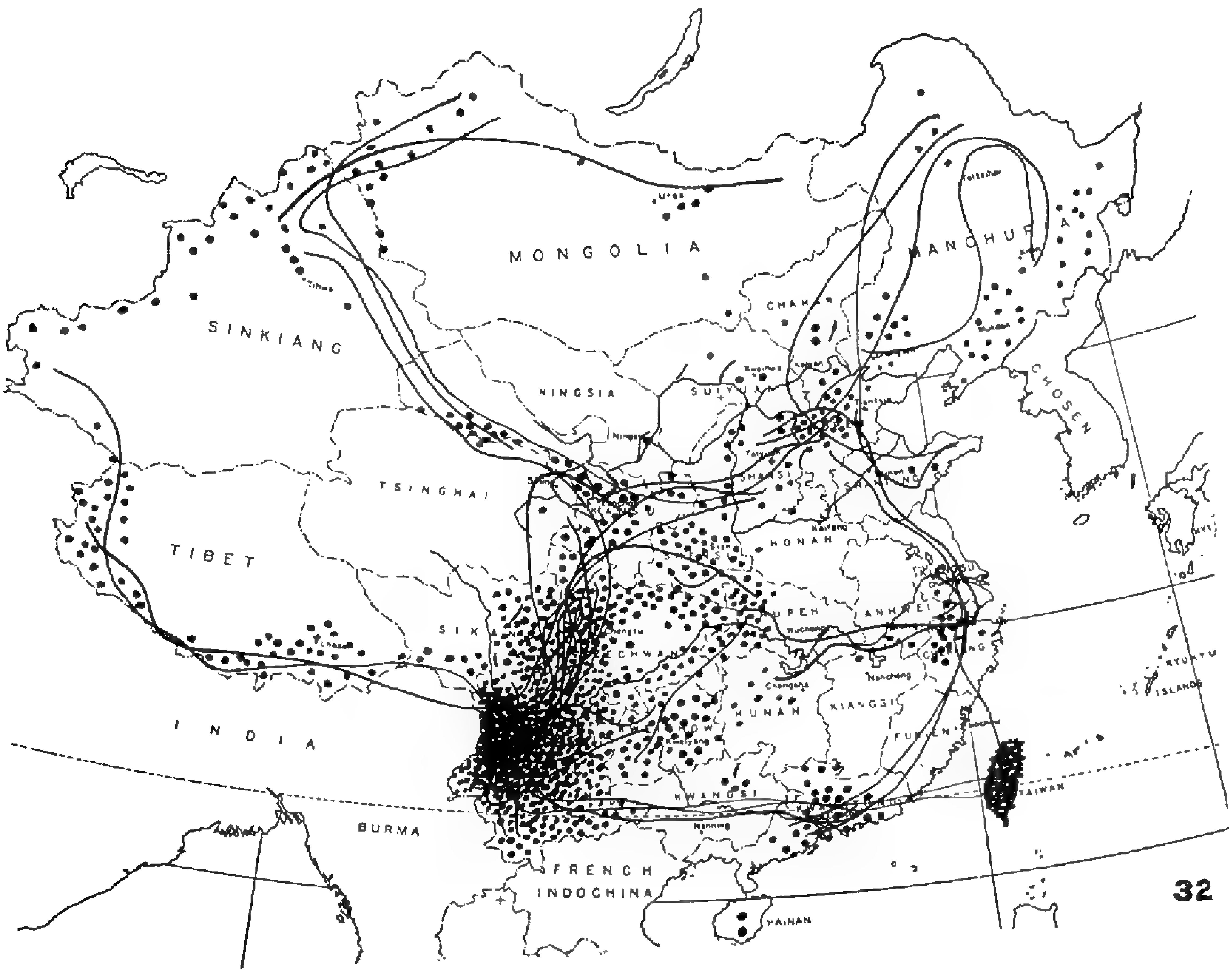
Another example of the S-shaped range is found in *Betula platyphylla*. This species is known to some botanists as *B. japonica* and to others as *B. mandshurica*. In this case the taxonomists are more conservative and the geographical variants are regarded as varieties. The five varieties of this species, *Betula platyphylla* vars. *rockii* (from Yunnan), *szechuanica* (Szechuan-Kansu-Shansi), *mandshurica*, *kamtschatica* and *japonica* form an elongated S-shaped range extending from Yunnan through the Meridional Ranges, the Tsingling, the Taihung Shan, the Yin Shan, the Khingan, the Changpo Shan to Kamchatka and Japan.

Many monotypic genera also have similar patterns of distribution. To cite a few examples, the two varieties of *Ostryopsis davidiana* (var. *cinerascens* and var. *nobilis* [Betulaceae]) form an S-shaped distributional pattern over northwestern Yunnan, western Szechuan, Kansu, Shensi, Shansi, Hopei and Chahar (MAP 28). *Tetracentron sinense* (Tetracentraceae) forms a shorter curve but with the same pattern over Yunnan, Szechuan, Shensi and Hupei (Map 29). *Euptelea pleiosperma* (Eupteleaceae) forms an even more symmetrical S-shaped distributional pattern covering Sikang, Yunnan, Szechuan, Shensi, Honan, Hupei and Kweichow (Map 30).

Many more cases can be cited from *Gentiana, Potentilla* and *Saxifraga* to illustrate the S-shaped distribution of subgeneric entities. In short it is conclusive that the mountain ranges including the Tsingling are bridges for the distribution of plants. It should also be noted that all the examples cited have small seeds which can be dispersed through adhesion to animals and man as well as by wind. In many cases closely related forms also occur in the northern Rockies. For example, *Larix occidentalis* and *L. potaninii, Philadelphus lewisii* and *P. tenuifolia* are morphologically twin species of the two continents.

4. Endemic Elements

About one-third of the 167 recognized genera of Compositae in China are endemic to that country. Most of them are monotypic or oligotypic genera but several of them, such as *Cremanthodium* and *Youngia*, have from 30 to 60 species. The occurrence of the endemic genera and species of Compositae is illustrated in Map 32. In this map the lines represent



Map 32. The occurrence of endemic genera (in lines) and species (in dots) of Compositae in China.

monotypic or oligotypic genera and the dots represent species known only from the type localities. Evidently the occurrence of the endemic genera and species of Compositae is a widespread phenomenon in the country. There seems to be no restriction on where endemism may occur, but it appears clear that there are definite areas of concentration of the endemics. The Compositae of various regions of the country have been studied by botanists of different nationalities. The Japanese botanists have published very liberally on the flora of Taiwan and on that of northern or northeastern China. The Russian botanists have described many new genera and species from Mongolia and Sinkiang. British botanists have published new taxa from Tibet and Yunnan. French, Austrian, Italian and German botanists have published voluminously on the material collected from central China. Individual differences in background, technique and temperament on the part of these botanists naturally affect the quality of the new genera or species they described. Some of them "split" more than the others. Consequently the areas they work on appear to support more endemics. In addition to these inevitable human defects, there is still another difficulty which affects the value of the map showing endemism of Compositae in China. This difficulty is that some areas are better explored and more endemic elements have become known than in other areas. For these reasons questions may be posed as to the validity of specific cases on the occurrences of narrow endemics. Nevertheless, for the general trend of endemism in the flora of China, the endemic genera and species of Compositae present remarkable examples.

The Meridional Ranges, especially in northwestern Yunnan, have the highest degree of endemism in the Compositae, both on the generic and on the specific level. Many monotypic genera like *Vierrhapperia*, *Formania*, *Vladimiria* and *Leucomeris* occur only in Yunnan and others like *Wardaster* and *Bolocephalus* occur only in Sikang. Many oligotypic genera occur throughout the region forming S-patterns in Yunnan, Sikang, Szechuan and Kansu or Shensi. *Myriactis*, *Stereosanthus*, *Nouellia* and *Dubyaea* are a few examples. Some of them such as *Faberia* extend the range to Kweichow while others such as *Soroseris*, *Tricholepis* and *Myriactis* extend the range to Chinghai and Sinkiang or Tibet and North India. The high degree of endemism in the Meridional Ranges and the extension of some genera to the Himalayas, to Tibet or to Kweichow represent common patterns of the occurrence of monotypic or oligotypic endemic genera in the flora of China. For example, *Docynia delavayi* (Rosaceae), occurs only in Yunnan, while *Tetracentron sinense* (Tetracentraceae) is very numerous at mid-high altitudes both in Yunnan and Szechuan. *Euptelea pleiosperma* (Eupteleaceae), *Decaisnea fargesii* (Lardizabalaceae), and *Sibiraea laevigata* var. *angustifolia* (Rosaceae) are abundant in this region but with their ranges extended to India, Shensi, Hupei, or to Kansu and Sinkiang.

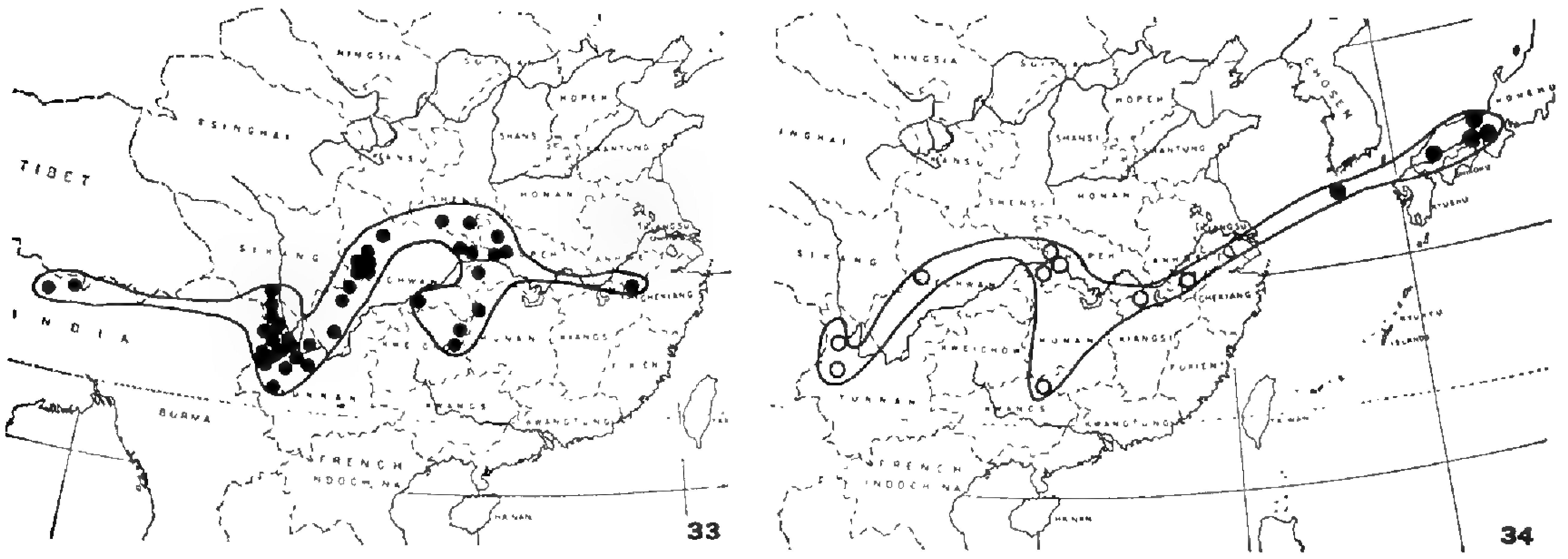
Taiwan is another area with a high degree of endemism, largely on the specific level. There are, however, a few oligotypic endemic genera which Taiwan shares with the mainland, especially with Yunnan. For example, there are 5 valid species of *Myriactis* on the mainland. These are concentrated in Yunnan and its adjacent regions, one as an endemic, one extending to Szechuan, two extending to Nepal and Kweichow. There are also one species and two varieties of the same genus in Taiwan. *Rhynchospermum verticillatum* is another species which occurs in Yunnan, Szechuan and Taiwan. There is a close tie between the flora of Yunnan and Taiwan. There are many subgeneric entities that are common to both regions and absent in areas between them. This tie is best expressed in some small endemic genera.

North China has several endemic genera of Compositae. Some of them are restricted only to one province. *Tugarinovi* and *Stilpnolepis* are known only from Suiyuan. *Takeikadzuchia* is restricted to Chahar. Others have wider ranges. *Myripnois* was first described from Peking. Additional collections have extended its range to Shansi and Kansu. *Filifolium* is known from Hopei to Heilungkiang. Probably many of these genera are due to the splitting activities of some Japanese and Russian botanists. The general flora evidently does not have a proportionate number of isolated endemics on the generic level. In general there are fewer endemics in North China. The genera characteristic of the flora of the region often extend to East China. *Xanthoceras sorbifolia* was first published from Peking. Additional collections extend its range to Shansi and Kansu. *Hemiptelea davidii* was also described from Peking but material in the herbarium of the Arnold Arboretum shows that it occurs in the Lower Yangtze Valley in the south, and in Manchuria and Korea in the north.

Northwestern China also has several endemic genera of Compositae. *Brachanthemum* is recorded from Kansu, Sinkiang and Mongolia. *Xanthopappus* from Kansu and Chinghai, *Olgaea* from Ninghsia, Shansi, Kansu, Sinkiang and Mongolia, and *Asterothamnus* is recorded from Sinkiang and Mongolia. The occurrence of these endemic genera of Compositae reflects the special character of the vegetation of the prevailing desert condition of this region. In the general flora endemic monotypic or oligotypic genera are not uncommon, especially in Caryophyllaceae, Tamaricaceae, Cruciferae and Zygophyllaceae. For example, *Acanthophyllum spinos* (Caryophyllaceae) occurs only in Sinkiang and the adjacent area of Mongolia. The monotypic genus *Tetradena* (*T. mongolica*, Zygophyllaceae), is endemic to the Kusuptschi desert of southwestern Suiyuan, and the oligotypic genus *Reaumuria* (Tamaricaceae) is represented in Kansu by *R. trigyna* and in Sinkiang and northwestern Mongolia by *R. soongorica*.

The region drained by the Middle Yangtze, that is, the Hupei-Szechuan border and the adjacent area of Shensi, marks the eastern end of Tsingling. Like the Meridional Ranges this is also a river-gorge country. But here the mountains walling the gorges of Yangtze, Hanshui and their numerous tributaries are only of moderate height. In general the river beds are about 600 ft. above sea level, and the altitudes of the mountains vary from 1800 to 7500 ft. The area is thickly populated and the vegetation is greatly disturbed. Some forests are preserved in the less accessible areas. Botanically this is the best known area of the country, for much has been published on the extensive collections made by A. Henry, E. H. Wilson, P. C. Silvestri and P. Farges from this region. In this region the endemism among Compositae is not as striking as that in the Meridional Ranges. On the generic level there is no genus which is limited to this region in particular. The genera that are endemic to China and also occur here seem to have their centers of distribution elsewhere. For example, *Ainsliaea* and *Pertya* both occur here but the center of their species concentration is evidently to the west of this area, in the Meridional Ranges. *Sheareria* also occurs here but the core of its range seems to be to the east of this area in the Lower Yangtze Valley. The endemics of this area are largely of the specific or subspecific levels, and they are relatively fewer than those of the Meridional Ranges. *Senecio doryotus*, *Ligularia fargesii*, *Ainsliaea henryi*, and *Pertya sinensis* are a few examples of the endemic species. *Ligularia hodgsonii* var. *pulchella* and *Anaphalis sinica* var. *calvescens* are some examples of the infraspecific endemics.

It seems that in this area endemism in Compositae does not reflect the picture of endemism in the general flora. It is true that this area seems to be on the periphery of the ranges of some endemic genera, for example, in the distribution of *Tetracentron sinense* (Tetracentraceae), which forms an S-shaped range over Yunnan, western Szechuan, southern Shensi and western Hupei (MAP 29). As remarked by E. H. Wilson, this monotypic genus is common in western Szechuan and rare in this area. Apparently western Hupei marks the eastern limit of the range of the genus. *Fortunearia sinensis* (Hamamelidaceae) is common in the lower Yangtze region, that is, the Anhwei-Chekiang-Kiangsu border. One collection from Chikungshan of southern Honan and one collection from Franghsien of western Hupei mark the western limit of the range of the species. *Loropetalum chinensis* (Hamamelidaceae) is widespread in the warmer region of China. It occurs in woods along the lower Yangtze valley and thence extends southward to Kwangtung and Kwangsi. Apparently its occurrence in the mid-Yangtze marks the northwestern limit of the range of this monotypic genus which is characteristic of the mesophytic forest in the warmer part of the country. On the other hand, this region constitutes the center of the ranges of some other monotypic or oligotypic endemic genera. For example, *Decaisnea fargesii* (Lardizabalaceae) and *Sinomenium acutum* (Menispermaceae) both have S-shaped distributions in Yunnan, Szechuan and Hupei. With *D. fargesii* the range extends bilaterally and with evident disjunction to Sikkim, on the west, and Huang Shan in Anhwei, on the east (MAP 33). With *S. acutum* the range extends eastward as a narrow band to Japan (MAP 34). In both genera the mid-Yangtze region is a part of the central core of their distribution. It is noteworthy that *Sinowilsonia henryi* (Hamamelidaceae) is restricted to the mountains of northwestern Hupei. *Cercidiphyllum japonicum* var. *sinense* (Cercidiphyllaceae) has an equiformal distribution from this region westward to western Szechuan and eastward to southern Anhwei. The occurrence of woody endemics in the mid-Yangtze and in the Meridional Ranges (which are sometimes called the Upper Yangtze) seems to tie the flora of the mid-high altitudes together. The relative paucity of endemics of Compositae in the mid-Yangtze region is apparently due to the absence of high mountains and alpine vegetation in the area.



MAPS 33, 34. Mid-Yangtze region as the center of two monotypic genera: 33, *Decaisnea fargesii*; 34, *Sinomenium acutum* and its variety.

The region generally called the lower Yangtze valley is another area characterized by a moderate degree of endemism. It covers northern Kiangsi, southern Anhwei, southern Kiangsu and the adjacent Chekiang. This area is a land of numerous hills. The botanically better-known ones are Lu Shan, Huang Shan, Tien-mu Shan, and the Nanking Hills, including the Ox Head Hills. Their altitudes vary from 900 to 4500 ft. The area is thickly populated and the vegetation is greatly disturbed. Endemism in the Compositae is at the specific or infraspecific level. For example, *Pertya desmocephala* is a narrow endemic which is known only from the type locality in Chekiang. *Youngia japonica* ssp. *elstonii* is known only from Chekiang and Kiangsu. At the generic level there are no Compositae limited to this area. *Sheareria* was first described from Kuling in northern Kiangsi. Additional collections extend its range to Chekiang, Hupei, Hunan and even northern Kwangtung. *Synurus* occurs in Kiangsi and Chekiang, but its range extends northward to Heilungkiang and to Japan. There are certain widespread endemic Chinese genera which are exceedingly abundant in this area. *Asteromoea, Hemistepta*, *Youngia*, and *Ixeris* are a few examples. They generally occur as weeds. Their origin is obscure and their ranges can hardly be regarded as illustrating certain distributional patterns. Endemism in the general flora of this area is more evident at the generic level than it is in the Compositae. The monotypic genera *Fortunearia* (*F. sinensis*, Hamamelidaceae) and *Fontanesia* (*F. fortunei*, Oleaceae) evidently have the center of their ranges in this area. The latter species apparently occurs more or less as a cultigen. The occurrence of several woody endemics in this area illustrates the same principle as expressed by the Composite genera. There is a close tie between the flora of this region and that of North, Central and South China. For example, *Hemiptelea davidii* (Ulmaceae) ranges from this area northward to Hopei, Shansi, Heilungkiang and Korea. The occurrence of *Decaisnea fargesii*

(Lardizabalaceae) and *Stephandra chinensis* (Rosaceae) in Huang Shan of southern Anhwei ties the flora of this area to that of Central and West China. *Fortunella hindsii* and *Ilex lohfauensis* are characteristic elements of the Wu-yi Range of southeastern China, and their northern limits are in southern Anhwei or Chekiang. The occurrence of *Cercidiphyllum japonicum* var. *sinensis* (Cercidiphyllaceae), *Sinomenium acutum* var. *cinereum* (Lardizabalaceae) in Huang Shan, Anhwei, and of *Ilex latifolia* in southern Kiangsu, Anhwei and Chekiang shows the very close relationship between the floras of this area and Japan.

The region drained by the Pearl River and its tributaries is generally known as South China. This area is a land of hills and mountains which are collectively called Nanling. The Nanling Range extends along with the tropic of Cancer from the border of Yunnan and Kwangsi eastward to the Fukien-Kiangsi-Chekiang border. The mountains are about 2000 to 4000 ft. above sea level. The vegetation is subtropical. In the last 50 years extensive botanical explorations have been made in the area largely through the coöperation of local Chinese universities and the Arnold Arboretum of Harvard University. Although much of the accumulated material awaits careful study, what has already been published is sufficient to indicate that this region possesses a relatively high degree of endemism. In the Compositae, at the generic level, there is the monotypic genus *Heteroplexis* (*H. vernonioides*) from Kwangsi. At the specific level, there are *Vernonia chingiana* from Kwangsi, *V. solanifolia* from Kwangtung, *Ainsliaea cleistogama* and *A. parvifolia* from Kwangtung, and *A. plantaginifolia* from southern Hunan. The general flora of this region shows the same pattern of endemism as reflected by the Compositae. In the north, the monotypic *Handeliodendron* (*H. bodinieri*, Sapindaceae) is restricted to the border region of Kweichow and Kwangsi. In the south, the monotypic genus *Mytilaria* (*M. laosensis*, Hamamelidaceae) is restricted to the Yunnan-Kwangsi and Indo-China border. Concentrated in this area but with wider distribution are *Bretschneidera sinensis* (Bretschneideraceae, a monotypic family) and *Eustigma oblongifolium* (Hamamelidaceae). The former species radiates in an equiformal area covering Kwangsi to northern Kwangtung on the east, eastern Yunnan on the west, southern Kweichow and Hunan in the north, and northern Indo-China in the south. The latter covers almost the same range and it extends even to Taiwan.

There are a few genera of Compositae which appear to be endemic to the flora of China as widespread weeds or as cultigens. They may be monotypic, as *Hemistepta* and *Callistephus*, or they may occur as oligotypic genera, each having one widespread variable species and a few isolated endemic species, such as *Asteromoea*, *Youngia* and *Ixeris*. This condition of endemism associated with man's activities is a common phenomenon in the general flora of China. For example, *Ginkgo* (*G. biloba*, Ginkgoaceae), *Metasequoia* (*M. glyptostroboides*, Pinaceae), *Broussonnetia* (*B. papyrifera*, Moraceae), *Platycarya* (*P. strobilacea*, Juglandaceae), *Pteroceltis* (*P. tatarinowii*, Ulmaceae), *Nandina* (*N. domestica*, Berberidaceae), *Chimonanthus* (*C. praecox*, Calycanthaceae), *Melia* (*M. azedarach*, Meliaceae), and *Ailanthus* (*A. altissima*, Simarubaceae) are all Chinese species or monotypic genera, the wild state of which is obscure, and their existence is associated with man. Probably this condition is brought about largely through man's continuous destruction of the natural vegetation. Since the period when the angiosperms became dominant features of the world's flora, there is no geological evidence that catastrophic changes have annihilated the plants of any extensive area in China as did the Pleistocene glaciers in Europe and America. Yet with the exception of the less accessible areas of the Meridional Ranges, there is hardly any area covered with natural vegetation. In most places poverty is a striking feature of the flora. Unless protected by the Buddhists as temple property, woods are rare. China is an old country, and it has long been extremely overpopulated. There has been a constantly greater demand for food than the arable land can produce. The conversion of forested areas into temporary farms by burning the hillsides is a common practice. Repeated intentional forest fires have denuded the mountains throughout the country, exterminated many species and left many others to represent isolated endemic genera or families.

In conclusion, the endemics in the Chinese Compositae reflect a very fair picture of endemism in the general flora of the country except in the mid-Yangtze region where there are proportionately more isolated woody endemics at the generic level. The lack of alpine vegetation in this area and the protection from human destruction which the steep gorges afford the vegetation of limited areas are probably the chief contributing factors of this situation.

5. Extra-Chinese Elements

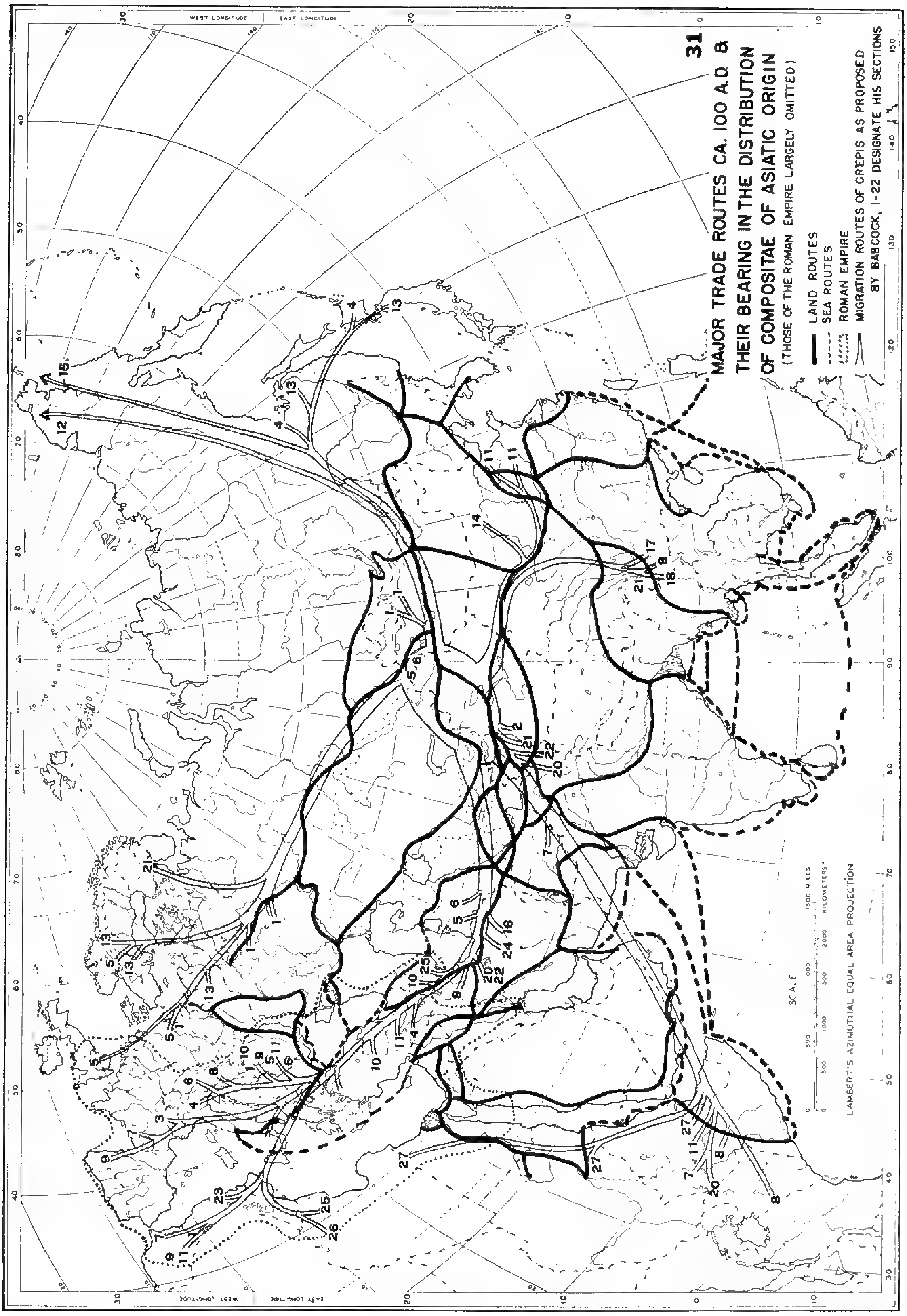
About 48% of the genera of Compositae in China are probably not of Chinese origin. Some of them have as many as 30 species, while others have only one or two or a few species. Their distribution in China is widespread either as weeds or cultigens or localized in coastal regions or port areas as adventives. In general, the tropical elements such as *Vernonia*, *Gynura*, *Blumea*, *Emilia*, *Erechtites*, etc. are concentrated in the south, especially in Yunnan, Kwangtung, Hainan and Taiwan. The Mediterranean, Central Asiatic and European elements such as *Tragopogon*, *Achillea*, *Cousinia*, *Echinops*, *Arctium*, *Matricaria*, etc. are limited to the west and the north, especially to Sinkiang, Tibet, Mongolia and Hopei. It is noteworthy that most of the widespread weeds like *Erigeron canadensis*, *Xanthium strumarium*, *Eclipta prostrata*, *Bidens pilosa*, etc. appear to be of New World origin.

As America is a melting pot of the modern world, so was China in the ancient historical times, and the flora of China is the result of this mingling. In 126 B.C. a general of the Chinese Empire subdued the people and annexed the country of the Iaxartes and Oxus rivers in Central Asia to the Han Dynasty. Since then, for approximately sixteen centuries, China has had more influence on land and sea in the Old World than most people realize. With the conquest of Central Asia began the silk trade, the most far-reaching large-scale overland commerce of the ancient time. It reached from the Pacific coast on the east to the shores of Britain on the west. Although the transactions were carried on through intermediate merchants, large-scale movement of men and animals provided the opportunity for the introduction of plants accidentally. Caravans of hundreds of horses, carts, yaks or camels passed back and forth over the great highways of Central Asia. The diary of a Taoist monk recorded that it took that 73-year-old man (Kiu Ch'ang-chung) and his 16 disciples 10 months to travel from Peking to northeastern Mongolia and thence westward to the Altai and Tien Shan mountains, and across the Pamir Plateau to reach Samarkand in 1222 A.D. (Bretschneider, 1875, p. 15–56). On their return trip it took them only three months and ten days to reach Peking through southern Mongolia, the regular postal route. The military, diplomatic, commercial and religious intercourse with Persia, India and Arabia overland (MAP 31), and through them with Europe and the Mediterranean world explain the presence of western Asiatic, Mediterranean and European elements in western and northern China.

Meanwhile, China was a sea power in the Pacific and Indian oceans for eleven centuries. There were regular communications between the mother country and the overseas Chinese in Malaysia. The commercial centers in Indo-China, Siam, India, Ceylon, Persia, Arabia and the East Coast of Africa were frequently visited by Chinese fleets (MAP 31). For example, in 1405 A.D. a fleet of 62 ships and 27,800 men, under the command of Cheng Huo went on regular patrol duties. The expedition took two and a half years. During his lifetime Cheng Huo made seven such expeditions and reached as far as Arabia and East Africa. With the periodical return of the overseas Chinese from the Malaysian islands and important ports of tropical Asia, and with the expeditions of the Chinese fleets, many tropical plants were either accidentally or intentionally introduced to the coastal regions of China. For example, *Chrysanthemum segetum* was brought in from the Arabian world to China for its edible young shoot. *Sphaeranthus africanus* has been introduced to Hainan Island and Taiwan, and a very closely related species, *S. senegalensis*, to Yunnan.

Unawareness of the interchange of plants as associated with human activities in the ancient historical times has created many unnecessary problems in plant taxonomy. *Chrysanthemum segetum* was brought in by a colony of Arabians who came to Canton about the fourth century. It has been adopted by the Cantonese as a vegetable and has spread with them to all warmer parts of China. Chinese plants in most herbaria have been named *C. coronarium*. Bailey in 1917 saw the plant in Chinese gardens and named it *C. coronarium* var. *spatiosum* in 1920. The same cultivar has been named by Loureiro as *Buphthalmum oleraceum* from Canton in 1790. Likewise, material of *Sphaeranthus africanus* from South China has been named *S. cochinchinensis* by Loureiro, *S. suberiflorus* by Hayata.

This confusion is not limited to the nomenclature of species of Compositae. It is a common disorder in the taxonomy of many Chinese plants. *Angraecum falcatum* was published from a plant supposedly of Chinese



Map 31. The major trade routes ca. 100 A.D. and their bearing on the distribution of Compositae of Asiatic origin. (Base map Goode's No. 205.)

origin. In the last 170 years orchidologists have placed it in nine different genera and a long list of synonyms has been created on its account. In China it has only been collected from the vicinity of Ningpo in Chekiang, a center of Chinese Buddhism. There is no other Chinese orchid that is closely related to it. In the Ames Orchid Herbarium of Harvard University I found its nearest relative to be an African species, *A. pusillum*. Perhaps this isolated Chinese cultigen was one of the ancient introductions from Africa.

The migration of plants accompanying the large body of human movement is always reciprocal. There were Chinese plants introduced and established in Africa long before Linnaeus' time. *Myrsine africana* Linn. was originally described from Ethiopia. The wide distribution of the species in the interior of China and concentration of related species of the genus in eastern Asia indicate that the natural origin of *M. africana* is Chinese.

VI. THE REFLECTION OF CHINESE COMPOSITAE ON THE ORIGIN AND ROUTES OF MIGRATION OF SOME MEMBERS OF THE FAMILY

It is well known that China is one of the most unique phytogeographical regions of the world. Before the data on the Compositae of this important phytogeographical region were available, James Small had proposed a hypothetical scheme for the origin and development of the Compositae of the world. Although his scheme has been questioned and disproved by competent monographers of special groups, such as Babcock and Stebbins, it has also been followed by synantherologists who work on the entire family of certain regions, like Kitamura. Now, what advancement can a better knowledge of the Chinese Compositae offer to the understanding of the origin of and routes of migration of some genera of Compositae?

Small's long article on the Origin and Development of the Compositae was published in thirteen issues of *The New Phytologist*. His main thesis "is that *Senecio* was the first genus of the Compositae to come into existence and that it has directly or indirectly given rise to all the other genera of the family." He considered "the origin of one definite kind of living organism from another definite kind of living organism as a normal, natural result of the actual *living* of the parent organism in a particular region," and, upon many suppositions, he derived *Senecio* from the *Siphocampylus-Centropogon* group of Lobelioideae. As these genera are natives of tropical America, he proposed that *Senecio* and, in turn, Compositae originated in or about the Bolivian region of South America. He suggested further that from tropical South America the genus migrated along the Andes northward to Central America and then along the Cordilleran system to Alaska, thence to the Old World. He maintained that throughout the world the path of migration of the genus is commonly along the mountain ranges, usually about 3000 ft. and frequently above 6000 ft. To illustrate his scheme of the development of the subdivisions of the family he made the large number of species of *Senecio* to represent the substantial trunk and constructed a family tree for the Compositae, employing this to show the evolution of the principal subdivisions through certain modern genera in time and space.

Although Small's article contains informative summaries of former works on Compositae and helpful observations which advance our understanding of the family, his conclusion on the origin and development of Compositae is unsupportable. It represents too much "mental effort," in Small's own words, and little truth. First, the origin of an inclusive family like the Compositae is not so traceable as to have a living parent, as Small put it. Recent researches in smaller categories of Compositae, for example Babcock's *Crepis*, Keck's *Artemisia* and Stebbins' *Dubyaea*, *Soroseris*, etc., all indicate that present evidences are not sufficient even to trace the precise progenitors of a genus, a section or a subtribe of Compositae. No one can pretend to know the exact origin and development of the Compositae. Secondly, *Senecio* is not a primitive genus in the Compositae. It is large, inclusive and heterogenous. It is inevitable that such an artificial genus is polyphyletic. Thirdly, in constructing the family tree to show the evolution of the Compositae in time and space, a very important geobotanical region, central and eastern Asia, including China, was not included. This omission of a region which is vital in the origin, development and distribution of plants, animals, men and culture, naturally shifted the actual points of origin of many genera or even tribes of Compositae to some assumed areas.

1. On the Origin of Compositae

The origin of Compositae is obscure and it may never be elucidated. There are many gaps in the fabric of the evolution of the angiosperms. The missing progenitor of the Compositae is but one of them. Paleobotanical evidences in the Cromerian Beds in England, in the Teglian and the Reuverian Beds in central and southern Europe and in the Wilcox Beds in North America indicate that members of Compositae were widespread throughout the northern hemisphere in the Oligocene era. Fossil remains of achenes distinctly resemble those of modern species including *Tussilago farfara*, *Lapsana communis*, *Picris hieracioides*, *Crepis fuscipappus*, *Carduus nutans*, *Cnicus palustris*, *Cirsium heterophyllum*, and *Eupatorium japonicum,* indicating that members of the Senecioneae, Cichorieae, Cynareae and Astereae were common in the Old World in the Pliocene era. Evidence for a progenitor of Compositae is lacking, and the home of the origin of the family is obscure, as is that of the angiosperms. Large genera with hundreds or thousands of species, like *Senecio* and *Aster* are heterogenous. Their subgenera or sections may possibly represent taxa of entirely different origins.

2. On the Asiatic Origin of Some Widespread Genera

Babcock's classical treatment of the genus *Crepis* elucidated the origin and routes of migration of a complicated, widespread genus of Compositae.

His conclusions throw light upon our understanding of the origin and distribution of many widespread genera which have distributional patterns similar to that of *Crepis* (e.g., *Aster*, *Leontopodium*, *Artemisia*, *Chrysanthemum* including *Tanacetum*, *Senecio* including *Cacalia*, *Ligularia* and *Cremanthodium*, *Saussurea*, *Jurinea*, *Taraxacum* and *Lactuca*). These genera were formerly regarded as of European or American origin. Additional evidence favors the suggestion that they are actually of Asiatic origin. As illustrated in TABLE V, China has the largest number of species in Asia in each of these genera. In China the Meridional Ranges appear to be the center of their species concentration. One may safely conclude that Meridional Ranges are the home of these large genera of Compositae.

TABLE V. **Widespread genera with an unusually large number of species in China**

	Indo-China	India	China	Japan	Korea	Pamir	Siberia
Aster	1	14	137	35	9	2	9
Leontopodium	1	1	57	6	3	1	2
Gnaphalium	3	7	20	3	4	0	4
Anaphalis	0	0	51	5	1	0	0
Carpesium	2	2	18	10	5	0	0
Artemisia	4	27	156	40	37	20	58
Chrysanthemum	2	4	73	30	10	7	3
Cacalia	0	0	60	25	7	0	1
Senecio	9	63	160	13	10	3	22
Ligularia	0	0	105	10	7	1	5
Cremanthodium	0	7	47	0	0	0	0
Saussurea	3	39	270	53	31	7	25
Jurinea	0	3	18	0	0	1	4
Ainsliaea	0	4	47	10	3	0	0
Taraxacum	0	2	57	37	2	22	2
Lactuca	9	22	57	6	4	1	7
Crepis	6	14	31	2	0	3	14
Youngia	0	0	30	6	6	0	0

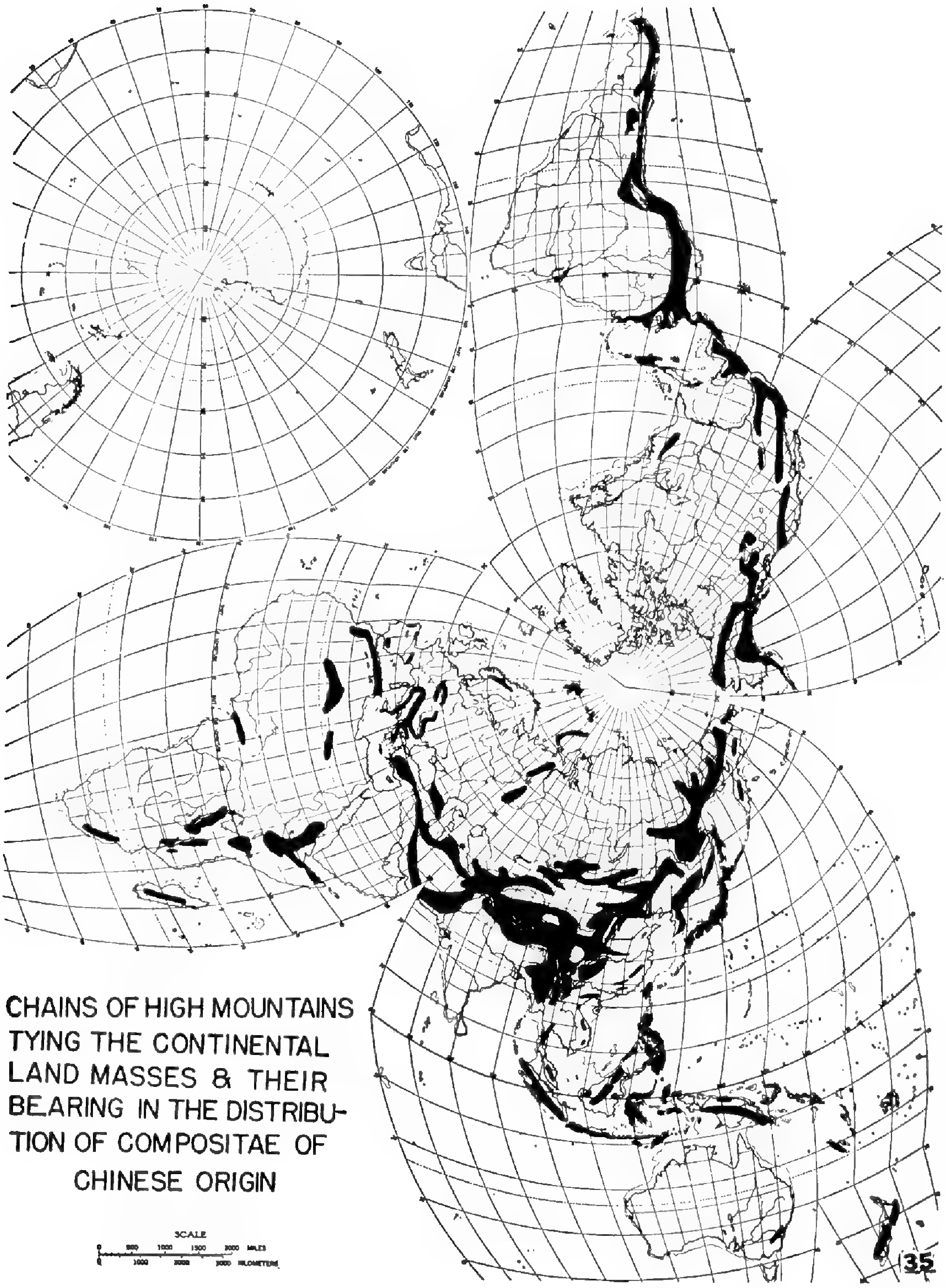
In our discussion on the area richest in Compositae we have pointed out the climatic conditions and the floristic character of the Meridional Ranges. The distribution maps of the large genera of Compositae of China, (MAPS 3, 6, 11–15, 17–19, 21–23), all indicate that these genera actually aggregate in this area. It is highly possible that the area richest in Compositae may also be the home of many of the large genera of Chinese Compositae. Geological, geographical, and floristic evidences seem to give support to this proposition.

Geological evidences seem to favor the suggestion that the Meridional Ranges are the home of montane and alpine genera such as *Leontopodium*, *Jurinea*, *Aster*, *Artemisia*, *Senecio*, *Ligularia*, *Cremanthodium*, etc. This region is geologically much older than the surrounding area. While the present Szechuan Basin and the Tibetan Plateau were still beneath the

Tethys Sea throughout the Cretaceous, rising land and mountains were already in existence in this region. Montane and alpine flora existed here before the Himalayan uplift in the late Eocene. Authorities on the flora of Tibet generally regarded the alpine elements of that region and the Himalayas as being derived from that of this river-gorge region (Ward, 1935, p. 264). Here, localized glaciation may have occurred at higher elevations, but the lower valleys, especially those nearer to the equator, have never been touched by the Pleistocene glaciers. Thus the Meridional Ranges have become a haven as well as a producer of many modern genera of angiosperms, including some Compositae.

Geographical evidences justify the consideration that the Meridional Ranges are the home of some widespread genera which occur in all important mountain ranges of the world. Map 35 represents a polar equal-area projection of the world with the continental land-masses developed radially from the north pole and the major mountain ranges plotted in black. It is worthy of note that the various continental masses are tied together by more or less continuous chains of high mountains, with the center of the tie falling in central and southeastern Asia. This phenomenon is of profound significance in the understanding of widespread genera or species of plants and animals. It is of special interest to us in our consideration of the possible origin and routes of migration of genera of Compositae of Asiatic origin. First, among all the living species of animals and plants there is one cosmopolitan species the origin of which is somewhere in this core and which is known to have immigrated gradually from here to all the major land-masses of the world in prehistoric times, without the aid of a land-bridge or continental drift. This species is *Homo sapiens*. Secondly, the Meridional Ranges are also a portion of the same core of the world's land-masses. It is highly possible that such montane and alpine genera as *Senecio*, *Aster*, *Artemisia*, *Leontopodium*, etc., have migrated throughout the world in the same direction as man did, but with better speed because of the moving forces contributed by wind, animals and, to some extent, by water, ice, landslides and other natural mechanisms of plant dispersal.

Finally, floristic evidences testify to the antiquity and prove the originality of the present flora of the Meridional Ranges and stamp the region as the home of the genera which have their species concentration there. Paleobotanical evidences indicate that the early flowering plants which became predominant during the Cretaceous period were mostly woody plants with generalized distributions. It is generally accepted that they lived for millions of years under fairly moist and rather warm conditions. The herbaceous forms represent later developments which came about with the climatic and altitudinal changes. The mesophytic forests of the middle altitudes of the Meridional Ranges and the alpine flora of the region were developed in accordance with these paleobotanical principles. The most striking fact is that the alpine flora of this region is actually situated as if it were on an island surrounded by mesophytic forest. The majority of its components are found only as fossils in other parts of the world. The earliest known angiosperm is believed to be *Homoxylon*, known through a piece of



MAP 35. Polar equal area projection of the world showing the continental land-masses tied together by more or less continuous chains of high mountains (dark), with the center of the core in central and southeastern Asia. (Base map Goode's No. 201.)

fossil wood of Jurassic origin from the Rajmahal Hills of India (Sahni, 1932, p. 4). In the mesophytic forest of the Meridional Ranges this primitive homoxylous structure reappears in *Tetracentron sinense*. In the same forest at different levels grow *Sassafras*, *Liriodendron*, *Cercidiphyllum*, *Magnolia*, *Cinnamomum*, *Machilus*, *Ailanthus*, *Cedrela*, *Dipteronia*, *Aleurites*, *Mallotus*, *Liquidambar*, *Paliurus*, *Grewia*, *Actinidia*, *Mahonia*, *Diospyros* and *Zizyphus*. All these are well-known fossil genera to botanists in other parts of the world. Together with numerous species of *Acer*, *Populus*, *Salix*, *Viburnum*, and species of Ericaceae, Menispermaceae and Coniferae, they form the mesophytic forest of the middle-high altitudes surrounding the alpine flora which is rich in Compositae. The antiquity and the originality of the flora of the Meridional Ranges is indisputable. This is true of the many Composite genera as well as of the general flora.

3. On the Migration of Compositae

The Compositae is one of the most ubiquitous families of the flowering plants. In the extent of areas covered this family is surpassed only by the Gramineae. Actually there are more genera and species in the Compositae than in the Gramineae, but unlike the latter, members of this family do not form continuous stretches and consequently they do not become so prominent in the vegetation of any area as do the Gramineae. General ubiquity is an expression of the possibility of wide dispersal of the disseminules of the members of the family. Ridley in his monumental work on the *Dispersal of Plants throughout the World* has cited many species of Compositae as his examples of dispersals by the action of wind, the force of water or ice and by the transport of animals, including fish, reptiles, insects, birds, mammals and man. There is no need to repeat his findings here. Nevertheless, there seems to be a necessity to supplement his summaries by pointing out how man's movement over the earth has accelerated the natural processes of plant dispersal, especially in connection with the migration of Compositae.

In preparing the enumeration of the Compositae of China and in trying to apply the findings of the enumeration to the advancement of a better understanding of the vegetation of China, I have referred to hundreds of articles and books. Most of them are involved in the taxonomy of the family and its subordinate groups. Some of them are reports of botanical explorations and lists of local floras. Not a few of them are on phytogeographical principles and the geography or geology of the country. This variety of literature gives me the impression that there is an evident lag on on the part of most taxonomists and many phytogeographers in giving due emphasis to the human effect on the distribution of plants. Although it is a well-known fact that man in five thousand years has altered the surface of the earth more than has Nature in five hundred million years, when phytogeographers attempt to explain the widespread or discontinuous genera they rather rely on hypotheses of land-bridges, continental drift, and nunataks, and pay no attention to what the prehistorical and historical man might have done to bring about the present picture of natural distribution. Their writings impress the reader with their belief that the world has been left to the operation of natural processes alone. They maintain that various floras have developed *in situ* and that they have not been disturbed until the arrival of the white man. They consider the plant specimens collected by the early European explorers, and described by post-Linnaean authors as indigenous to the particular area. They believe that those plants have been left there since the Tertiary time. Such a concept is incorrect.

From the standpoint of the colonization of the world by the Europeans, there is an Old World and a New World, but from the standpoint of the inhabitation of the land surface by man, the major land-masses of the world are all old. With the exception of a few islands where active volcanoes explode periodically, there is no land surface too young to have been inhabited by man. It is true that where the land-masses are connected, as in the case of Asia-Europe-Africa, man has traveled freely to and fro. It was not uncommon for people like Abraham of Ur to wander on foot with large companies of herds and herdsmen from Iraq through Jordan to Cairo and then back to get settled in Israel. Nor was it strange for a monarch such as the Queen of Sheba to travel through the tropical heat from Ethiopia to Jerusalem for a visit. In prehistorical and historical time man has traveled far and wide. Accompanying every human movement is the deliberate or accidental introduction of plants. To overcome the barrier created by large bodies of water prehistorical man made boats long before the invention of a written language. The Neolithic culture of the tribes inhabiting the Pacific Islands and of some of the Indians in the Americas seems to indicate that these land-masses have been occupied and their vegetation disturbed for from seven to ten thousand years. The migratory races and their domesticated animals carry plants far and wide. In Asia and Polynesia the origin of many of them is obscure. This type of introduction extends over a long period of time. The early stages are beyond elucidation. In regard to the distribution of Compositae, the achenes of fifteen modern species of the family have been unearthed with the Neolithic remains in Europe. This indicated that man has been associated with these species for a long time and it is inevitable that he became instrumental in their migration.

There are some botanists who have an excellent range of knowledge of plants of certain areas, but who because of their prejudice against what they call "closet botanists" have made some hasty conclusions concerning the vegetation of isolated areas. Upon finding some colonies of plants which are closely related to a geographically remote ally, they concluded that the taxon is a relict species, implicitly ruling out the possibility that it was introduced (accidentally) by man and that what they have interpreted as an ancient survivor may actually be a recent arrival. The area that appears undisturbed to a twentieth century botanist may have been visited many times by indigenous peoples and an isolated colony may be an accidental introduction. In exchanging experiences of exploration in China, an entomologist who had surveyed the Tsingling from an airplane, and caught some ants on one of the peaks, told me that the area appeared to be uninhabitable, but my association with the hunters and medicine diggers and the collectors of wild edible plants leads me to a different conclusion. It is amazing how far-reaching is the influence of the village dwellers on the vegetation of the region, and how exact is their knowledge of where certain things grow. For the reward of a couple of sewing needles a woman had walked with me into the deep wilderness of a mountain of the Meridional Ranges to show me a special kind of bamboo. For a few pennies a fifteen-year-old medicine digger led me to an apparently virgin forest of *Tsuga*, *Picea*, *Betula* and *Acer*, to collect a species of *Cimicifuga* which yields certain medicine. What appears to a city dweller as vast wilderness is to tribal people like a playground is to school children. They seem to have visited everywhere, and know exactly where to find certain things. This is true with tribal people everywhere, in Africa and America as well as in Asia. Thus what appears to be relict species may be an accidental introduction of tribal people.

It does not take long to change vegetation through man's unintentional activities. Allan in 1940 in *A Handbook of the Naturalized Flora of New Zealand* reported that in less than two and a half centuries over 1000 species of alien plants have been recorded from that country. Many of them have firmly established themselves, and have even become dominant features in the vegetation of New Zealand. On the basis of 500 well-established aliens, Allan estimated that approximately 56% of them have entered the country in seed mixtures and been further spread by sowing. About 15% were introduced through adhesion to animals. Among the common aliens which have become abundant throughout that country are these Compositae: *Arctium lappa*, *Cirsium arvense*, *C. vulgare*, *Chrysanthemum leucanthemum*, *Senecio vulgaris*, *S. jacobaea*, *Hypochoeris radicata*, *Crepis capillaris*, and *Sonchus arvensis*. If in 200 years man can unwittingly create "a new flora and a new vegetation" in a distant land, how much more could he have done in intermingling the flora of the land he has occupied for many thousands of years? The modern man has speed, whereas the prehistoric, ancient and medieval man had time.

To illustrate man's instrumentality both directly and indirectly in the distribution of some Composite genera, I redraw Babcock's diagrammatic representation of the principal migration routes of *Crepis*, and superimpose it upon a map of the ancient trade routes (MAP 31). In so doing a striking correlation between the principal routes of migration of *Crepis* and the major ancient highways is revealed. It is undeniable that the dispersal of *Crepis* is accelerated by man's activities. As the species of *Crepis* are normally of little or no economic importance to man, one may conclude that this distribution has been unintentional. It is very possible that the dispersal has been effected through the attachment of the seeds to man and his animals.

It is customarily accepted among botanists that the fruits of *Xanthium*, *Arctium*, *Bidens*, etc., which have specially modified mechanisms for adhesion, are dispersed through attachment to animals, and that the fruits of *Taraxacum*, *Artemisia*, *Crepis*, *Senecio*, etc., which are small and plumed, are specially modified for wind dispersal. Small had demonstrated by a specially designed wind dispersal apparatus that a light breeze of 1.97 m.p.h. is sufficient to carry the seed of *Taraxacum* to indefinite distances, and that a moderate breeze of 4.4 m.p.h. can transport the seed of *Leontopodium*. Few people realize, however, that the seeds of many Compositae which have small size, light weight and achenial hairs can be transported more effectively through adhesion than by wind. When man and animal travel in nature, their feet and clothes or fur are usually wet because of dew, rain or wet ground. When the momentum of the walking feet or running animal knocks against the partially disintegrated ripe head of *Saussurea*, *Senecio*, *Crepis*, *Taraxacum*, *Leontopodium*, *Artemisia*, *Lactuca*, etc., hundreds of small, light, hairy achenes naturally adhere to the wet surface of the feet of man or to the body of an animal, and are thus carried away from the parent plant. The distance may be long or short. The German botanists have attributed the migration of a Chinese species, *Lactuca tatarica*, to Europe through its adherence to a Steppenkuhn, *Syrrhaptes paradoxus* (Hegi, 1928, p. 1133, *fig. 809*). This is a widespread species in China. As man is the only species that has spread over the land surfaces of the earth in an era when there is no known continental drift or land-bridge, his effect on the migration of small-seeded species with disjunct or widespread distribution, especially those with small, light seeds like the Compositae, should be given serious consideration.

SUMMARY

1. The Compositae is the largest family of flowering plants in China. It contains 167 genera and 2027 species.

2. A large number of the genera are small. Thirty-two per cent of the 167 genera have only one species each. Twenty-two per cent contain two or three species each. This is due to the presence of large numbers of endemic genera in the interior and to the numerous introduced adventives in the border areas.

3. The Composite flora of China is characterized by an unusually large number of endemic species in the genera *Aster*, *Leontopodium*, *Anaphalis*, *Senecio*, *Ligularia*, *Cremanthodium*, *Cirsium*, *Saussurea*, *Jurinea*, *Ainsliaea*, *Taraxacum*, *Lactuca*, *Crepis*, *Youngia*, *Pertya* and *Ixeris*. Like *Dubyaea*, *Soroseris*, *Callistephus* and other local endemics, these genera should be considered to be Chinese in origin. Although some of them occur in China's neighboring countries, their numbers there are much smaller.

4. The distribution of the Chinese Compositae is very uneven. Many of them concentrate at the river-gorge area on the Yunnan-Szechuan-Sikang-Kansu borders, known also as the Meridional Ranges. The distribution of many species forms an S-shaped range over these mountains and thence extends north-eastward or westward.

5. About 48% of the Chinese Composite genera are extra-Chinese elements. Species of these genera generally are concentrated in the bordering areas. The bordering provinces in adjacent Central Asia and Siberia, that

is, Sinkiang, Mongolia, Heilungkiang and Tibet, have a considerable number of central or western Asiatic, European or Mediterranean genera such as *Echinops, Carduus, Achillea,* etc. Their distributions seldom extend south to the Yangtze River. The Composite flora of the coastal provinces, namely, Kwangtung, Fukien, Taiwan and Hainan contains a considerable number of pantropic elements such as *Blumea, Vernonia, Elephantopus, Sphaeranthus, Spilanthus,* etc. The distribution of these genera seldom extends north of the Yangtze River.

6. The immigration and emigration of Composite genera in and out of China correlate fairly well with the ancient trade routes and modern waterways. Evidently the distribution of many widespread genera as well as some localized adventives are associated with man's activities. The more widespread genera have had longer periods of association with man and the localized adventives are recent arrivals.

7. The origin of the Compositae is obscure. The Meridional Ranges of China constitute an area of origin of widespread large genera as well as of small narrow-endemic ones. Geologic, geographic and floristic evidence all favor this conclusion.

8. The degree of endemism is relatively high in Chinese Compositae. About 30% of the genera are endemic. There is no regional limit of endemism at the species level. The endemic genera are concentrated largely in the Meridional Ranges.

LITERATURE CITED

ALLAN, H. H. 1940. A handbook of the naturalized flora of New Zealand. Dep. Sci. Ind. Res. Bull. **83**: 1–344.

BABCOCK, E. B. 1947. The genus *Crepis* I. The taxonomy, phylogeny, distribution and evolution of *Crepis*. Univ. Calif. Publ. Bot. **21**: 1–198.

BARTHOLOMEW, J. G. 1922. The Time Survey Atlas of the World, *t. 3.*

BRETSCHNEIDER, E. 1875. Notes on Chinese Mediaeval Travellers to the West. iii + 130 pp.

DALLA TORRE, C. G. DE, AND H. HARMS. 1900–1907. Genera Siphonogamarum. [Compositae, p. 523–583.]

CRESSEY, G. B. 1934. China's Geographic Foundations. xviii + 436, map.

FERNALD, M. L. 1926. The antiquity and dispersal of vascular plants. Quart. Rev. Biol. **1**: 212–245.

———. 1929. Some relationships of the floras of the northern hemisphere. Proc. Internat. Congr. Plant Sci. Ithaca **2**: 1487–1507.

———. 1931. Specific segregations and identities in some floras of eastern North America and the Old World. Rhodora **33**: 25–63.

———. 1931. The home of *Kerria japonica*. Rhodora **33**: 199–200.

———. 1944. Continental drift and plant distribution (a review). Rhodora **46**: 249–251.

———. 1950. Gray's Manual of Botany, ed. 8. Compositae: 1357–1567.

FEDTSCHENKO, O. A. 1905. Flore du Pamir. Compositae, 108–137.

GAGNEPAIN, F. 1924. Composées. Flore Générale Indo-Chine **3**: 448–663.

GOOD, R. 1929. The taxonomy and geography of the Sino-Himalayan genus *Cremanthodium* Benth. Jour. Linn. Soc. Bot. **38**: 259–316.

———. 1953. The Geography of the Flowering Plants, ed. 2. xiv + 452 pp.

GOODSPEED, T. H. 1936. Essays in Geobotany. xxv + 319 pp.

GRAY, A. 1840. Bibliographical Notices. 7. Dr. Siebold, Flora Japonica; sectio Prima, Plantae ornatui vel usui inservientes, digessit Dr. J. G. Zuccarini. Am. Jour. Sci. Arts **39**: 175–176.

———. 1856–1857. Statistics of the flora of the northern United States. Am. Jour. Sci. Arts **22**(2): 1–30. 1856; **23**: 62–84, 369–403, 1857.

———. 1884. Synoptical Flora of North America **1**(2): 48–448.

HALENIUS, J. P. 1750. Plantae Camschatcenses Rariores. Linnaeus, Amoenitates Academicae **2**: 332. 1752.

HEGI, G. 1928. Illustrierte Flora von Mittel-Europa **6**(2): 394–1386.

HERRMANN, A. 1935. Historical and Commercial Atlas of China, Harvard-Yenching Inst. Monogr. Ser. **1**: 1–112.

HITCHCOCK, C. L., ET AL. 1955. Vascular Plants of the Pacific Northwest. Pt. 5, Compositae. 343 pp.

HOOKER, J. D. 1881. Flora of British India **3**: 219–419.

JAMES, P. E. 1943. An Outline of Geography, xvi + 475 pp. *pl. 1–24.*

KECK, D. D. 1946. A revision of the *Artemisia vulgaris* complex in North America. Proc. Calif. Acad. IV. **25**: 421–468. *fig. 1–19.*

KITAMURA, S. 1937–55. Compositae Japonica. Mem. Coll. Sci. Kyoto Univ. Ser. B. **13**: 1–421. 1937; **15**: 285–446. 1940; **16**: 155–292. 1942; **22**: 76–126. 1955.

KRYLOVA, P. 1949. Flora Zapadnoi Sibiri [Florae Sibiriae Occidentalis] **11**: 2649–3070.

LEE, J. S. 1939. The Geology of China. xv + 528 pp.

LI, C. C. 1228. Kiu Ch'ang-chun's Travels. (In Chinese, also see Bretschneider, Notes on Chinese Mediaeval Travellers, 15–56.)

LI, H. L. 1952. Floristic relationships between eastern Asia and eastern North America. Trans. Am. Phil. Soc. II. **42**: 371–429. *56 maps.*

———. 1953. Endemism in the ligneous flora of eastern Asia. 7th Pac. Sci. Congress **5**: 1–5 (reprint).

LINNAEUS, C. 1750. Plantae Camschatcenses Rariores. Publico Examini submisis Jonas P. Halenius. Amoenitates Academicae **2**: 332. 1752.

LYDE, L. W. 1933. The Continent of Asia. xxii + 777 pp.

MARSH, G. P. 1874. The Earth as Modified by Human Action, a new edition of Man and Nature. xvii + 656 pp.

OSTENFELD, C. H. AND C. SYRACH-LARSEN. 1930. The species of the genus *Larix* and their geographical distribution. Biol. Medd. Dansk. Vid. **9**(2): 1–107. *fig. 1–35. maps 1–8.*

RIDLEY, H. N. 1930. The Dispersal of Plants throughout the World. xx + 744 pp.

ROSS-CRAIG, S. 1954. A revision of the genus *Sphaeranthus.* Hook. Ic. Pl. **36**: 1–90. *t. 3501–3525.*

SAHNI, B. 1932. *Homoxylon rajmahalense*, gen. et sp. nov. A fossil angiospermous wood devoid of vessel, from the Rajmahal Hills, Behar. Palaeont. India II. **22**: 4.

SMALL, J. 1917–19. The origin and development of the Compositae. New Phytol. **16**: 157–177, 198–221, 253–276. 1917; **17**: 13–40, 69–94, 114–142, 200–230, 1918; **18**: 1–35, 65–89, 129–176, 201–234. 1919.

SMALL, J., AND I. K. JOHNSTON. 1937. Quantitative Evolution in Compositae. Proc. Roy. Soc. Edinb. **57**(3): 26–54.

STEBBINS, G. L., JR. 1933. A new classification of the tribe Cichorieae, Family Compositae. Madroño **12:** 65–81.

———. 1940. Studies in the Cichorieae. Mem. Torrey Bot. Club. **19:** 1–76.

WARD, F. K. 1935. A sketch of the geography and botany of Tibet, being materials for a flora of that country. Jour. Linn. Soc. Bot. **50:** 239–265.

———. 1937. Plant Hunter's Paradise. *maps 1–347.*

WULFF, E. V. 1950. An Introduction to Historical Plant Geography. (Transl. by E. Brissenden.) xv + 223 pp.

A NEW SPECIES OF PHALERIA (THYMELAEACEAE) FROM NEW GUINEA *

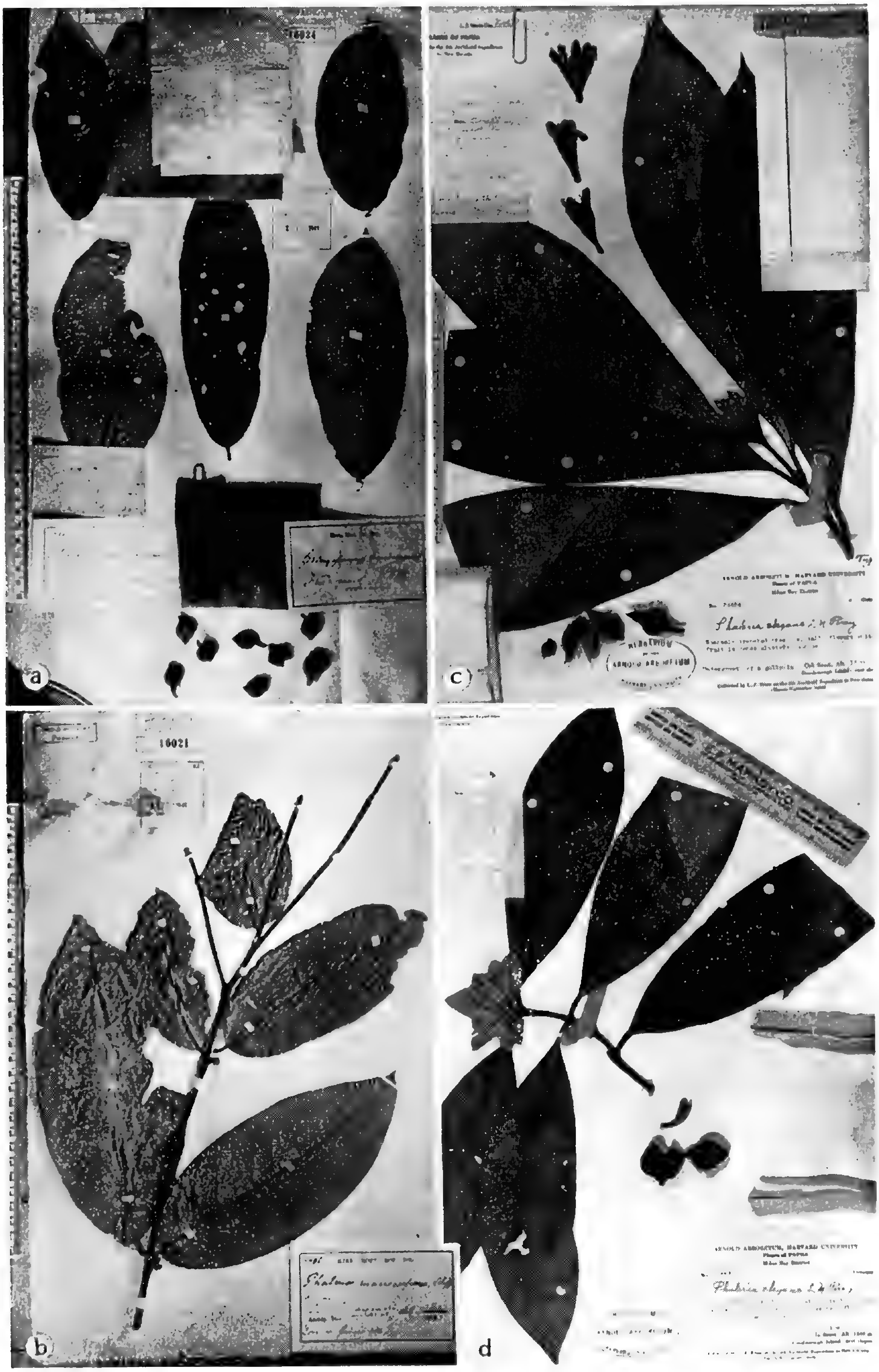
LILY M. PERRY

THE COLLECTIONS of the Fourth Archbold Expedition to New Guinea include two numbers of *Phaleria* with flowers having an unusually broad perianth-tube. I have searched both herbaria and literature but up to now have found nothing to match it. For a long time it has been a recognized fact that the species of this thymelaeaceous genus are difficult to separate. Mr. C. T. White (1919) drew up a key to the species of Queensland, based on the position of the flower-heads, the pubescence (or the lack of it) on the outside of the perianth-tube, the relative length of the latter, and the relative length of the leaves. Dr. A. C. Smith (1942) presented a key to the Fijian species with the following introductory paragraph: "The Fijian species are difficult to separate; one finds that such characters as leaf-texture, shape, and size, position of inflorescence, length of peduncle, size and internal pubescence of perianth, shape of faucial scales, length of filaments, and pubescence of ovary are variable within a species and not very dependable. The only specific characters which are more or less constant appear to be the 4- or 5-merous condition of the flower, the external pubescence of the perianth (in one species), the degree of persistence of the floral bracts and their size, and, in some cases, the length of petioles."

I was unable to find a key to the Malaysian species of the genus, and perhaps a look at the synonymy given in critical works such as those of Valeton (1913) and Hallier f. (1922) might suggest a reason. To draw up a workable key, it would be necessary not only to make a complete study of the material designated by the various epithets but also supplementary collections from the type-localities with both flowers and fruits. This is not feasible at present. However, the two collections under consideration have flowers with perianth-tubes so much more broadly infundibular than any which I have seen, or found indicated in the literature, that I believe this difference to be of specific importance. Perhaps among the species described from Malaysia, the fruits are nearest in size to those of *P. macrocarpa* (Scheff.) Boerl., a species apparently not included in Hallier's list of Malayan representatives with critical synonymy, and, other than the original publication as *Drymispermum* (1876) and the nomenclatural transfer to *Phaleria* (1900), I have not found it mentioned in the literature. To facilitate the comparison of *P. macrocarpa* with the two *Brass* collections, I am indebted to Mr. J. Leandri, Muséum National d'Histoire Naturelle, Paris, for negatives of the type and three duplicates which he has on loan from the Bogor Herbarium. Of these, two are reproduced in the plate ac-

---

* Botanical Results of the Richard Archbold Expeditions.



FIGS. a, b. Type and duplicate of *Phaleria macrocarpa* (Scheff.) Boerl. (coll. Teysmann, near Doré, New Guinea). FIG. c. Type of *P. elegans* L. M. Perry. FIG. d. Paratype of *P. elegans*.

companying this note: the type, (*fig. a*) bearing Teysmann's field label and another label with the name *Drymispermum macrocarpum* Scheff. in Scheffer's handwriting, consists of separate leaves and fruits (young, fide Mr. Leandri); the other (*fig. b*) shows the tip of a branchlet with the leaves attached and axes of inflorescences in the lower axils. Mr. Leandri affirmed that Scheffer's "pedicels" are actually very short peduncles, each bearing many fruit-scars. The reproductions of the two Brass collections (*figs. c, d*) include flower-buds, flowers and fruit. Of the three flowers attached to the sheet, the uppermost is laid open to show the inside of the flower; the leaves are elongately narrowed toward both base and apex, whereas those of Scheffer's species are obtuse with an abrupt acumen, and with obviously shorter petioles. The similarity in the shape of the fruits is probably a sectional rather than a specific character.

Phaleria elegans sp. nov.

Frutex arborescens 2–3 m. altus, sparsim ramosus; foliis magnis 18–30 cm. longis, 5.5–9 cm. latis, lanceolatis vel oblanceolatis, utrinque angustatis, apice acutis vel breviter acuminatis, basi cuneatis, glabris, crasse membranaceis vel subcoriaceis, nervis lateralibus utrinsecus 8–12 patentibus ante marginem arcuatis, venis costalibus pluribus, reticulo laxo, petiolo 1.3–1.7 cm. longo in sicco nigrescente; inflorescentiis terminalibus et axillaribus subsessilibus vel breviter pedunculatis, pedunculo 5–9 mm. longo (in fructu), apice bracteis circiter 8 instructo, interioribus majoribus ovatis vel oblongis acutis vel obtusis 2–3 cm. longis 6–14 flores involucrantibus; floribus sessilibus extus puberulis; perianthio (post compresso sicco) late infundibulari 3.8–4.2 cm. longo, ima basi 3–4 mm. juxta medium ca. 1 cm. sub lobis 1.3 cm. lato, tubo 2.9–3.3 cm. longo, intus infra medium puberulo superne fere glabro, lobis 5, ca. 8–9 mm. longis rotundatis intus praecipue prope marginem puberulis; staminibus 10, filamentis perianthii lobis subaequantibus; disco cupulari ca. 2 mm. alto crenulato; stylo filamentis breviore; ovario glabro biloculari, loculo uniovulato; fructibus in sicco late fusiformibus, 2.7–3.3 × 1.6–1.9 × 1.3–1.4 cm., utrinque acuminatis, spermis duobus.

Papua. GOODENOUGH ISLAND: sparsely branched tree 2 m. tall, flowers white, fruit in dense clusters, undergrowth of an oak forest, east slopes, alt. 1750 m., Oct. 1953, *Brass 24484* (A, type; LAE); tall shrub, sparsely branched, up to 3 m. high, leaves somewhat fleshy, petioles red, flowers and bracts cream-colored, occasional in forest gullies, east slopes, alt. 1600 m., Oct. 1953, *Brass 24883* (A, LAE).

The characters of this species might be indicated as follows: lanceolate or oblanceolate leaves elongately narrowed at both apex and base; flower-cluster terminal or axillary; large ovate cream-colored bracts surrounding the flower-cluster about to open, but missing on the cluster of fairly large but unripe fruits; the broadly infundibular perianth pubescent outside, with only very narrow scales in the throat.

LITERATURE CITED

White, C. T. Queensland Department of Agriculture Botany Bulletin **19:** 21. 1919. (*Phaleria*, 19–21.)

Smith, A. C. Fijian Plant Studies II. Sargentia **1:** 1–148. 1942. (*Phaleria*, 67–73.)

Valeton, Th. Thymelaeaceae. Icones Bogorienses **4:** *pls. 368–371.* 1913.

Hallier, H. Beiträge zur Kenntnis der Thymelaeaceen und ihrer natürlichen Umgrenzung. Mededeelingen van 's Rijks Herbarium Leiden no. 44: 1–31. 1922. (*Phaleria*, 20–24.)

Scheffer, R. H. C. C. Enumeration des plantes de la Nouvelle-Guinée, avec déscription des espèces nouvelles. Annales du Jardin Botanique de Buitenzorg **1:** 1–60. 1876. (*Drymispermum*, 46.)

Arnold Arboretum
Harvard University

A TAXONOMIC REVISION OF PODOCARPUS, XI
THE SOUTH PACIFIC SPECIES OF SECTION PODOCARPUS, SUBSECTION B

NETTA E. GRAY *

THE SPECIES OF PODOCARPUS in subsection B (*2*) of section *Podocarpus* (*Eupodocarpus* of previous papers in this series) are trees and shrubs of southeastern Asia, Australia, and the islands of the western Pacific Ocean, the area covering almost 100° in longitude and 80° in latitude. At present there are twenty-nine species in this group, and in some varieties have been recognized. This subsection is about as large as subsection C (*2*) of South and Central America. The extent of the southerly range is about the same as subsection C but native specimens of subsection B are found about 10° farther north than are those of the former. Of the twenty-nine species, only three (*Podocarpus neriifolius*, *P. glaucus*, and *P. polystachyus*) have been found both north and south of the Equator. *Podocarpus neriifolius* is found, usually in mountainous regions, throughout the entire area except Australia; *P. polystachyus* occurs at lower altitudes and in the coastal regions of both large and small islands and also in the Malay Peninsula of Asia; *P. glaucus* is of very limited distribution in the mountains of the Philippine Islands and New Guinea.

The observations on leaf anatomy included here were made from transverse sections taken from near or below the middle of the leaf. Sections from other parts of the leaf were also made but it was not found that these added pertinent information. Observations were most easily made from unstained sections dehydrated in glycerine; for permanence some sections were mounted in glycerine jelly. Both the upper and the lower epidermis were examined in flat mounts stained with safranin O in examples of all species.

As in all other subsections of sect. *Podocarpus*, the leaves are hypostomatic and have a single vascular bundle flanked by winglike areas of transfusion tissue. There is always at least one resin canal below the phloem; in all species of this section except *Podocarpus drouynianus* and *P. spinulosus* there are three. In several species a pair of resin canals has also been observed below the vascular bundle near, or even imbedded in, the transfusion tissue (*P. ridleyi* [*Fig. 1*], *P. deflexus*, usually in *P. salomoniensis*, rarely in *P. elatus*, *P. neriifolius* and *P. archboldii* var. *crassiramosus*). These additional vascular resin canals have not previously been described for this subsection of *Podocarpus*.

---

* The author wishes to express her appreciation to Prof. M. Y. Orr of the Edinburgh Botanical Garden and to Dr. Rudolph Florin of Stockholm for fragments of critical specimens. She is also grateful for a research grant from the Georgia Academy of Science.

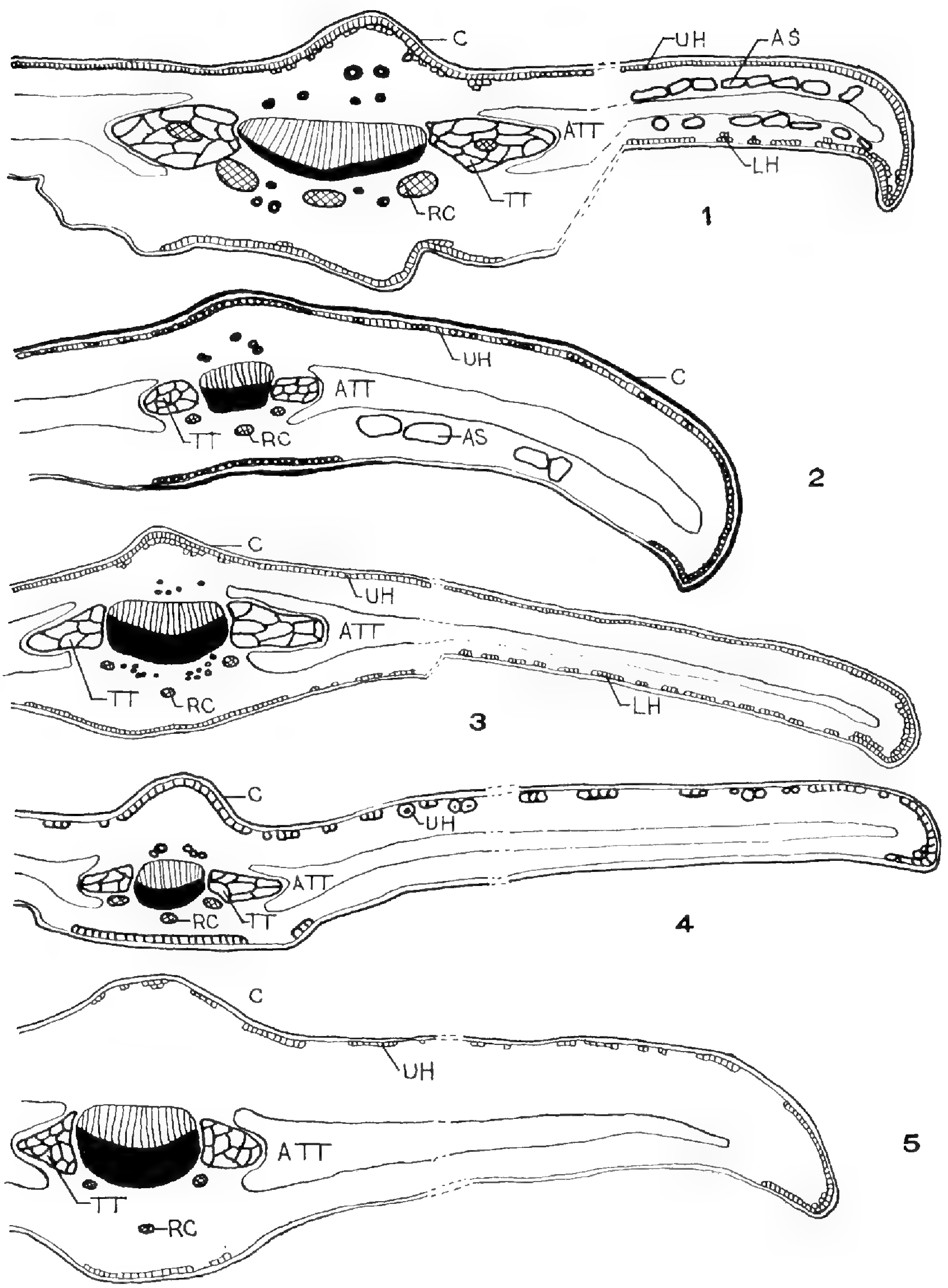
The well-developed accessory transfusion tissue (*Fig. 1*) extends from the transfusion tissue proper to the margins of the leaf, between the layers of mesophyll. The full extent of lignification is observed only in the most mature leaves, but the horizontal orientation of the elongated cells of this tissue may be seen in leaves which are still quite young.

A layer of hypodermis of variable pattern is found between the mesophyll and the epidermis of the leaves. In many species this pattern is consistent and can be used as a reliable taxonomic character. The upper hypodermis is a continuous layer from the midrib to the margin only in *Podocarpus elatus* (*Fig. 3*), *P. philippinensis*, *P. novae-caledoniae*, *P. gibbsii* (*Fig. 2*), *P. koordersii*, and *P. ridleyi* (*Fig. 1*). The use of this diagnostic character was strikingly successful in the identification of a large number of cultivated specimens of *P. elatus* from many parts of the world. In *P. novae-caledoniae* the hypodermis is rarely interrupted. In all the others, it is interrupted between the margin and the midrib, sometimes being represented by only a few fibers. In some cases, the diameter of the fibers can be relied on for specific determinations; for example, they are always large (50μ or more) in *P. polystachyus* (*Fig. 4*) and always small (20μ or less) in *P. macrophyllus* (*Fig. 5*). Lower hypodermal fibers are not found between the stomatal rows in most species. They have been found consistently in *P. novae-caledoniae*, *P. philippinensis*, *P. ridleyi*, *P. elatus*, *P. drouynianus*, *P. spinulosus*, *P. archboldii* var. *crassiramosus*, *P. dispermus*, *P. ledermannii* from New Guinea, *P. sylvestris*, and *P. affinis*. They were found occasionally in *P. rumphii*, *P. neriifolius*, *P. idenburgensis*, *P. polystachyus* var. *rigidus*, *P. pilgeri* and *P. archboldii*; in some of these species, only a few specimens showed these fibers, while in others only a few fibers were found in most of the specimens.

The presence or absence of auxiliary sclereids in the mesophyll was rarely found to be consistent enough for use as a distinguishing character. However, they were always absent in *Podocarpus philippinensis*, *P. glaucus*, *P. brassii*, *P. drouynianus*, *P. spinulosus*, *P. idenburgensis*, *P. dispermus*, *P. macrophyllus* vars. *maki* (*Fig. 5*) and *chingii*, *P. neriifolius* vars. *atjehensis*, *degeneri*, and *polyanthus*, *P. forrestii*, *P. thevetiifolius*, *P. costalis*, *P. pilgeri* in the Philippines, and *P. nakaii*. They were present in only one specimen of *P. elatus*, two specimens each of *P. rumphii* and *P. archboldii*, and several specimens of *P. neriifolius*.

The presence of vascular fibers or sclereids either below or above the bundle was not consistent enough to be diagnostic.

The combination of characters consistent for this subsection as observed in transverse sections of the leaves is: (1) no marginal resin canals (as found in subsection A); (2) no resin canals above the vascular bundle (as found in subsection F); (3) organized accessory transfusion tissue (absent in subsection D); (4) three resin canals below the vascular bundle (with the exception of *P. drouynianus* and *P. spinulosus*; not found in subsections C and D). Subsections B and F are the only subsections of sect. *Podocarpus* with a pair of small, subulate bracts beneath the receptacle which bears the ovule.



FIGURES 1–5. TRANSVERSE SECTIONS OF LEAVES OF PODOCARPUS. FIG. 1. **P. ridleyi** (Wasscher) Gray [*Eyma 4911*], showing relative thickness of cuticle (C), continuous upper hypodermal layer (UH) and extent of lower hypodermal fibers (LH), location of vascular resin canals (RC) with two lateral canals embedded in the transfusion tissues (TT), accessory transfusion tissue (ATT), and auxiliary sclereids (AS) in the mesophyll. FIG. 2. **P. gibbsii** Gray [*Clemens 32021*], with upper hypoderm of alternating thick- and thin-walled fibers and auxiliary sclereids only below the accessory transfusion tissue. FIG. 3. **P. elatus** R. Br. [*Laseron 435*], showing upper hypoderm continuous and auxiliary sclereids lacking. FIG. 4. **P. polystachyus** R. Br. [*G. L. Smith s.n.*], with scattered large upper hypodermal fibers. FIG. 5. **P. macrophyllus** var. **maki** Endlicher, illustrating thickness of leaf and small, scattered upper hypodermal fibers. All figures ca. × 20.

Within subsection B, anatomical characters of the leaves alone are not sufficient to determine the species. Nor have leaf-size and -shape, terminal bud shape, buds or cones of male strobili, length of peduncle, or size and shape of seed, proved to be reliable when used individually. Combinations of some or all of these characters are needed to differentiate the various species. Because so many of the specimens encountered are sterile, vegetative characters have been used insofar as possible in the preparation of the following key.

Key to Sect. Podocarpus (South Pacific Species), Subsection B

A. Leaves with continuous upper hypoderm (*Figs. 1, 2, 3*).

B. Leaves rarely over 5 cm. long; Borneo. . . . . 1. *P. gibbsii.*

BB. Leaves over 5 cm. long.

C. Leaves not more than 5 mm. wide, the midrib flat or concave above; New Caledonia. . . . . 2. *P. novae-caledoniae.*

CC. Leaves over 5 mm. wide, the midrib prominent above.

D. Leaves without lower hypodermal fibers between the stomatal rows; Java & Celebes. 3. *P. koordersii.*

DD. Leaves with lower hypodermal fibers between the stomatal rows (*Figs. 1, 3*).

E. Leaves 13–23 cm. long; terminal buds globose; Philippine Islands. . . . . 4. *P. philippinensis.*

EE. Leaves usually less than 15 cm. long; terminal buds ovate.

F. Apex of leaves usually long-acute or -acuminate; leaves with 3–5 vascular resin canals, upper hypodermal fibers large; Malay Peninsula & Borneo. . . . . 5. *P. ridleyi.*

FF. Apex of leaves obtuse, often mucronate; leaves with 1–3 vascular resin canals, hypodermal fibers not over 22 μ in diameter; Australia. . . . . 6. *P. elatus.*

AA. Leaves with interrupted upper hypoderm (*Figs. 4, 5*).

G. Leaves not over 6.5 mm. broad.

H. Leaves not over 2.5 cm. long, rarely over 5 mm. wide.

I. Terminal buds large, globose; pollen cones thick; New Guinea, above 3000 m. . . . . 7. *P. brassii.*

II. Terminal buds small; leaves glaucous when young; pollen cones slender; Mindoro & New Guinea. . . . . 8. *P. glaucus.*

HH. Leaves over 2.5 cm. long.

J. Leaves not over 5.5 cm. long, erect and adpressed to twig; Philippines, Borneo, China. . . . . 9. *P. brevifolius.*

JJ. Leaves usually over 5.5 cm. long.

K. Leaves pungent; seed strongly beaked; southeastern Australia. . . . . 10. *P. spinulosus.*

KK. Leaves rarely pungent; seed with rounded apex.

L. Leaves 5–12 cm. long, sessile, grasslike, with 1 vascular resin canal; western Australia. . . . . . 11. *P. drouynianus.*

LL. Leaves 6–9 cm. long, petiolate, with 3 vascular resin canals; New Caledonia. . . . . 2a. *P. novae-caledoniae* var. *colliculatus.*

GG. Leaves (at least some of them) over 6.5 mm. broad.

M. Leaves with lower hypodermal fibers between the stomatal rows.

N. Leaves mostly less than 10 cm. long.

O. Leaves less than 5.2 cm. long; Fiji. .... 12. *P. affinis.*

OO. Leaves usually over 5.2 cm. long.

P. Midrib of leaves channelled below; Borneo. .... 28a. *P. polystachyus* var. *rigidus.*

PP. Midrib of leaves not channelled below.

Q. Twigs very stout; leaves with acute or acuminate tips; New Guinea. .. 20a. *P. archboldii* var. *crassiramosus.*

QQ. Twigs slender; leaves with rounded obtuse apex; New Caledonia. .... 13. *P. sylvestris.*

NN. Leaves over 8 cm. long.

R. Leaves 9–15 mm. wide; New Guinea. . 14. *P. idenburgensis.*

RR. Leaves 17–30 mm. wide.

S. Seeds solitary, 8 mm. long; New Guinea. .... 15. *P. ledermannii.*

SS. Seeds usually in pairs, 2.5 cm. long; Australia. .... 16. *P. dispermus.*

MM. Leaves mostly without lower hypodermal fibers between the stomatal rows.

T. Leaves with auxiliary sclereids.

U. Leaves narrow, 6.5–9 mm. wide; Solomon Islands. .... 17. *P. salomoniensis.*

UU. Leaves wider, over 9 mm.

V. Leaves strongly deflexed, with 5 vascular resin canals; Malay Peninsula. .... 18. *P. deflexus.*

VV. Leaves not deflexed, with 3 vascular resin canals; Annam, Indochina, Hainan. .... 19. *P. annamiensis.*

TT. Leaves usually without auxiliary sclereids.

W. Leaves for the most part deflexed; Sumatra. .... 27a. *P. neriifolius* var. *atjehensis.*

WW. Leaves erect, spreading or divaricate.

X. Terminal buds globose or ovate, obtuse.

Y. Margins of leaves revolute; New Guinea. .... 20. *P. archboldii.*

YY. Margins of leaves not revolute.

Z. Leaves 8–11 mm. broad; Formosa. . 21. *P. nakaii.*

ZZ. Leaves mostly more than 10 mm. broad.

a. Leaves with parallel margins, the apex usually short-angustate; Borneo, New Guinea, etc. .... 22. *P. rumphii.*

aa. Leaves lanceolate, the apex caudate-acuminate; Sumatra, etc. .... 27d. *P. neriifolius* var. *teysmannii.*

XX. Terminal buds ovate, conical, acute.

b. Upper midrib of leaf broadly prominent or flat.

c. Peduncles of female cones 2 mm. long; Philippines, Formosa, shores. .... 23. *P. costalis.*

cc. Peduncles of female cones over 2 mm. long.

d. Upper hypoderm of large fibers; New Guinea. .... 24. *P. thevetiifolius.*

- dd. Upper hypoderm of small fibers; China. . . . . 25. *P. forrestii.*
- bb. Upper midrib of leaf narrowly prominent.
  - e. Male cones usually solitary.
    - f. Leaves usually less than 8 cm. long, apex usually obtuse, apiculate; Philippine to Solomon Islands. . . . . 26. *P. pilgeri.*
    - ff. Leaves usually 8 cm. long or more, the apex usually acute to acuminate; entire area except Australia. . . . . 27. *P. neriifolius.*
      - g. Leaves usually less than 10 mm. wide; Fiji. . . . . 27b. *P. neriifolius* var. *degeneri.*
      - gg. Leaves usually over 10 mm. wide; female cones numerous all over youngest growth; Sumatra & New Guinea. . . . . 27c. *P. neriifolius* var. *polyanthus.*
  - ee. Male cones usually clustered.
    - h. Leaf with upper hypoderm of very large fibers; Philippines to Bangka. . . . . 28. *P. polystachyus.*
    - hh. Leaf with upper hypoderm of small fibers.
      - i. Leaves 9–11 mm. broad; China & Japan. . . . . 29. *P. macrophyllus.*
      - ii. Leaves less than 9 mm. broad.
        - j. Leaves more than 4.5 mm. broad.
          - k. Leaves 5.5–12 cm. long × 5.5–8 mm. broad; China, Japan & Burma. . . . . . . 29a. *P. macrophyllus* var. *angustifolius.*
          - kk. Leaves 3.5–7 cm. long × 4.5–8 mm. wide; China, Japan, Formosa & Burma. . . . . . . 29c. *P. macrophyllus* var. *maki.*
        - jj. Leaves less than 4.5 mm. broad; China. . . . . 29b. *P. macrophyllus* var. *chingii.*

1. **Podocarpus gibbsii**, sp. nov.

Arbor 10–20 m. alta, ad 20 cm. diametro; ramulis erectis; alabastris perminutis ovatis, 1.5 mm. diametro, squamis paucibus exterioribus lanceolatis, carinatis, rectis, ad 6 mm. longis, apiculatis longi-acuminatis, aliquando foliaceis; foliis 1.3–2.1 cm. longis, 4–6 mm. latis, spathulatis, interdum ellipticis vel lanceolatis, coriaceis, planis, apice obtusis vel acutis, basi in petiolum brevem crassum angustatis; costa supra manifesta, subtus plana et inconspicue; strobilis masculis axillaribus, sessilibus, solitariis vel duobus, squamis exterioribus confertim imbricatis, deltoideis, apice longe acuminatis; strobilis femineis et seminibus ignotis.

DISTRIBUTION: Edges of low jungle, 1600–2300 m. altitude, Mt. Kinabalu, British North Borneo.

British North Borneo. Marai Parai, near camp, *Clemens 32021* (TYPE, A; †BM,

---

† This symbol preceding the abbreviation of an herbarium signifies that the details of the leaves of this specimen have been examined in transverse section.

†NY, †UC);* Marai Parai spur, *Gibbs 4092* (†BM); Colombon Basin, *Clemens 40001* (A, †NY, †UC).

This small tree of apparently very limited range may be described in somewhat further detail. The inner scales of the very small vegetative terminal buds are thinner than the outer ones and have merely acuminate tips. The extreme margins of the short, spatulate leaves are slightly recurved and the sharply prominent midrib above becomes flat toward the apex. Juvenile leaves may be up to 5.2 cm. long and 9 mm. wide. Transverse sections of the leaves (*Fig. 2*) show three vascular resin canals, upper hypoderm in a continuous single layer except at the margin and midrib (some fibers with large lumen), lower hypodermal fibers absent between stomatal rows, vascular sclereids abundant above and rare below the bundle, the single layer of palisade mesophyll composed of large cells often almost as broad as long, mesophyll cell walls, expecially the lower, lignified but not pitted and thickened as much as is usual for most auxiliary sclereids.

Podocarpus gibbsii differs from the other species in having continuous upper hypoderm in its very short, broad, spatulate leaves. The two Clemens specimens were used by Wasscher (11) for his discription of *Podocarpus glaucus* but these differ from Foxworthy's description of that species in that the young foliage is not glaucous and, in addition, the leaves have a continuous upper hypoderm. Only *Clemens 40001* is fertile, bearing male cone buds and immature cones. I do not understand the description "tiny yellow pistils" written on the label of this specimen, for the species is dioecious and I cannot find any structures to which the note might apply. The upper hypodermal fibers in the leaves of the Clemens specimens show clearly the alternation of groups of fibers with open and closed lumina. This was erroneously described by Orr (9) for *Podocarpus glaucus*. Orr did not observe the lignification of cell walls in the mesophyll, particularly the lower, where an almost continuous layer is formed. This is very apparent in cleared and stained whole mounts of leaves. *Gibbs 4092* has more scattered, larger, acute-tipped leaves which are a normal juvenile variation in most podocarps.

This species is named in honor of Dr. L. S. Gibbs, who first collected it on Mt. Kinabalu.

* The following symbols indicate the location of the specimens cited: Academy of Natural Sciences of Philadelphia (PH); Arnold Arboretum (A); Bernice P. Bishop Museum, Honolulu (BISH); Brisbane Herbarium of Agriculture (BRI); British Museum of Natural History (BM); Brussels Botanical Garden (BR); University of California at Berkeley (UC) and at Los Angeles (UCLA); California Academy of Science (CAS); Chicago Natural History Museum (Field Museum) (F); Cornell University (CU); Dudley Herbarium at Stanford (DS); Edinburgh Royal Botanic Garden (E); Gray Herbarium (GH); University of Illinois Herbarium (ILL); Royal Botanic Gardens, Kew (K); McGill College Herbarium, Montreal (MTMG); Missouri Botanical Garden (MO); Department of Forests of New Guinea and Papua (LAE); New Jersey College for Women (Rutgers) (RUT); New York Botanical Garden (NY); Paris Muséum National d'Histoire Naturelle (P); Pennsylvania University Herbarium (PENN); United States National Herbarium (US); Victoria National Herbarium, Melbourne (MEL).

Stapf, when determining and describing the specimens for Gibbs (6), described but did not identify two specimens of *Podocarpus* (*Gibbs 4089*, *4092*). *Gibbs 4092* (BM), which I examined, resembles Stapf's description of *Gibbs 4089*. Either the numbers were reversed in attaching the labels to the specimens or Stapf reversed the descriptions. Stapf's description of *Gibbs 4092*, "a very striking species with fairly crowded leaves, oblong-linear, obtuse or sub-obtuse at the apex, attenuated at the base, 1.5–2 cm. long, 3.5–4.5 mm. broad, with the margins recurved, the midrib raised above and rather broad and flat beneath," shows that this plant is like the two Clemens specimens and is, therefore, *Podocarpus gibbsii*, the new species. The other specimen, *Gibbs 4089*, is said to have "leaves, in shape and size, intermediate between those of *P. brevifolius* and *P. polystachyus* but thinner and much more loosely arranged than either." This is like the British Museum's specimen of *Gibbs 4092* and, therefore, is probably also *P. gibbsii*. Wasscher (11, p. 471) lists these specimens under doubtful species. His suggestions that *Gibbs 4089* is *P. pilgeri* and *Gibbs 4092* is *P. glaucus* are untenable.

2. **Podocarpus novae-caledoniae** Vieillard ex Brongn. & Gris, Bull. Soc. Bot. France **13**: 425. 1866; Parlatore, DC. Prodr. **16**: 513. 1868; Pilger, Pflanzenreich IV. 5(Heft 18): 76. 1903, Nat. Pflanzenfam. ed. 2. **13**: 248. 1926; Compton, Jour. Linn. Soc. Bot. **45**: 425. 1922; Dallimore & Jackson, Handb. Conif. 53. 1923, 1931, 78. 1948; Florin, Svenska Vet.-Akad. Handl. III. **10**: 279. 1931.

P. ensifolia Carrière, Traité Conif. ed. 2. 655. 1867 (non R. Br.).

A shrub (seldom a small tree up to 3 m. high) with erect crowded branches. Terminal buds ovate, 2–3 mm., the long triangular scales with acuminate apex. Leaves linear, crowded, more or less erect, leathery, 4–9 cm. long, 3–5 mm. broad, the apex short-acuminate or rarely long-attenuate and sometimes pungent, gradually narrowing at the base to a short obscure petiole; margins blunt with sharply recurved edges but not revolute; midrib shallowly concave or flat above. Transverse sections of the leaves with three vascular resin canals (rarely only one); upper hypoderm usually in a single continuous layer except at the margin and midrib where it is doubled, lower hypodermal fibers not abundant between stomatal rows, fibers averaging 20–30 μ in diameter; vascular fibers few above but numerous between the vascular bundle and central resin canal; auxiliary sclereids in the mesophyll so abundant as to form a distinct layer between the palisade mesophyll and accessory transfusion tissue; cuticle thick. Male cones axillary, in pairs, sessile, surrounded at the base by stiff obtuse scales. Microsporophylls densely imbricate, each with a short rotundate apiculus. Female cones axillary and solitary on peduncles 7–10 mm. long, the fleshy receptacle subtended by two minute scales and bearing 1–2 ovules. Seeds ellipsoid, shiny, 7–8 mm. long, 4 mm. wide.

DISTRIBUTION: Stream banks, at low altitudes, New Caledonia.

New Caledonia. River Dumbea, *Vieillard 1266* (ISOTYPE, A, BM, GH, K, P), *Compton 402, 419* (BM), *Buchholz 1133, 1137, 1139, 1255, 1477* (ILL), *1759* (†ILL), *Franc 96* (BM, NY, UC), *Anon. s.n.* (BM), *Pancher* (P), *Balansa 189* (P), *Godefroy 552* (P), *LeRat 603, 1587* (P); Rio des Pirogues, *White 2231* (A–2 sheets, BRI, DS, K, P, UC–2 sheets, US), *Buchholz 1340* (ILL); Rivière Camboui, *Compton 2017, 2169* (BM); Couvélée, *Franc 2408* (A–2 sheets, BRI, †F, K, NY, P, UC, US); Table Unio, *Lecard s.n.* (BM, P), *Lecard 92* (P); Port Bouquet, *Balansa 704* (NY), *2504* (K, P); Bourail, *Pennel s.n.* (P); Mt. Mou, *Franc 107* (K), *Glandoger* in 1906 (†MO); Mt. Dore, *Vieillard & Pancher 396* (P); Mt. Koghi, *LeRat 2372* (P); Rive gauche de la Toutouta, *Virot 369* (A); Prony, *Franc 94A* (BM), *96A* (BM, K–2 sheets, US), *s.n.* (BM), *Franc* in 1913 (A–7 sheets, F, GH, NY, UC–2 sheets), *MacDaniels 2540* (†CU), *Juillet 96* (BRI, US). Locality unknown: *Pancher* ex Hennecart in 1879 (K, NY), *Pancher* in 1870 (†BR, K–2 sheets, †UCLA), *Franc 90* (†UC), *Baudouin 635* (P).

Podocarpus novae-caledoniae is a low, rounded shrub rarely forming a small tree when growing in a thicket with other vegetation. The young leaves are glaucous, becoming dark green when older (3). According to Buchholz (ms.), there seem to be differences in the thickness of the leaves, as specimens found in Plaine des Lacs and near Prony have leaves more coriaceous than those found in the Dumbea valley. This is not apparent in transverse sections of the leaves. Compton (3) described the fleshy receptacle as becoming bright scarlet or purple, soft, translucent, and sweet to the taste, whereas Buchholz (ms.) says that it turns yellow or brick red. These variations may merely be due to different stages of maturity of the fruit.

Orr (9) examined the leaf anatomy of *Podocarpus novae-caledoniae* and described most of the above characters. He does not seem to have observed the lower hypodermal fibers between the stomatal rows since he did not include this species in his list of those showing this character.

2a. **Podocarpus novae-caledoniae** var. **colliculatus**, var. nov.

Frutex vel arbuscula, 1 m. alta; foliis coriaceis, linearibus, saepe falcatis, 6–9 cm. longis, 5–6.5 mm. latis, apice coarctis acutis vel rare acuminatis, basi in petiolum 1–4 mm. longum sensim angustatis; strobilis masculis alabastris immaturis, globosis, cum squamis brevibus adpressis; strobilis femineis seminibusque ignotis.

DISTRIBUTION: Isle of Pines, New Caledonia, at 80 m. altitude, and possibly on New Caledonia itself.

New Caledonia. *Germain* in 1874–76 (†P). ISLE OF PINES: Pic N'Ga, *Virot 1053* (Type, †ILL; NOUMEA).

The description of *Podocarpus novae-caledoniae* var. *colliculatus* was prepared only from *Virot 1053.* I am in doubt as to whether the *Germain* specimen really came from New Caledonia. The terminal buds of the twigs of this variety have short, thin, appressed scales very similar to those of the species. The midrib of the leaf is flat or broadly rounded above and broadly prominent or ridged below. Transverse sections of the leaves of both collections cited above are very similar. These show three vascular resin canals, an interrupted upper hypoderm, rare lower hypodermal fibers, vascular sclereids above and below the bundle and auxiliary sclereids in the mesophyll. That the upper hypoderm is occasionally interrupted instead of being a continuous layer is in contrast to the main species. The low, shrubby habit is in agreement but the broader leaves with a definite petiole and the occasionally interrupted upper hypoderm differentiate the variety. In these latter characters it is like *P. sylvestris* but this is a tree and the leaves are mostly broader. The vegetative buds of all three of these taxa are similar.

3. **Podocarpus koordersii** Pilger ex Koorders & Valeton, Meded. Lands Plant. [Batavia] **68**: 268. 1904; Nat. Pflanzenfam. ed. 2. **13**: 248. 1926; Florin, Svenska Vet.-Akad. Handl. III. **10**: 279. 1931; Wasscher, Blumea **4**: 433. 1941.

A small tree, to 14 m. tall, with stout twigs. Vegetative buds globose with thick, broad, obtuse or roundish scales, the outer ones sometimes acuminate. Leaves spreading, thickly coriaceous, rigid, glossy above, straight or somewhat falcate, linear or linear-lanceolate, 9–21 cm. long, 6–13 mm. wide (larger on sterile twigs), gradually narrowing to a short thick petiole and acute apex; midrib broad and usually roundly prominent on both surfaces. Transverse sections of the leaves with 3 vascular resin canals below the bundle, with vascular fibers always above and sometimes below, isolated auxiliary sclereids in the mesophyll both above and below the accessory transfusion tissue, upper hypoderm fibers in a continuous layer, doubled at the margin and midrib, absent below between the stomatal rows, small, 16–24 μ in diameter. Male cones axillary, sessile, in fascicles of 2–8, the buds globose with thick rounded scales; mature cones 4.5 cm. long, 2 mm. in diameter. Microsporophylls broadly triangular, each with a small apiculus. Female cones unknown.

Distribution: From sea level to 50 m. in Java and up to 300 m. in Celebes.

Java. *Koorders 39480* (Type, †via Florin ex Leiden Herbarium); *Anon.* (†via Florin ex Berlin Herbarium); Banjumas, *Koorders 40251 β* (†A); *Horsfield s.n.* (†BM), *Horsfield* in 1859 (†MEL). **Celebes.** Malili, Oesoe, *Cel/II–285* (A), *Cel/II–287* (†BRI), *Cel/II–288* (†BISH). **San Cristobal.** BSIP on ridge, *Logie BSIP 356* (†LAE).

Podocarpus koordersii differs from *P. neriifolius* in having leaves with margins parallel over a greater length, a broader, less prominent midrib and a continuous upper hypoderm (as seen in transverse sections). The specimens from Java all have rounded or obtuse vegetative bud scales but those from Celebes have acuminate tips on the outer bud scales. In most of the leaves of *P. koordersii* the upper hypodermal fibers show alternate groups of thick-walled cells with small lumina and thinner-walled cells with large lumina. This is especially apparent in the specimens from

Celebes, in which I find also that the mesophyll above and below the accessory transfusion tissue is an almost complete layer of thin-walled sclerenchymatous cells with simple pits, very large and empty of cell contents. Wasscher (11) referred to *P. rumphii* a group of specimens from Celebes with related collection numbers, including those I have examined, but he says that they have very small, more lanceolate leaves. This and the continuous upper hypoderm readily refer them to *P. koordersii*. Orr (9) also examined *P. rumphii* and agrees that this species has interrupted upper hypoderm while in *P. koordersii* it is continuous.

4. **Podocarpus philippinensis** Foxworthy, Philip. Jour. Sci. Bot. **6**: 163. 1911; Pilger, Nat. Pflanzenfam. ed. 2. **13**: 248. 1926; Florin, Svenska Vet.-Akad. Handl. III. **10**: 280. 1931.

Large, straight trees, 20–30 m. tall, with smooth reddish-brown flaky bark and erect branchlets. Terminal buds globose with thick ovate scales, the tips rather acute but sometimes very blunt. Leaves erect or erect-spreading, straight to subfalcate, linear-lanceolate, 13–23 cm. long, 9–18 mm. wide (juvenile to 31 cm. long, 25 mm. wide), the apex acute to acuminate, gradually narrowing at the base to a short petiole; midrib mostly flat or somewhat depressed, broadly prominent below. Transverse sections of the leaves show three vascular resin canals, vascular sclereids or fibers rare above and absent below the bundle, no auxiliary sclereids, upper hypoderm in a continuous single layer except at the margin and midrib where it is doubled, lower hypodermal fibers abundant between stomatal rows, the small fibers 15–22 μ in diameter. Male cones unknown. Female cones axillary, on peduncles 5–8 mm. long; receptacle fleshy, subtended by two small bracts, bright red. Seeds ellipsoid-globose, 12–15 mm. long, 11 mm. wide, the crest suppressed.

DISTRIBUTION: On mountain slopes in the Philippine and Selangan Islands.

Philippine Islands. LUZON. Bataan Prov.: Lamao Forest Preserve, For. Bur. 6326, *Curran* (BISH, BRI, †MO, NY); For. Bur. 8987, *Curran* (†MO, NY); For. Bur. 17523, *Curran* (†BR), For. Bur. 17592, *Curran* (NY), For. Bur. 17594, *Curran* (†BM); Mt. Mariveles, For. Bur. 2743, *Borden* (NY). Pampanga Prov.: Mt. Arayat, For. Bur. 17664, *Curran* (†NY, †P), *Merrill 3917* (†NY). Tabayas Prov.: *Merrill 1992* (MO); Alikad, *Jones 63* (†F–2 sheets). Locality unknown: *Anon. s.n.* (†UC). **Selangan Islands.** *Cons. For. N. Borneo s.n.* (†E).

Podocarpus philippinensis was distinguished by Foxworthy from *P. rumphii* by the smooth reddish-brown flaky bark, the leaves narrowing more gradually toward the petiole and the seeds with shorter peduncles. With the exception of *Jones 63* and *Merrill 1992*, all the collections listed by Foxworthy were examined and all are either female or sterile. Foxworthy (5) left under *P. rumphii* several specimens, one of which (*Merrill 3917*) is certainly *P. philippinensis,* for an examination of a transverse section of a leaf showed the same continuous upper hypoderm characteristic of this species. I have not seen the other specimens, but they are probably also *P. philippinensis* as the larger leaves and longer peduncles which they may show seem to be natural variations in most species of *Podocarpus*. Wasscher (11), who does not recognize *P. philippinensis*, saw many of the same collections and included them under *P. rumphii* without comment. The upper hypoderm is so consistently continuous in *Podocarpus philippinensis* that his treatment of these specimens is not tenable.

Orr (9) agrees that the leaves of *Podocarpus philippinensis* differ from those of *P. rumphii* by the continuous hypoderm, an evident but not very prominent upper midrib, the absence of sclereids in the mesophyll, and no auxiliary sclereids. This description of the leaf anatomy resembles that of *P. elatus*, an Australian species. It differs from *P. koordersii* only in the lower hypodermal fibers between the stomatal rows and the absence of auxiliary sclereids. I do not find that the hypodermal fibers are as large compared with those of *P. koordersii* as described by Orr (9).

Orolfo 3919, from the Selangan Islands, agrees with *Podocarpus philippinensis*. It had been identified by Orr (9) as *P. teysmannii* but, on examination of authentic material of this latter species, I find that it is quite different.

5. **Podocarpus ridleyi** (Wasscher), stat. nov.

Podocarpus neriifolius var. *η ridleyi* Wasscher, Blumea **4**: 453. 1941.

A small tree with stout branches but small verticillate twigs. Terminal buds ovate with long-acuminate outer scales up to 13 mm. long. Leaves crowded on new growth, spreading, stiffly coriaceous, linear-lanceolate, straight or falcate, 10–15 cm. long. 9–12 mm. wide (rarely to 17 cm. long, 19 mm. wide), narrowing at the base to a short petiole, gradually narrowing to an acute or acuminate apex; midrib flat or broadly prominent above, more prominent below. Transverse sections of the leaves show 3–5 vascular resin canals, the two outermost often located within the transfusion tissue on either side of the bundle, vascular fibers above the bundle and usually below, upper hypodermal fibers in a continuous layer, usually large, 22–50 μ in diameter, lower hypodermal fibers also large and scattered or abundant between the stomatal rows, auxiliary sclereids often abundant in the palisade layer and mesophyll both above and below the accessory transfusion tissue. Male cones axillary, sessile or on peduncles up to 2 mm. long, fascicled 1–3, buds small, ovate, the outer scales keeled, acute, 2–4 mm. long, with erose scarious margins; mature cones large, cylindric, up to 8 cm. long, 4 mm. wide. Female cones solitary, axillary; peduncles to 9 mm. long; immature receptacle subtended by two subulate bracts 2.5 mm. long. Mature seed not seen.

DISTRIBUTION: On mountains, up to 1000 m. altitude, Malay Peninsula, Borneo, and New Guinea.

Malay Peninsula: Johore, Gunong Blumut, *Holttum 10720* (TYPE, †A); Malacca, Padang Bata, *Ridley 10016* (A). **Borneo:** western part, G. Semedoen, *Hallier 720* (†NY, UC). **Netherlands New Guinea:** Seroei, Japen, *Boschpr. bb30484*, (†A), *bb30650* (†A); Japen, Soemberbaba near Seroi, *Van Dijk 830* (†A); Wissel Lake region, environs of Post, on foot of Mt. Boebeiro, *Eyma 4911* (†A). **Cultivated.** JAVA: Buitenzorg Botanic Garden, *V.F.31* (†MO–3 sheets).

Podocarpus ridleyi is a common tree on Gunong Blumut and, according to Holttum in Wasscher (11), it is a very striking plant with its yellow-green leaves. Leaves of these specimens are superficially similar to those of *P. koordersii*, *P. philippinensis*, *P. rumphii* and *P. neriifolius*, but can be distinguished from each of these species by the anatomy of the leaf as observed in transverse sections (*Fig. 1*). The most striking feature is the presence of five vascular resin canals in the leaves of all specimens except *Hallier 720*. Five vascular resin canals have been found elsewhere only in *P. deflexus* (Malay Peninsula), *P. salomoniensis* (Solomon Islands), some specimens of *P. neriifolius* and *P. decipiens* (Fiji Islands), and *P. ulugurensis* (Africa). Only the first three of these are in this subsection of sect. *Podocarpus*. The continuous upper hypoderm is similar to that of *P. koordersii* and *P. philippinensis*, but *P. koordersii* does not have lower hypodermal fibers between the stomatal rows and *P. philippinensis* does not have auxiliary sclereids; the hypodermal fibers are larger in *P. ridleyi* than in either of these species. In most of the specimens of *P. ridleyi* the upper hypoderm consists of alternating groups of thick- and thin-walled fibers as has been described for some specimens of *P. koordersii*.

The specimens of *Podocarpus ridleyi* have had various identifications. Both *Holttum 10720* and *Hallier 720* have been identified with *P. neriifolius* and Wasscher lists them in his new variety *ridleyi* under this species. Both the continuous upper hypoderm and hypodermal fibers between the stomatal rows differ from *P. neriifolius* and the specimens are an entirely distinct species. Two of the specimens from Java had been named as *P. macrophyllus*, a species having smaller leaves with interrupted upper hypoderm of very small fibers and a very prominent midrib. The other specimen was called *P. rumphii* which I have found to be a species also with interrupted upper hypoderm.

In *Hallier 720*, from Borneo, the upper hypodermal fibers are smaller in diameter, usually not over 18 μ, and only three vascular resin canals have been observed. Rare interruptions were found in the upper hypoderm of *Holttum 10720*. There seem to be no vascular fibers below the bundle in the three cultivated specimens (two male, one sterile) from Buitenzorg collected by *Sargent* in 1903.

6. **Podocarpus elatus** R. Brown ex Mirb. Geogr. Conif. in Mém. Mus. **13**: 75. 1825 (nomen!); Endlicher, Syn. Conif. 213. 1847; Gordon, Pinetum, ed. 1. 273. 1858, ed. 2. 334. 1875; Carrière, Traité Conif. 656. 1867; Parlatore in DC. Prodr. **16**: 517. 1868; Bentham, Fl. Austral. **6**: 246. 1873; Van Tieghem, Bull. Soc. Bot. France **38**: 169. 1891; Hemsley, Jour. Linn. Soc. Bot. **30**: 199. 1894; Bailey, Queensl. Fl. **5**: 498. 1902; Pilger, Pflanzenreich IV. **5**(Heft 18): 75. 1903, Nat.

Pflanzenfam. ed. 2. **13**: 248. 1926; Gibbs, Jour. Linn. Soc. Bot. **39**: 183. 1909; Baker & Smith, Res. Pines Austr. 435. 1910; Dallimore & Jackson, Handb. Conif. 43. 1923, 1931, 66. 1948; Florin, Svenska Vet.-Akad. Handl. III. **10**: 279. 1931.

P. ensifolia R. Br. ex Gordon, Pinetum ed. 1. 275. 1858; ed. 2. 335. 1875 (non Carr.).
P. acicularis Van Houtte ex Gordon, Pinetum ed. 1. 275. 1858.
P. falcata A. Cunn. Herb. fide Baker & Smith, Res. Pines Austr. 435. 1910.
Nageia elata F. Mull. Cens. 109. 1882.

An erect tree up to 30 m. high with solitary or verticillate branches bearing spreading, rather lax leaves. Vegetative buds small, ovate or subglobose with short, more or less sharply acute scales. Leaves light green and shiny above, coriaceous, straight or subfalcate, linear-lanceolate, the acute to obtuse apex often mucronate, gradually tapering at the base to a short petiole, 5–11 cm. long, 7.5–10 mm. wide (occasionally up to 20 cm. long, 16 mm. wide). Midrib broad and slightly prominent above, scarcely evident below; leaf margins sometimes slightly thickened, never revolute. Transverse sections of the leaves (*Fig. 3*) usually show three vascular resin canals (only one resin canal in the leaf examined of the type, *Brown 3117*, one to three in *Laseron 435*, one in *Anon. 10545* from Mt. Spergeon, and one to three in two cultivated specimens from Rome and California), vascular fibers rare above the bundle but usually abundant below, auxiliary sclereids absent in the mesophyll, palisade mesophyll thick but of a single layer of cells, upper hypoderm in a neat single continuous layer except at the margin and midrib where it is doubled, lower hypodermal fibers abundant between stomatal rows, both upper and lower fibers averaging 15–22 μ in diameter. Pollen cones axillary and sessile, in groups of 2 or 3, 5 cm. long, 4–5 mm. wide, surrounded at the base by numerous thick broad obtuse scales. Microsporophylls densely imbricate, broadly triangular with a short apiculus. Female cones solitary in the axils of the leaves, on stout peduncles 3–10 mm. long; receptacle of two fused thickened equal bluish scales scarcely free at the tips and subtended by a pair of small subulate bracts. Seeds globose, 12–14 mm. wide (22 mm. long on Mt. Spergeon), with very blunt inconspicuous crest.

DISTRIBUTION: Native to southeastern Australia (Queensland, New South Wales) and Tasmania. Cultivated as an ornamental around the world.

Australia. QUEENSLAND: Cape York Peninsula, 100 mi. south of Cape York, *Hartmann* in 1886 (†MEL); Fitzroy Island, *Moore 39* (†MEL); Rockingham Bay, *Mueller* in 1864 (2 sheets, ♂ and ♀, †MEL); Barron River, Kenevunga, *Cowley 52* (BRI); Mt. Spergeon, *Anon. 10545* (†BRI); South Kennedy Dist., Dalrymple Heights, *Sclemers* in 1947 (BRI); Bundaberg, *Keep* in 1898 (BRI); Gympie Dist., *Kenny* in 1907 (BRI); Beech Mountain, *White* in 1923 (BRI, †BR), *Wilson* in 1921 (†A, seedling); Brisbane River, Ithaca Creek, *Bailey* in 1875 (BRI), Moreton Bay, *Mueller* in 1855 (MEL); Pioneer River, *Griffiths* in 1889 (MEL). NEW SOUTH WALES: Moore Park near Kyogle, *White 12579* (MO, UC); Richmond River, *Henderson 106* (MEL); Casino, *McLean* in 1918 (BRI); Ballina, *Baker* in 1892 (†BR); Clarence River, *Beckler* s.n. (MEL); Hastings River, *Beckler* s.n. (MEL); Gloucester River, *Betche* in 1882; Tiona, south of Forster, *Garden 19004* (A, MO); Hunder and Paterson Rivers, *Brown* in 1802–5 (MEL), *Brown 3117* (TYPE, †BM); Ourimbah, *Laseron 435* (†A); Illawarra Distr., near Bulli, *Kirton 8* (MEL), *Anon. 152* (BRI); *Anon.* (MEL). LOCALITY UNKNOWN: Dundowran, Nichenbach, Sandy Flat, *Tryon* in 1928 (BRI); Bennett's River, *Leichhardt* in 1943 (MEL); Ash Island, *Leichhardt* s.n. (MEL). Tasmania: Van Diemen's Land, *Caley* in 1805 (†BM).

Cultivated. AUSTRALIA. Queensland: Brisbane Botanic Garden, *White 2337* (A, BRI), *Everist 75* (MO). New South Wales: Sydney, The Domain, *Boyce 19005* (A, MO, UC), Botanic Garden, *Camfield* in 1896, 2 sheets, ♂ and ♀ (†UC), *Eames* s.n. (CU). ASIA: Nepal (?), Villa Thuret, *Martio* in 1889 (A), *Wallich s.n.* (†P); Singapore, *Scheidweiler* s.n. (†BR). AFRICA: Tunis, *Anon.* in 1868 (†MO, 2 sheets), *Anon.* in 1870 (†MO); Natal, behind Durham Botanic Garden, *Wilson* in 1922 (†A); Cape Colony, Capetown State Nursery, *Bowman* in 1921 (†A). EUROPE: Italy, Rome, Mont. Pinario, *Anon.* in 1869 (†MO); England, Kew, Royal Botanic Garden, *Cook* in 1937 (†ILL) *Anon.* in 1832 (†BR). SOUTH AMERICA: Brazil, Rio de Janeiro Botanic Garden, *Curran 341* (†US); Chile, Valparaiso, Los Zooras, Jardin Suizo, *Harshberger 1031* (PENN, †US); site unknown, *Anon. s.n.* (PH). NORTH AMERICA. United States. New York: New York Botanical Garden, 3740 ex DPM in 1900, *Nash* in 1905 (†NY), *Hartling* in 1919 (†NY), 3750 ex DPM in 1900, *Nash* in 1905 (†NY), 4788 ex DPM in 1900, *Taylor* in 1906 (†NY), 8766 ex MBG in 1901, *Nash* in 1901 (†NY), 11800 ex DPB in 1902, *Taylor* in 1905 (NY), 14415 ex Edinburgh in 1902, *Taylor* in 1905 (NY); Manhattan, Dept. of Parks 3740, *Hartling* in 1900 (†ILL). New Jersey: cult. in greenhouse from CU56 from Atkins Garden, Cuba, *Johnson* in 1952 (RUT). District of Columbia: Washington, *Foxworthy* in 1903 (†CU, NY), *Anon. s.n.* (ILL). California: Stanford University, *Dudley* in 1909 (†DS); San Francisco, Golden Gate State Park, *Walther* in 1936 (CAS), *Buchholz* in 1942 (†ILL); Mill Brae, Mills' Place, *Walther* in 1921 (CAS); Berkeley, *Eastwood* in 1913 (CAS), *Curran 23* (A); Goleta, Sexton's place near Santa Barbara, *Eastwood* in 1917 (†CAS), *Van Rensselaer 1716* (ILL), *Buchholz* in 1941 (†ILL); Santa Barbara, *Eastwood* in 1926 (A, †CAS); Hueneme, Bord's place (Ventura Co.), *Walther* in 1921 (CAS), *Vijos* in 1917 (CAS); San Diego, *Wongenheim* in 1941 (ILL); Jefferson's, *Walther* in 1926 (CAS), *Wilson* in 1937 (CAS), Hawaiian Islands: Oahu, *Curran 122* (†US).

Podocarpus elatus is not represented in our herbaria by many specimens collected directly from native habitats in Australia, but there are a large number of specimens from cultivation both here and abroad. The cultivated specimens have masqueraded under a number of different names: *P. macrophyllus* (China), *P. neriifolius* (Nepal), *P. coriaceus* (West Indies), *P. polystachyus* (Singapore), *P. latifolius* (Africa), *P. purdieanus* (Jamaica) and *P. spinulosus* (Australia). These specimens were first recognized as being identical by the striking uniformity in general appearance and by the transverse sections of the leaves (*Fig. 3*) in which the single layer of upper hypoderm and three vascular resin canals proved to be distinguishing characters. Later it was found that the broad, straight, often mucronate leaves also served to identify this plant.

An undetermined specimen collected in Tasmania by Caley in 1805

(BM) proves to be *Podocarpus elatus.* The early date of this collection precludes the possibility that this species could have been planted by Europeans and grown to a reproductive size by the time of its collection. A leaf from a specimen (P) supposedly collected by Wallich in Nepal and determined by Lindley, first as *P. macrophyllus*, later as *P. neriifolius*, was examined. This specimen is also *P. elatus*, but it is very doubtful that this species is really to be found in Nepal. Either this specimen was picked up by Wallich en route and not given clear collection data or it has been mislabelled subsequently. Gibbs (6) lists *819* from Fiji as *P. elatus.* This is also very unlikely, as I have examined numerous specimens from Fiji and never found this species. Orr (9) included *P. elatus* in Fiji and also suggests that it is in New Caledonia and the islands of Polynesia, but it has not appeared among any specimens I have examined from these places.

Both Stiles (10) and Orr (9) examined the anatomy of the leaves of *Podocarpus elatus* and are in agreement as far as they report their observations. However, Stiles includes it with *P. polystachyus*, attributing the differences in hypoderm and auxiliary sclereids to external conditions. This does not seem to be the case since both the native collections and the large number of cultivated specimens from other climates exhibit unexpected uniformity in the leaf anatomy.

Baker and Smith (1) included photographs of the mature tree (p. 432), male cones and mature seeds on branches (p. 434), photomicrographs of transverse and longitudinal sections through the leaves (pp. 436–37) and wood and bark anatomy (p. 438).

Orr (9) stresses that the three vascular resin canals found in this species are exceptional among the Australian members of sect. *Podocarpus.* It is interesting to note that there are rare specimens in which only one vascular resin canal is developed, and also that one specimen has as many as five, two being in the transfusion tissue; however, the regular number is three. Orr observed auxiliary sclereids in the mesophyll, but I found a few in only a single specimen, *Anon. 10545* from Mt. Spergeon. This specimen also differed from the type in the large seed, 22 mm. long and 13 mm. wide, with three distinct ridges on the back and a strong beak.

Other specimens from northern Queensland differ from the type in having long leaves (up to 18 cm.), with apices not mucronate but long-acute (*Mueller* in 1864, Rockingham Bay, and *Hartmann* in 1886, Cape York). The leaves of *Moore 39* from Fitzroy Island are up to 30 cm. long and 22 mm. wide, thus reaching the lower limits of *Podocarpus dispermus*, but the leaves in this latter species have interrupted hypoderm. The specimen also shows five vascular resin canals, three below the vascular bundle and two in the wings of transfusion tissue, and a flat or depressed upper midrib. Its general appearance is that of a juvenile specimen.

Allen Cunningham, a well-known Australian explorer of early days, in the diary (7) of his travels mentions seeing a *Podocarpus* several times in the vicinity of Paramatta and Liverpool, very near Sydney, New South Wales. We now know that this species was *P. elatus.*

7. **Podocarpus brassii** Pilger, Engler Bot. Jahrb. **68**: 246. 1938; Wasscher, Blumea **4**: 469. 1941.

An erect tree, 10–12 m. tall, densely branched, with thick, stiff, verticillate, ridged branchlets. Terminal buds large, globose, the scales often spreading, rigid, ovate-lanceolate, keeled, with membranous margins, up to 8 mm. long, apex stiffly acuminate. Leaves crowded, erect to patent, thick, very stiffly coriaceous, broadly lanceolate, 1–1.8 cm. long, 3–7 mm. broad (juvenile 2.5–4 cm. long), the apex acute or obtusely apiculate, narrowing at base to a short broad petiole, shiny above, duller beneath with the exception of a broad marginal band; margins revolute; midrib narrow and prominent or scarcely prominent above, broader below. Transverse sections of the leaves show three (rarely one) vascular resin canals, upper hypoderm of scattered fibers, rare isolated lower hypodermal fibers between the stomatal rows, rare vascular sclereids and no auxiliary sclereids. Leaves quite thick with more than one layer of palisade mesophyll. Pollen cones axillary, solitary, sessile, surrounded at the base by ovate-triangular scales, cylindric, 2.5–3 cm. long, 3–7 mm. thick. Microsporophylls densely imbricate, each with long triangular acute apiculus. Female cones solitary in upper leaf axils; peduncles thick, 2–9 mm. long; receptacle of 2–3 fused fleshy scales, 5–9 mm. long, 2.5–7 mm. broad, subtended by 2 narrowly triangular bracts, 3 mm. long; ovule usually solitary. Seeds elliptical-globose, rounded at the base and apex, 7–10 mm. long, 5–6 mm. broad.

DISTRIBUTION: High mountains, above 3000 m. altitude, New Guinea.

New Guinea. NETHERLANDS NEW GUINEA: Lake Habbema, 3225 m. Camp, *Brass 9341* (†A), *9342* (†A), *9560* (†LAE), *Brass & Meyer-Drees 10435* (A), *10436* (A). TERRITORY OF NEW GUINEA. Eastern Highlands District: Mt. Wilhelm, Lake Piunde, *Womersley 8866* (LAE). PAPUA. Central Division: Mt. Albert Edward, *Brass 4295* (ISOTYPE, †A–2 sheets; †BRI), *Brass 4395a* (BRI), *Brass 4396* (BRI).

The leaves of *Podocarpus brassii* are smaller than those of *P. brevifolius*, which are usually over 2 cm. long. It also differs from *P. glaucus* in that its young foliage is not glaucous and the pollen cones are thick instead of slender. Orr (9) agrees with the above description of the leaf anatomy. I have observed that the upper hypodermal fibers are larger in *Brass 9342* than *Brass 4395.*

8. **Podocarpus glaucus** Foxworthy, Philipp. Jour. Sci. **2**: 258. 1907, **6**: 159. 1911; Pilger, Nat. Pflanzenfam. ed. 2. **13**: 248. 1926; Florin, Svenska Vet.-Akad. Handl. III. **10**: 262, 266. 1931; Wasscher, Blumea **4**: 468. 1941.

A small bushy tree, 5–6 m. tall, with branchlets crowded toward tips of branches, light colored. Terminal buds very small, the outer scales spreading, up to 2 mm. long, with acuminate apex. Leaves densely crowded, erect-patent, coriaceous, glossy, pale beneath and glaucous when young, oblong, elliptic-oblong or spatulate, 0.9–1.7 cm. long, 3.5–5.5 mm. wide, apex obtuse or rounded, the base gradually narrowed to 1–2 mm. petiole and somewhat decurrent; margins thickened; midrib prominent near base on upper side, becoming flat and indistinct toward the apex, very prominent beneath. Transverse sections of the leaves show three resin canals below the vascular bundle, upper hypodermal fibers large and scattered, no lower hypodermal fibers between the stomatal rows, no vascular fibers nor auxiliary sclereids. Pollen cones solitary in upper leaf axils, scattered, slender cylindric, 1–1.5 cm. long, 2–3 mm. thick. Microsporophylls densely imbricate. Female cones and seeds not known.

DISTRIBUTION: Mt. Halcon, 2400 m. altitude, on Mindoro in the Philippine Islands and the slopes and summit of Mt. Moetaro in New Guinea.

Philippine Islands: MINDORO: Mt. Halcon, *Merrill 5672* (†ex Florin, Berlin Herbarium). **Netherlands New Guinea:** Wissel Lake region, Mt. Moetaro, *Eyma 5208* (†A).

Podocarpus glaucus is a little-known species and its position in the genus has been doubtful until the present time. The examination of the transverse sections of the leaves shows three resin canals under the phloem of the vascular bundle, transfusion tissue, accessory transfusion tissue, and hypodermal fibers on both sides of the leaf. These characters definitely place it in subsection B of section *Podocarpus*; it seems to be most closely related to *P. brevifolius,* which has larger leaves with parallel margins, and *P. brassii,* which has very thick pollen cones.

Florin (4) listed *Podocarpus glaucus* as a hypostomatic species of section *Stachycarpus.* The solitary pollen cones and the leaf anatomy show that it could not belong to this section. Wasscher (11) concluded correctly that it belongs in section *Podocarpus,* but he did not see *Merrill 5672*, the specimen on which the species is based. *Clemens 32032* and *40001,* which he lists, have continuous upper hypoderm and belong elsewhere, invalidating his description for this species. I have not seen the other two specimens which he lists, but I do not believe that *P. glaucus* has yet been collected in Borneo.

Orr (9) followed Florin in including *Podocarpus glaucus* in section *Stachycarpus* and he described the leaf anatomy correctly, but unaccountably treated the species along with *P. amarus* and *P. rostratus* as aberrant species in this group. His suggestion that the three species comprise a separate group is not tenable as they differ greatly from each other and each species must have separate consideration. By not placing this species in section *Podocarpus* with others from the Pacific islands, he missed seeing its similarity to *P. brassii* and *P. brevifolius.*

9. **Podocarpus brevifolius** Foxworthy, Philipp. Jour. Sci. **6**: 160. 1911; Pilger, Bot. Jahrb. **54**: 40. 1916; Florin, Svenska Vet.-Akad. Handl. III. **10**: 279. 1931; Wasscher, Blumea **4**: 466. 1941; Metcalf, Fl. Fukien **1**: 21. 1942.

P. neriifolius var. *brevifolius* Stapf, Trans. Linn. Soc. Bot. II. **4**: 249. 1894; Pilger, Pflanzenreich IV. **5**(Heft 18): 93. 1903.

P. wangii C. C. Chang, Sunyatsenia **6**: 26. 1941; Metcalf, Fl. Fukien **1**: 21. 1942.

A small tree or shrub with verticillate, spreading, stout branchlets. Terminal buds small, 2.5 mm. wide, with outer scales keeled, 3–7 mm. long, tardily deciduous, the tips acute to long-acuminate sometimes spreading. Leaves densely crowded, erect, thick-coriaceous, rigid, quite flat, straight or slightly falcate, elliptic to lanceolate, sessile or subsessile, 1.5–5.5 cm. long, 4–6 mm. wide, shining above, duller beneath, apex acute or somewhat rounded; upper midrib prominent and narrow, broader below; margins flat or revolute. Transverse sections of the leaves show three vascular resin canals below the phloem (rarely only one), interrupted upper hypoderm of small or often quite large fibers, no hypodermal fibers between the stomatal rows below, no auxiliary sclereids and no vascular fibers above the xylem, rarely below the phloem. Male cones solitary in the upper leaf axils, sessile, cylindric, thick, 2–3 cm. long, 4–5.5 mm. in diameter, scales at the base triangular. Microsporophylls imbricate, triangular, with obtuse apiculus. Female cones solitary, axillary near the tip of the branchlet; peduncles 2–4 mm. long, broad and flattened; receptacle of two fused fleshy scales, free at the tips, subcylindrical, 5–6.5 mm. long, 2.5–4 mm. thick, subtended by a pair of subulate to narrow-triangular, keeled, acute bracts, 3–5 mm. long. Seed ovoid, 1.2 cm. long, apex obtuse.

DISTRIBUTION: High mountain slopes in the Philippine Islands, on Mt. Kinabalu in British North Borneo and on Hainan island.

Philippine Islands. LUZON: Zambales, Bur. Sci. 5002, *Ramos* (A, NY), For. Bur. 9511, *Curran & Merritt* (†MO, NY, †US). **Hainan.** *Wang 36533* (A, NY). **British North Borneo.** Mt. Kinabalu: Paka Cave to Low's Peak, *Clemens 10657* (A, GH, †UC); upper Kinabalu, *Clemens 27825–27103* (†NY); above Paka, *Clemens 28901* (A, †NY); Gurulau Spur, *Clemens 50825* (A, †UC); Penibukan, *Clemens* in 1933 (A, NY, UC).

Podocarpus brevifolius was first described as a variety of *P. neriifolius* by Stapf from an early collection from Mt. Kinabalu. He included it under this species only because Hooker had combined *P. neriifolius* and *P. polystachyus* and he believed it to be more closely related to the latter. Foxworthy (5) suggested that it is more closely related to *P. pilgeri*, with which I would agree. According to Wasscher (11), it is "a very distinct species in its adpressed, small, lanceolate, thick-coriaceous leaves."

This examination of a number of specimens of *Podocarpus brevifolius* shows that the layer of upper hypodermal fibers is always interrupted. I believe that Orr (9), who is not in agreement with this, examined only *Clemens 32021* from the British Museum since his description fits this specimen perfectly. It is here included in the new species, *P. gibbsii.*

Metcalf (8) who lists this taxon from China, assigns to it three specimens: *Wang 36533* from Hainan and Wang *39578* and *40196* from Kwangsi. I agree on the specimen from Hainan but I question the two from Kwangsi on the mainland as I have not seen them and they may be *Podocarpus macrophyllus* var. *chingii.*

10. **Podocarpus spinulosus** (Smith) R. Brown ex Mirb. Geogr. Conif. in Mém. Mus. **13**: 75. 1825; Endlicher, Syn. Conif. 213. 1847; Carrière, Traité Conif. 653. 1867 (in part); Parlatore in DC. Prodr. **16**: 513. 1868; Bentham, Fl. Austral. **6**: 247. 1873; Mahlert, Bot. Centralbl. **24**: 281. 1885; Pilger, Pflanzenreich IV. **5**(Heft 18): 78. 1903, Nat. Pflanzenfam. ed. 2. **13**: 247. 1926; Brooks & Stiles, Ann. Bot. **24**: 305. 1910; Baker & Smith, Res. Pines Austr. 443. 1910; Dallimore & Jackson, Handb. Conif. 56. 1931, 81, 1948; Florin, Svenska Vet.-Akad. Handl. III. **10**: 280. 1931.

P. bidwillii Hoibrenk ex Endlicher, Syn. Conif. 213. 1847.
P. excelsa Loddiges ex Endlicher, Syn. Conif. 213. 1847.
P. pungens Don ex Lamb. Pinus, ed. 1. **2**: 21. 1824; ed. 2. **2**: 124. 1828.
Nageia spinulosa F. Müll. Cens. 109. 1882.
Taxus spinulosa Smith in Rees Cyclop. **35**. 1819.

A small tree, sometimes shrublike, with scattered or subverticillate branches. Terminal buds small, ovate with erect triangular, narrowly acuminate or attenuate scales up to 8 mm. long. Leaves scattered, coriaceous, erect to patent, linear, subsessile, 2–6.5 cm. long, 2–4.5 mm. wide, shiny above, apex long-acuminate and often pungent, base tapering abruptly to a very short petiole, or sessile; midrib narrow and evident above, broader and less prominent below. Transverse sections of the leaves show only one vascular resin canal, interrupted upper hypoderm often scarce between margin and midrib, no hypodermal fibers between the stomatal rows below, often two layers of palisade parenchyma, and regular transfusion tissue, upper vascular fibers rare. Male cones often very abundant, solitary or in clusters of 3–5 at the tips of very short, 1–3 mm., axillary peduncles subtended by 5–6 mm. long bracts, apiculate, simulating leaves; each cylindric cone, 4–8 mm. long, surrounded at the base by a few stiff scales. Microsporophylls densely imbricate, obtuse, apiculate. Female cones axillary to prophylls or true leaves in basal part of young shoot; peduncle slender, up to 1 cm. long; receptacle of 2–3 fused fleshy unequal scales, free at the tips, subtended by 2 subulate bracts 1–4 mm. long, glaucous, deep purple and edible when mature, bearing one ovule. Seed broadly ovoid, 1–2 cm. long, 7–10 mm. wide, often with a stout beak.

Distribution: In light forest, usually in sandy soil; southeastern New South Wales near Sydney.

Australia. New South Wales: Sydney, *Anon. s.n.* (†CAS), *Anon.* in 1897 (A), *Anderson 34* (NY), *Wright* in 1853–56 (NY, Y), *Prajerus* in 1889 (MTMG), *Kenny* s.n. (BRI–2 sheets); Port Jackson, *Mueller* in 1855 (MEL), Manly Beach, *Dawson* s.n. (MEL); Lake Narrabeen, beyond Manly, Wheeler's place, *Maiden* in 1887 (MEL); Paramatta, North Rocks, *Anon. s.n.* (MEL); Loftus, *Camfield* in 1897 (†MO); Collarez, *Burges* in 1930 (NY); Mosman, *Cannon 443* (A); Blackdown Tableland, *Simmons 76* (BRI); Lake Tabourie, *Baker* in 1892 (BRI); Beerwah, *White 12858* (BRI–2 sheets, ♂ and ♀); *R. Brown* in 1802–5 (†E); Jervis Bay, Naval Reserve, *Willis* in 1954 (MEL). Stradbrooke Island: *White 1665* (BRI); *White 1708* (A, BRI). Locality unknown: *Anon. s.n.* (BRI).

Podocarpus spinulosus resembles *P. drouynianus* in having long, slender crowded leaves, but in *P. spinulosus* the leaves taper to a definite short petiole and the midrib is prominent. In the transverse sections of the leaves the cuticle is a little thinner, the accessory transfusion tissue is more regular and the palisade layer is thicker. Orr (9) agrees with the description of the leaf anatomy and the specimen, *R. Brown* in 1802–05 (E), is probably a duplicate of the one he used.

11. **Podocarpus drouynianus** F. Müller, Fragm. **4**: 86, *t. 31.* 1863–64; Bentham, Fl. Austral. **6**: 274. 1873; Bertrand, Ann. Sci. Nat. V. **20**: 64. 1874; Van Tieghem, Bull. Soc. Bot. France **38**: 169. 1891; Pilger, Pflanzenreich IV. **5**(Heft 18): 77. 1903, Nat. Pflanzenfam. ed. 2. **13**: 247. 1926; Baker & Smith, Res. Pines Austral. 443. 1910; Dallimore & Jackson, Handb. Conif. 48. 1931, 66. 1948; Florin, Svenska Vet.-Akad. Handl. III. **10**: 279. 1931.

P. brownii Bertrand, Ann. Sci. Nat. V. **20**: 64. 1874 (nomen).
Nageia drouyniana F. Müll. Cens. 104. 1882.

A small tree or shrub, 1 m. high, with erect branches. Terminal buds ovate, with narrow, acute or attenuate scales up to 5 mm. long. Leaves spirally arranged, erect to patent, thin, leathery, linear, straight, subsessile, 2–12 cm. long, 2–5 mm. broad, green above, glaucous beneath, apex acute-acuminate, rarely pungent, short angustate at the base; margins somewhat revolute and thickened; midrib scarcely prominent or flat above, broad and prominent beneath. Transverse sections of the leaves with only one resin canal below the vascular bundle, the upper hypoderm interrupted, no hypodermal fibers between the stomatal rows, often very little transfusion tissue, accessory transfusion tissue usually of very irregularly elongate cells which are quite thick, vascular fibers very abundant below the phloem and forming a tissue several cells thick; cutin very thick and rounded over each epidermal cell; epidermis of very large cells, up to 207 μ long and 11–46 μ wide, pitted, with somewhat wavy walls. Pollen cones solitary or clustered at the ends of slender axillary peduncles 1–2.5 cm. long, or widely scattered, up to six on special axillary branches, each cone on a separate peduncle with a subulate bract at the base, sometimes with sterile bracts; mature cones short, thick, cylindric, 4–10 mm. long, 4 mm. wide. Microsporophylls densely imbricate, minutely apiculate. Female cones solitary in the axils of prophylls or the lowermost true leaves of new growth; peduncles variable, up to 2.0 cm. long; receptacle of 2 or 3 fleshy fused unequal scales with the tips free, 2.5 cm. long, subtended by 2 narrow bracts 2–3 mm. or more long, sometimes foliaceous and unequal (up to 11 mm. long, 2 mm. wide on *Gilbert 45*), waxy-coated, purple at maturity, sometimes bearing 2 ovules when young but only one maturing. Seeds broadly ovoid, 1–1.7 cm. or more long, not crested.

Australia. WESTERN AUSTRALIA: Busselton, *Pries* in 1870 (MEL); Warren Dist., Manjimup, *Koch 2499* (BRI, MEL, †MO), Warren River, *Mueller* in 1877 (MEL); Tom River, *Mueller* s.n. (MEL); Dape River, *Oldfield s.n.* (MEL); Preston Gordon River, *Mueller* in 1877 (MEL); Greenbushes, *Cook* in 1939 (MEL); Bow River, *Jackson* in 1912 (BRI); Blackwell River, *Mueller* s.n. (PH); Fly River, *Wilson 263* (†A); Vasse River, *Dept. Agr.* in 1898 (A); Denmark, Jarrah Forest, *White 5377* (A, BRI, †NY), *Dept. Agr. 443* (†A); southwest, *Eames* in 1937 (CU); *Baker* in 1904 (†A); *Gilbert 45* (†BM, MO); *Drummond 154* (MEL).

Podocarpus drouynianus has grass-like leaves which differ from those of *P. spinulosus* in having broad bases and in being sessile or very nearly so. The upper surface of the leaf is nearly flat at the midrib. The leaf anatomy differs little except for the very thick cuticle and the loose construction of the accessory transfusion tissue.

Orr (9) examined the leaf anatomy of this species and reported the single vascular resin canal; the thick cutin was also a distinguishing character.

Mueller in 1877 (MEL) from the Warren River is an excellent example of the reduction from normal vegetative leaves to the scale-like prophylls of the reproductive portion of the stem. The specimen twig is about 45 cm. long and the basal portion, 5–6 cm. long, is bare, the old leaves having fallen away. The next 20 cm. bears short, 2.5 cm. long, spreading leaves which decrease upward to narrow triangular scales 5 mm. long with spreading tips. In the following 10 cm. the prophylls are up to 8 mm. long and in the axils are solitary peduncled fruit. The remaining 14 cm. has large linear, mucronate leaves, 4–7 cm. long and 2–3 mm. wide, terminating in a bud which has just burst with new growth without having yet elongated.

12. **Podocarpus affinis** Seem. Fl. Vitiens. 266. 1865–73; Parlatore in DC. Prodr. **16**: 517. 1868; Warburg, Monsunia **1**: 193. 1900; Pilger, Pflanzenreich IV. **5**(Heft 18): 78. 1903, Nat. Pflanzenfam. ed. 2. **13**: 248. 1926; Florin, Svenska Vet.-Akad. Handl. III. **10**: 279. 1931; Dallimore & Jackson, Handb. Conif. 38. 1931, 60. 1948.

A tree with short, spreading branchlets, densely leafy toward the tips. Leaves spirally arranged, patent, linear-elliptic, 3–5.2 cm. long, 6–9.5 mm. wide, reddish-brown underneath when dry (young leaves glaucous), the apex obtuse with pointed tip, the base narrowed into a short distinct petiole; midrib narrow and often very prominent above, narrow and sometimes with shallow groves on either side below. Transverse sections of the leaves show three vascular resin canals with vascular fibers usually present both above and below the bundle, an interrupted hypoderm of fibers 18–30 μ in diameter, usually quite abundant on the upper side, but very rare on the lower between the stomatal rows, auxiliary sclereids in the mesophyll between the palisade mesophyll and the accessory transfusion tissue and also a few in the palisade making that layer discontinuous, palisade tissue occasionally doubled in thicker leaves, the cuticle sometimes thick. Male and female cones unknown.

Fiji. VITI LEVU: Namosi, Voma Peak, *Seemann 574* (TYPE, †BM, †GH, K), *Gillespie 2721* (†UC), *Horne 769* (K), *973* (†GH, K).

Orr (9) examined the leaf anatomy of *Podocarpus affinis* and his account agrees with the above description. The short leaves distinguish this species from the others in Fiji but only the vegetative characters are known.

13. **Podocarpus sylvestris** Buchholz, Bull. Mus. Paris II. 21: 285. 1949.

A tree becoming 15–18 m. high with the trunk up to 2 m. in diameter; outer bark gray and furrowed between longitudinal plates, the inner bark reddish brown; twigs very slender, subverticillate. Vegetative buds spherical or ovoid, solitary or in groups of three, with thin, slightly carinate, ovate, apiculate or obtuse, appressed scales. Leaves aggregated toward the ends of twigs, linear-lanceolate, 5–9 cm. long, 7–9.5 mm. wide (sometimes up to 17 cm. long and 15.5 mm. wide), narrowed above to an obtusely rounded apex, narrowed at the base to a short petiole, bright shiny green becoming gray-green above, lighter dull green beneath; midrib flat on both surfaces or broadly prominent. Transverse sections of the leaves show 3 vascular resin canals, hypoderm interrupted above with small fibers rarely more than 20 μ in diameter, few and scattered fibers between the stomatal rows below, vascular sclereids usually above and sometimes below, auxiliary sclereids present in the palisade mesophyll and abundant in the mesophyll above the accessory transfusion tissue. Pollen cones axillary, in clusters of 3, sessile or the peduncle 1 mm. long, cylindrical, 8–16 mm. long, 2–2.5 mm. in diameter when fully expanded; surrounded at base by 7–9 thin imbricated bud scales, the outer acute, the inner obtuse. Microsporophylls with a scarious obtuse apiculus. Female cones axillary on slender peduncles 5–9 mm. long; receptacle of 2 fused fleshy unequal scales 6–7 mm. long, subtended by a pair of small deciduous bracts and bearing a single ovule. Seed elongated, becoming 13 mm. long and 8–9 mm. wide, with only a minute or suppressed crest.

DISTRIBUTION: Scattered in mixed angiosperm forests of southern New Caledonia at 150–400 m. altitude.

New Caledonia: Plaine des Lacs, foret du Mois de Mai, *Buchholz 1696* (TYPE, †ILL, P), *1351* ♂ (†ILL, P), *1352* ♀ (†ILL, P), *1354* (†ILL), *1360*, *1372* — juvenile (ILL, P) *1392* (ILL), *Bernier 158* (P), *219* (P), *Bernier* in 1947 (ILL); Baie des Pirogues, *White 2118* (†A, BRI, P), *White s.n.* (K–2 sheets); north of St. Louis, Thy River, *Buchholz 1233* (†ILL); Mt. Canala, *Compton 1273* (†BM); North Prony, *Cribs 4718* (†P); Mt. Balade, *Vieillard 1265* (A, P); Wayap, *Vieillard 1265* (P); Pic du Pin, *Virot 598* (A); Mont Mi, *Virot 735* (A). Locality unknown: *Kay 34* (†P), *Vieillard 1265* (P).

It is likely that *Podocarpus sylvestris* has been confused in the past with *P. longifoliolatus* Pilger in subsection F, a tree which occurs on Mt. Mou in high coniferous rain-forests above 1000 m. It differs from the latter in its more slender twigs and globose vegetative buds with closely appressed ovate or obtuse, apiculate scales. Transverse sections of the leaves show only three vascular resin canals and smaller hypodermal fibers. *Podocarpus longifoliolatus* has, in addition, two or more resin canals above the vascular bundle. The female cones of *P. sylvestris* bear solitary ovules.

According to the manuscript notes of Prof. Buchholz, the vegetative buds of this species are more like those of *P. novae-caledoniae*. It differs from the latter in the much wider leaves with interrupted hypoderm. *Podocarpus novae-caledoniae* is the only other species in New Caledonia belonging in this subsection and its shrubby habit distinguishes it readily.

The wood is light, reddish, of excellent quality and is used for lumber. It is called "False Kauri" where it is marketed. One specimen, *Buchholz 1392*, has white wood but does not seem to differ otherwise.

14. **Podocarpus idenburgensis,** sp. nov.

Arbor 12–33 m. alta; ramulis tenuibus gemmis terminalibus parvis, ovatis vel globosis; foliis apice ramulorum congestis, lineari-lanceolatis vel lineari-ellipticis, 8–15 cm. longis et 9–15 mm. latis, apicibus acutis, petiolis 6–10 mm. longis, strobilis masculis alabastris axillaris cicatricorum foliorum oppositis positis, pedunculo tenue, 3–12 mm. longo, strobilis maturis 4 cm. longis, 5 mm. crassis; strobilis foemineis solitariis, pedunculo tenue, 8 mm. longo; semine globoso, 9 mm. longo, apice tenue rotundato.

A tree 31–57 cm. in diameter, the outer scales of the terminal buds on the twigs narrowly triangular, erect or spreading, up to 6 mm. long, the tips long acute or acuminate. Leaves straight or falcate, coriaceous, gradually or more abruptly narrowing to a definite petiole and gradually narrowing to an acute apex; midrib usually narrowly prominent above, almost flat below. Male cone bud scales acutely triangular, erect; microsporophylls imbricate, tips broadly obtuse, scarious, somewhat erose. Female cones axillary; receptacle very fleshy of 3 fused scales almost 1 cm. long.

DISTRIBUTION: In high mountain rain-forests in Netherlands New Guinea.

New Guinea. NETHERLANDS NEW GUINEA: 6 km. sw of Bernhard Camp, Idenburg River, *Brass & Versteegh 12581* (TYPE, †LAE); 2 km. sw of Bernhard Camp, Idenburg River, *Brass & Versteegh 13530* (†A, LAE); Bele River, 18 km. NE of Lake Habbema, *Brass & Versteegh 11133* (†A, LAE).

This species must be distinguished from both *Podocarpus neriifolius* and *P. rumphii* in New Guinea. It differs from these species in its large male cones, usually solitary or rarely paired, on peduncles up to 12 mm. long. The shape of the leaves is like that of both of the other species, while the terminal buds are more like those of *P. neriifolius*. Transverse sections of the leaves did not show any auxiliary sclereids and there were no lower hypodermal fibers in *Brass & Versteegh 11133*.

The name refers to the Idenburg River which flows adjacent to the region in which the species is found most abundantly.

15. **Podocarpus ledermannii** Pilger, Bot. Jahrb. **54**: 210. 1916, Nat. Pflanzenfam. ed. 2. **13**: 248. 1926; Florin, Svenska Vet.-Akad. Handl. III. **10**: 279, 283. 1931; Wasscher, Blumea **4**: 456. 1941.

A tree up to 20 m. high with gray bark and slender spreading branchlets; terminal buds small and ovate with long-triangular apiculate bud scales. Leaves scattered or crowded at the tips of the branches, thinly coriaceous, flexible, elliptic-lanceolate or narrow-elliptic, broadly cuneate or cuneate-rounded at the base, obtuse or abruptly narrowed and acute at the apex, often almost caudate at the tip, scarcely shiny above, dull below, 8–12 cm. long, 12–27 mm. wide; midrib abruptly prominent above, broader below. Transverse sections of the leaves show 3 vascular resin canals, interrupted hypoderm of large scattered or isolated fibers, some hypodermal fibers scattered below between the stomatal rows, vascular sclereids both above and below the bundle, auxiliary sclereids in the mesophyll both above and below the accessory transfusion tissue. Pollen cone buds in groups of 2 or 3 on very short peduncles; scales ovate-triangular, acute, keeled, 2 mm. long, inner ones more obtuse. Microsporophylls ovate-triangular obtuse or with acute apiculus. Female cones solitary, axillary, on peduncles 6.5–9 mm. long; receptacle of 2 or 3 fused fleshy scales with free tips, subtended by 2 subulate bracts 2.5 mm. long. Seed elliptic or globose, about 8 mm. long, crested.

DISTRIBUTION: In mountain forests of New Guinea, Java and Borneo.

New Guinea. NETHERLANDS NEW GUINEA: Bele River, 18 km. NE of Lake Habbema, *Brass 11058* (†A); Idenburgh River, 6 km. SW of Bernhard Camp, *Brass 12749* (†A). TERRITORY OF NEW GUINEA. Sepik District: Lordberg, *Ledermann s.n.*, ex Berlin Herbarium (†ex Florin). Eastern Highlands District: Chimbu, *Cavanaugh NGF3336* (†LAE). Morobo District: Yungaing, *Clemens 2352* (†A). **Java.** *Horsfield s.n.* (†GH); Preanger, *Warburg 2678* (†NY). **Borneo.** SARAWAK: *Foxworthy 377* (†US); Mt. Poi, *Clemens 20348* (†A, NY).

Podocarpus ledermannii differs from *P. neriifolius* in the more oval or oblong shape of the leaves and from *P. rumphii* in its abruptly or narrowly prominent midrib. Transverse sections of the leaves differ from *P. neriifolius* and *P. rumphii* in the large hypodermal fibers, hypodermal fibers between the stomatal rows and more abundant auxiliary sclereids. Orr (9) examined this species and found the same differences. The leaves of the specimens from Java show five vascular resin canals below the bundle and those from Borneo show three to five and there are few if any hypodermal fibers between the stomatal rows.

16. **Podocarpus dispermus** White, Contrib. Arnold Arb. **4**: 10. 1933.

A small tree up to 17 m. high with light brownish-gray, slightly flaky bark. Vegetative buds small; the scales narrow, acute, stiff and erect, up to 6 mm. long, longer than bud. Leaves dark glossy green, straight, broad-linear or narrow-lanceolate, apex acute, often pungent, gradually narrowing at base to a short petiole, 10–20 cm. long, 20–30 mm. wide; midrib broadly prominent above and below. Transverse sections of the leaves show usually 3 vascular resin canals (rarely one or five), an interrupted upper hypoderm of fibers 18–33 μ in diameter, lower hypodermal fibers between the stomatal rows, vascular sclereids present above and below, and auxiliary sclereids absent in palisade and spongy mesophyll. Pollen cones sessile, in clusters of 1–3, 3 cm. long, 3 mm. broad, surrounded by acute scales at the base. Microsporophylls crowded, imbricate, with the apiculus short, broad, and acute. Female cones axillary, on thick peduncles 5–15 mm. long; the very fleshy receptacle subtended by two small deciduous scales, turning scarlet when the fruit is ripe. Seeds usually in pairs, ellipsoid, 2.5 cm. long, 1.7 cm. broad.

DISTRIBUTION: In rain forests in northeast Queensland.

Australia. QUEENSLAND: Atherton Tableland, Gadgarra Reserve, *Kajewski 1192* (TYPE, †A, BRI, ILL, NY), *Kajewski 1107* (†A, BRI, NY–3 sheets); Millea Millea, *Tardent* in 1930 (A, BRI); Johnstone River, *Michael 97* (BRI).

Podocarpus dispermus differs from *P. elatus* in having broader and usually longer leaves with interrupted hypoderm. The receptacle and seeds are larger and the ripe receptacle of *P. dispermus* is red instead of blue-black. This species is not very abundant and has a restricted range in the region of Atherton in northern Queensland. Orr (9) did not see any specimens of *P. dispermus*, but he correctly included it in section *Podocarpus*.

The pollen cones on *Michael 97* are on short (1.5 cm.) branches arising from stems more than one year old, which also bear leaves. This is the only specimen I have seen with pollen cones.

17. **Podocarpus salomoniensis** Wasscher, Blumea **4**: 430. 1941.

Tree up to 20 m. tall with pale yellowish-brown, thin bark, usually smooth but sometimes fissured and flaking, the scattered drooping branches with stout twigs. Terminal buds large, ovoid, with long-attenuate scales up to 11 mm. long, the outer spreading and keeled, the inner erect. Leaves spirally arranged, spreading or crowded, linear to linear-lanceolate, sometimes falcate, 12–18 cm. long, 6.5–9 mm. wide, shiny above, dull beneath, long-tapering to an acuminate apex or sharp point, very gradually narrowed at base to a short, more or less distinct petiole; midrib sharply prominent above (in dried leaves sometimes located in a broad channel or fold), broader below; margins revolute. Transverse sections of the leaves usually show five vascular resin canals, the outer two of which are commonly found in the transfusion tissue, interrupted upper hypoderm of small fibers, lower hypodermal fibers absent between stomatal rows, vascular fibers above but not below the midvein, auxiliary sclereids in the mesophyll usually quite rare. Pollen cone buds solitary in the axils of upper leaves of new growth, large, 4–5 mm. diameter, connate; scales broadly triangular, apex acute, as long as bud. Female cones solitary in the leaf axils; peduncles divaricate, 11–15 mm. long; receptacle fleshy, 8–9 mm. long, of four decussate bracts, of which only the two lower are fertile, subtended by two narrow bracts, 4 mm. long, just beneath its base. Seed elongated, rounded at the apex and somewhat narrowed toward the base, 11 mm. long, 8 mm. broad.

DISTRIBUTION: On slopes in rain forests at 400–900 m. altitude in the Solomon Islands.

Solomon Islands. SAN CRISTOBAL ISLAND: Hinuahaoro, *Brass 2881* (TYPE, BM, BRI, †ex Florin, Leiden Herbarium); Waimasi River, *Walker BSIP. 254* (A, BRI, †K).

Podocarpus salomoniensis is quite distinct from *P. neriifolius* which is also found in the Solomon Islands. It has long, much narrower leaves which are usually quite crowded, the receptacle has four fleshy scales instead of two and the bracts are very close to its base. Transverse sections of the leaves show five vascular resin canals. Wasscher (11) recognized a relationship between *P. deflexus* Ridley and *P. salomoniensis* in the leaf and fruit, but he distinguished the latter by its "non-deflexed leaves, with the midrib usually not channelled beneath." In the leaf transverse sections I find these species similar, except for the smaller hypodermal fibers, 10–26 μ in diameter, in *P. salomoniensis*.

18. **Podocarpus deflexus** Ridley, Fl. Malay Peninsula **5**: 283. 1925; Florin, Svenska Vet.-Akad. Handl. III. **10**: 279. 1931; Wasscher, Blumea **4**: 427. 1941.

A small tree, 5–8 m. tall, the divaricate branches with stout branchlets showing numerous leaf scars. Terminal buds large, globose, with the outer scales narrow-triangular and reflexed, the inner scales almost triangular and adpressed. Leaves densely crowded at the ends of the branches, strongly deflexed, thick-coriaceous, rigid, linear or linear-lanceolate, 10–27 cm. long, 7–12 mm. broad, long-tapering to a shortly rounded (rarely acute) apex, gradually narrowing at the base to a very short petiole; midrib prominent above, broad and flat or deeply and broadly channelled below; margins of the blade sometimes recurved. Transverse sections of the leaves show 3–5 vascular resin canals, the center one often with the lumen closed due to the channel below and the outer pair located in the transfusion tissue; upper hypoderm of small groups of large fibers, 30–70 μ in diameter, and usually two fibers deep, no lower hypodermal fibers between the stomatal rows, vascular sclereids above and more rarely below the bundle, auxiliary sclereids in both palisade and mesophyll. Male cone buds 1–3 in the upper leaf axils, globose; mature cones unknown. Female cones solitary in the upper leaf axils; peduncle thick, 9–15 mm. long; receptacle large and fleshy, up to 8 mm. thick. Seeds obovoid, narrowed at the base, 11–12 mm. long, 8–9 mm. broad.

DISTRIBUTION: On rocky slopes, 1650–2300 m. altitude, in Gunong Tahan, Pahang.

Malay Peninsula. PAHANG: Gunong Tahan, *Ridley 16024* (†K).

The leaves of both *Podocarpus deflexus* and *P. salomoniensis* are large, crowded, and have five vascular resin canals, but there are several striking differences. The former species has strongly deflexed leaves, which may become longer, and are twice as wide, with the midrib channelled below. In transverse section, the small groups of very large hypodermal fibers contrast with the larger groups of much smaller fibers in a neat single layer in

P. salomoniensis. *Podocarpus deflexus* differs from *P. neriifolius* in its reflexed leaves, five vascular resin canals and the large upper hypodermal fibers. These large hypodermal fibers of *P. deflexus* are most like those of *P. polystachyus* and its relatives but the latter species has only three vascular resin canals. Orr (9) also observed the interrupted upper hypoderm of large fibers of *P. deflexus*, the absence of lower hypodermal fibers and the presence of auxiliary sclereids. He apparently did not see the five vascular resin canals as he reported no such condition for any species of *Podocarpus*. Florin (4) was impressed by the thick cuticle in this species.

19. Podocarpus annamiensis, sp. nov.

Arbor media, 5–12 m. alta; ramulis plerumque crassis, oppositis vel verticillatis; gemmis terminalibus ovatis vel saepe globosis, 2.5–4 mm. diametro, squamis exterioribus saepe quam alabastris longis, ad 5 mm. longis; foliis apicibus ramulorum congestis, erectis vel tantum interdum divaricatis, 4–10.5 cm. longis, 5–10 mm. latis, late linearibus vel lineari-lanceolatis, apicibus abrupte angustatis, obtusis, orbiculatis vel acutis, petiolo gradatim angustato, 2–6 mm. longo, marginibus interdum revolutis; strobilis masculis ex alabastris solitariis, vel 2–3-fasciculatis, sessilibus, subglobosis, 1.5–3.0 mm. diametro, strobilis maturis ignotis; strobilis femineis solitariis, pedunculo 2–10 mm. longo; semine ovoideo inferne haud angustato, apice obtuso, apiculato vel orbiculare, 8–10 mm. longo, 6 mm. lato.

DISTRIBUTION: Frequent summit tree of mountains in the coast range of Annam and Cochin China in Indochina and nearby Hainan.

Indochina. ANNAM: Mt. Bana, *Poilane 1561* (TYPE, A–2 sheets, †P–2 sheets); Mt. Bana, 25 km. from Tourane, *Clemens 3475* (†A, NY, †P, UC); Nhatrang Prov., *Poilane 3541* (†P); Nhatrang Prov., Hoi Li, *Chevalier 38692* (†P); Quang-trî Prov., massif de Dong-co-pah, *Poilane 3541* (A). COCHIN CHINA: in cacumine montis Dink propé Baria, *Pierre 354* (A–2 sheets, NY–3 sheets); Biuh Biuh, *Pierre 354* (†P–5 sheets); Chin'a Chiang, prov. Bienhoa, *Pierre 5532* (†A, †P–2 sheets). **Burma:** site unknown, *Brandis 38* (†MEL). **Hainan:** in mountain forests, *Liang 63510* (A, †NY), *Liang 65091* (A, †NY, P), *Liang 65554* (†NY–juvenile), *Liang 65555* (NY), *C. Wang 35031* (A, NY); Ng Chi Leng, Fan Yah, *Chun & Tso 44217* (A, †NY); Lingshiu, *How 73776* (†A).

The trunks of the trees are usually 0.5–1 m. in diameter with dark brown bark. The outer scales of the terminal bud are broadly triangular, keeled, stiff, erect with apex acute and apiculate or acuminate; the inner scales are shorter with rounded or minutely apiculate apex. The leaves are usually straight but are sometimes falcate, and rarely they may be up to 18 cm. long and 20 mm. wide; the midrib is from broadly prominent to flat above, rarely narrowly prominent, and below it may be broadly prominent, flat or even channelled. The pollen cone buds are found in the axils of the lower leaves of the new growth and the bud scales are tightly appressed, broadly triangular, stiff, with obtuse to acute apices and scarious margins, strongly keeled. The young cones are greenish white. The female cones are axillary and widely scattered; receptacle 4–8 mm. long, of two fused fleshy almost equal scales with free tips.

Podocarpus annamiensis differs from *P. neriifolius,* which is found in nearby regions, in the smaller stiff leaves which are crowded toward the ends of the twigs and in the abruptly obtuse or acute apex of these leaves. The habit and shape of the leaves is much like that of *P. macrophyllus* but it differs from this species (see no. 29) in the leaf anatomy. The stiff leaves also suggest *P. polystachyus,* but this is a tree of the strand rather than of the mountains, and the pollen cones occur in clusters of as many as five.

Transverse sections of the leaves of *Podocarpus annamiensis* show three vascular resin canals with the median one usually very small and the lateral very large and conspicuous, vascular fibers both above and below the bundle, upper hypodermal fibers 20–40 μ in diameter, very rare or in small groups and always interrupted at the midrib, hypodermal fibers absent between the stomatal rows, auxiliary sclereids in the mesophyll not abundant, cuticle thick. The two large lateral vascular resin canals distinguish transverse sections of this species from the three mentioned above. It is also distinguished from *P. macrophyllus* by the auxiliary sclereids and usually only one layer of palisade mesophyll.

The specimens listed from Annam and Cochin China are all quite similar. *Poilane 11121* with falcate narrower leaves deviates the most from the type specimen. Upper hypodermal fibers are quite rare in *Pierre 354* and abundant in *Poilane 3541.* Auxiliary sclereids have not been observed in the mesophyll of leaves from *Pierre 354.* Arnold Arboretum and New York Botanical Garden herbarium specimens of *Pierre 354* bear labels giving the site as Mt. Dink near Baria but the Paris Museum specimens give the site as Mt. Biuh Biuh.

The smaller-leaved specimens from Hainan have a more sharply acute apex to the leaves. Transverse sections of the leaves show abundant hypoderm and thick palisade which is often in more than one layer. The large-leaved specimens from the same locality have auxiliary sclereids only on the lower side of the leaf. Herbarium labels of these specimens indicate larger trees than those in Annam, reaching 16 m. in height and 3 m. in diameter.

20. **Podocarpus archboldii,** sp. nov.

Ramuli aliquando crassi, verticillati; alabastris terminalibus magnis globosis, squamis exterioribus late triangularibus ad 6 mm. longis, apicibus obtusis, recurvatis, marginibus tenuibus scariosis; foliis 3–9.5 cm. longis, 5–11 mm. latis, apicibus acutis vel acuminatis, marginibus revolutis; strobilis masculis 3–4 mm. latis; semine sphaeroideo, sine crista distincta.

A tree 6–38 m. high, 60–90 cm. in diameter with gray scaly bark 2–4 mm. thick and shallowly fissured. Leaves crowded, erect to patent, coriaceous, narrowly lanceolate, almost sessile or narrowed to a petiole 2 mm. long, green above, paler and brownish beneath; midrib narrowly prominent above, broader below. Pollen cone buds axillary, solitary, sessile or on short 2–3 mm. peduncles, large, globose, with obtuse scales. Female cones on stout peduncles 3–14 mm. long, solitary, axillary; receptacle of several thick fleshy fused scales, 7–8 mm. long, subtended by 2 deciduous bracts 2–3 mm. long. Seeds sometimes up to 15 mm. long, 13 mm. wide.

DISTRIBUTION: Occasional trees in high primary rain-forests of New Guinea, 1820–3000 m. altitude, more common at the higher altitudes.

New Guinea. NETHERLANDS NEW GUINEA: Idenburg River, 4 km. SW of Bernhard Camp, *Brass 13121* (TYPE, ♀ †A, LAE); 15 km. SW of Bernhard Camp, *Brass 11946* (♀ †A, LAE); 18 km. SW of Bernhard Camp, *Brass 11946A* (♂ A, †LAE); 9 km. NE of Lake Habbema, 2800 m. Camp, *Brass & Versteegh 10452* (†A). TERRITORY OF NEW GUINEA. Morobe District: Samanging, *Clemens 9503* (†A), *9525* (†A), Mt. Sarawaket, *Clemens 10073* (†A). Eastern Highlands District: above Goroka, J. Leahey's logging area, *Womersley & Floyd NGF6137* (A, †LAE); Wai, High country, *Jacobs NGF53* (†LAE). PAPUA. Central Division: Wharton Range, Murray Pass, *Brass 4605* (†A, BRI), Mt. Tafa, *Brass 5118* (†NY).

In New Guinea this species is distinguished from *Podocarpus neriifolius* by smaller leaves with revolute margins and from *P. pilgeri* by larger leaves with gradually acute or acuminate tips. The large globose terminal buds distinguish it from both species.

Transverse sections of the leaves show three vascular resin canals, an interrupted upper hypoderm of fibers of medium diameter, hypodermal fibers rarely between the stomatal rows, vascular fibers both above and below the bundle, and usually no auxiliary sclereids in the mesophyll. Only *Jacobs NGF53* and *Brass & Versteegh 10452* show rare auxiliary sclereids.

Clemens indicated that his specimen *10073* from Mt. Sarawaket had red fruit. *Brass & Versteegh 10452* had a seed of larger size, 15 mm. long and 13 mm. wide.

This species is dedicated to Mr. Richard Archbold who sponsored the expedition to New Guinea on which this species was first found.

20a. **Podocarpus archboldii** var. **crassiramosus**, var. nov.

Arbor gracilis, 8–20 m. alta; ramulis crassissimis, alabastris terminalibus magnis, globosis vel globosi-ovatis, supra 5 mm. diametro; foliis congestis tenue lanceolatis, apicibus longe acutis, interdum acuminatis 6–13 cm. longis, 7–11.5 mm. latis; strobilis masculis ignotis; strobilis femineis solitariis, pedunculo 6–11 mm. longo; semine globoso-elliptico, ad 10 mm. longo et 9 mm. lato, apice rotundato vel obtuse apiculato.

Outer scales of terminal buds triangular, keeled, erect, to 9 mm. long, with long acute or acuminate tips which are sometimes recurved. Leaves divaricate, straight or falcate, gradually narrowing to short, thick petioles at the base and with long, acute tips; midrib narrowly prominent above, flat or even channelled below. Female cones axillary among lower leaves of new growth; receptacle of 2–3 fused fleshy scales with free tips, 6–8 mm. long, and subtended by 2 small subulate bracts.

DISTRIBUTION: In high mountain forests of New Guinea, 1850–2650 m. altitude.

New Guinea. NETHERLANDS NEW GUINEA: 9 km. NE of Lake Habbema, *Brass 10874* (TYPE, †A, LAE); Wissel Lake Region, s. of border of Lake Paniae, foot of Mt. Poti, *Eyma 4538* (†A). TERRITORY OF NEW GUINEA. Western Highlands District: Al River mountains, Nondugl, *Womersley NGF5361* (†A, LAE). Eastern Highlands District: Chimbu, *Cavanaugh NGF3329* (†LAE). Morobe District: Oberamnang, *Clemens 5434* (†A); Sattelberg, *Clemens 2276* (A); Mongi valley, below Salawaket, *Lane-Poole 524* (†BRI).

This variety differs from the species in the very thick twigs and widely spreading leaves which do not have revolute margins. The hypodermal fibers are somewhat larger. Transverse sections of the leaves of *Cavanaugh NGF3329* and *Lane-Poole 529* have three very large vascular canals and the latter specimen has two smaller ones in addition. Auxiliary sclereids were seen only in *Clemens 5434 and Eyma 4538.*

21. **Podocarpus nakaii** Hayata, Ic. Pl. Formosa **6**: 66. 1916; Pilger, Nat. Pflanzenfam. ed. 2. **13**: 248. 1926; Florin, Svenska Vet.-Akad. Handl. III. **10**: 279. 1931.

A tree with terete, glabrous branchlets. Terminal buds globose, outer scales short, 3 mm. long, with acute or short-acuminate spreading tips. Leaves crowded at the ends of twigs, spreading, linear-lanceolate or linear, 5–10 cm. long, 8–11 mm. broad (sometimes up to 14 mm. broad), straight or falcate, shiny above, paler beneath, the apex acute or shortly attenuate, at the base gradually narrowing to petioles 5 mm. long; midrib broadly prominent or flat above, rarely narrow, very broad below. Transverse sections of the leaves show 3 vascular resin canals (sometimes obscure), upper hypoderm of few and scattered small fibers 13–28 μ in diameter interrupted at the midrib, no hypodermal fibers between the stomatal rows, vascular sclereids absent above and rare below the bundle, auxiliary sclereids absent. Pollen cones unknown. Ovulate cones solitary in the leaf axils; peduncles 2–7 mm. long; receptacle fleshy and subtended by two thick triangular bracts 1.5 mm. long, 1 mm. wide. Seed oblique-globose, crested, 1 cm. long, 8 mm. thick.

DISTRIBUTION: Known only from Formosa on mountain slopes.

Formosa: Hassen-zan, *Kanehira 21184* (A, †UC, UCLA); Sui-sya, *Kanehira 740* (†UC); Rengeti, *Hayashi 21208* (A, NY, †UC), *Kanehira 316* (A); Nanto, Tahiken, *Wilson 9935* (A–5 sheets, †US), *Wilson* in 1918 (P); above Shushu, *Wilson 10023* (A–3 sheets); around Honsha, *Wilson 9937* (A–3 sheets); Shinchiku Prov., forests beyond Nanoaherzan, *Wilson 10319* (†A).

Podocarpus nakaii, according to the description, differs from *P. neriifolius* by the very short (2–4 mm.) peduncle of the fruit and the short, thick triangular bracts subtending the receptacle; and I find the terminal buds have shorter acute scales. The peduncles on *Kanehira 740*, however, are 7 mm. long. Transverse sections of the leaves show thicker palisade than is found in *P. neriifolius.* As Orr (9) suggests, the species is not readily distinguished from *P. macrophyllus* by means of leaf anatomy.

22. **Podocarpus rumphii** Blume, Rumphia 3: 214. 1847; Gordon, Pinetum 282. 1858, ed. 2. 346. 1875; Carrière, Traité Conif. ed. 2. 663. 1867; Parlatore, DC. Prodr. **16**: 515. 1868; Bertrand, Ann. Sci. Nat. V. **20**: 59. 1874; Van Tieghem, Bull. Soc. Bot. France **38**: 169. 1891; Warburg, Monsunia **1**: 193. 1900; Pilger, Pflanzenreich IV. **5**(Heft 18): 81. 1903, Bot. Jahrb. **54**: 210. 1916, Nat. Pflanzenfam. ed. 2. **13**: 248. 1926; Foxworthy, Philip. Jour. Sci. **6**: 164. 1911; Dallimore & Jackson, Handb. Conif. 55. 1923, 1931, 80. 1948; Wasscher, Blumea **4**: 432. 1941.

A tree 20–33 m. high with straight branches and subverticillate twigs. Terminal buds on the twigs globose or ovate, with thick, keeled outer scales which are acute or acuminate, rarely obtuse. Leaves erect or patent, coriaceous, linear-lanceolate, straight or subfalcate, more or less abruptly narrowing to the short-angustate (rarely caudate-acuminate) apex, narrowing abruptly to the short thick petiole, 6–25 cm. long, 10–29 mm. broad, margins parallel or nearly so; midrib broadly prominent above or scarcely evident, less so below. Transverse sections of the leaves show 3 vascular resin canals, interrupted upper hypoderm with fairly small fibers, no hypodermal fibers between the stomatal rows below, almost always vascular fibers but rarely auxiliary sclereids. Male cones axillary, solitary or clustered 1–3, sessile, or on short 1.5–3 mm. peduncles, strobili to 4 cm. long, 3 mm. in diameter. Microsporophylls nearly ovate-triangular, apiculate. Female strobili solitary, axillary; peduncle 2–16 mm. long; receptacle of 2–4 fused fleshy scales with narrow, obtuse free apex, subtended by 2 subulate bracts, 6–10 mm. long, 3.5–8 mm. in diameter. Seeds 1 or 2, globose-ellipsoid, grayish when ripe, 10–13 mm. long, not crested.

DISTRIBUTION: Usually a mountain tree in forests of Borneo, New Guinea and some of the smaller islands in this region.

Borneo. BRITISH NORTH BORNEO. Mt. Kinabalu: Gurulau Spur, *Clemens 50691* (A, †BM, †UC); Penibukan Ridge, *Clemens 50051* (A, UC), For. Dept. 2174, *Apostal s.n.* (UC). SARAWAK: Bidi Cave, near top of mountain, *Clemens 20656* (†NY). SOUTHEAST BORNEO: Sampit, *Buwalda 7793* (†A), peak of Balikpapan, *Kostermans 7408* (†LAE). JAMBONGAN ISLAND: Sanakan, *Cabiling, For. Dept. 3710* (UC).

Moluccas. Weda, Weda, *Anon. Boschpr. bb24924* (A). MOROTAI: G. Pare 2, *Kostermans 1210* (A, LAE). AROE ISLANDS: Dosinamalaoe, P. Kobroor, *Boschpr. bb 25289* (A), *Buwalda 4988* (†A); Selibatabat, P. Wokam, *Boschpr. bb 25415* (†A), *Buwalda 5271* (†A); Wakatoebi, P. Oedjir, *Boschpr. bb25438* (†A). AMBOINA: *Robinson 309* (NY).

New Guinea. TERRITORY OF NEW GUINEA. Sepik District: Aitape, *Smith NGF1241* (BRI, †LAE–2 sheets). Eastern Highlands District: Aiyura, *Smith NGF1102* (BRI, †LAE); Tumoma River, *Masters 1341* (†BRI); Chimbu, *Cavanaugh NGF3336* (†A). Morobe District: Matap, *Clemens 11133* (†A). PAPUA. Central Division: Rona, *Brass 6208* (†A); Koitaki, *Carr 12842* (†A). Gulf

Division: Kikori River delta, *Hart NGF4545* (†LAE–2 sheets). Milne Bay District: Misima Island, *Schacht NGF2762* (†BRI, LAE).

Solomon Islands. SAN CRISTOBAL: ridge forest, *Logie BSIP357* (†LAE).

The description for this species was taken from the specimens examined and from Pilger (1903). These specimens all show leaves with a broad, scarcely prominent midrib and abruptly acute apex which distinguish *Podocarpus rumphii* from *P. neriifolius*; I find that these characters also distinguish it from *P. ledermannii.* Wasscher (11) included in *P. rumphii* specimens of *P. philippinensis* and some specimens from Celebes which I am excluding from *P. rumphii.*

The male specimen, *Buwalda 7795,* has solitary sessile, globose male cone buds. The seeds on the female specimens are very immature. Wasscher includes *Clemens 50691 and 50051* under *P. neriifolius,* but the broad midrib and the leaf anatomy are so like *Buwalda 7795* that these should both be considered as *P. rumphii. Cabiling s.n.* has a narrowly prominent midrib and caudate-acuminate apex on the leaves, but their very large size, 19.3 cm. long and 24 mm. wide, suggest that it is a juvenile example of this species.

Orr (9) examined the leaf anatomy of *Podocarpus rumphii* in transverse section and described lower hypodermal fibers between the stomatal rows. I do not know what specimens he used, but I found a few fibers only in *Smith NGF1102.*

Wasscher's description excluded caudate-acuminate apices of the leaves, but I find that some specimens which have such leaves must be included in *P. rumphii.*

The specimens listed from the Moluccas have large, broad leaves with nearly parallel margins and tips abruptly acute or acuminate. The midrib is broadly or scarcely prominent above. One of the specimens with seeds, *Buwalda 4988,* has peduncles 6–16 mm., longer than the type, and the seed is up to 13 mm. long. The male cones are solitary or clustered and sessile or short peduncles in *Kostermans 1210* and *Buwalda 5271.*

Most of the specimens from New Guinea had been tentatively ascribed to *Podocarpus neriifolius,* but the very broadly prominent upper midrib and the parallel margins of the leaves proved to be satisfactory criteria for their inclusion in *P. rumphii.* The foliage on these specimens is usually much larger.

Smith 1102, from Aiyura, is a sterile specimen with very large drooping leaves clustered at the tips of the twigs and reminds one of *Podocarpus deflexus* from the Malay peninsula. Transverse sections of the leaves show 5 resin canals below the vascular bundle but the hypodermal fibers are smaller, there are no auxiliary sclereids and the lower hypodermal fibers are fairly numerous; these are not characteristics of *P. deflexus.*

23. **Podocarpus costalis** C. Presl, Epimel. Bot. 236. 1849; Pilger, Pflanzenreich IV. 5(Heft 18): 78. 1903, Pflanzenfam. ed. 2. **13**: 248. 1926; Florin, Svenska Vet.-Akad. Handl. III. **10**: 279. 1931; Dallimore & Jackson, Handb. Conif. 42. 1931, 64. 1948.

Tree or shrub (?) with thick, short, densely leafy spreading branchlets. Terminal buds short, 2–2.5 mm. long, ovate with thick, stiff, keeled, closely appressed scales with obtuse apex, as long as the bud. Leaves erect to patent, crowded, coriaceous, oblanceolate, sometimes rounded, obtuse, or even emarginate at the apex, narrowing rather gradually from above the middle to a short, thick petiole, 3.8–7.0 cm. long, 7–10 mm. broad; midrib broadly prominent above, rarely embedded in shallow grooves, below broad and scarcely evident or shallowly impressed. Transverse sections of the leaves show uniformly three vascular resin canals, interrupted upper hypoderm, no hypodermal fibers between the stomatal rows and no auxiliary sclereids. Male cone buds subglobose, 2–2.5 mm., solitary, sessile, with obtuse-rotundate outer scales; mature cone thick cylindric, 3 cm. long. Female cones solitary, axillary; peduncles 2 mm. long; receptacle of two fused fleshy equal scales with rounded tips, 7 mm. long, subtended by two very minute bracts. Seed elliptical, obtusely crested at the tip, dark when dry, 7–9 mm. long.

DISTRIBUTION: Shores of several of the Philippine Islands and Formosa.

Philippine Islands. BABUYAN ISLANDS: Dalupiri, *Bartlett 15138* (A), *15192* (†A). BATANES ISLANDS: Mahatow, For. Bur. 80397, *Ramos* (†NY). POLILLO ISLAND: For. Bur. 29682, *Salvoza* (†NY, UC). BUCAS ISLAND: For. Bur. 5268, *Merrill* (†NY). **Formosa:** Isl. Koto-syo, *Mori 315* (†A).

The description of *Podocarpus costalis* was drawn up from the specimens cited and from Pilger's description (1903). The only likely suggestion as to the locality of the original collection by Haenke is Luzon, but I have seen no other collections of this species from there. The only specimen included here which has been examined previously is For. Bur. 5268, *Merrill*; it was placed in *P. polystachyus* by both Foxworthy and Wasscher in spite of the spatulate shape of the leaves. Foxworthy's description (5) under *P. costalis* is referred to *P. pilgeri* since all of the specimens he used are cited under that species, no doubt rightly, by Wasscher (11).

Podocarpus costalis differs from *P. polystachyus* in the thick, spatulate leaves which are usually erect on the twigs. Transverse sections of the leaves show more abundant upper hypodermal fibers of smaller diameter in *P. costalis*. Orr (9) included *P. costalis* with those species having lower hypodermal fibers but I did not find these in any case. Both species are found at sea level in coastal areas.

The Formosan specimen (*Mori 315*) differs from the others in having vascular fibers.

24. **Podocarpus thevetiifolius** Zippel, Flora **12**: 287. 1829 (nomen!); Blume, Rumphia 3: 213. 1847; Carrière, Traité Conif. ed. 2. 669. 1867; Parlatore, DC. Prodr. **16**: 518. 1868; Gordon, Pinetum ed. 2. 349. 1875; Warburg, Monsunia 1: 192. 1900; Pilger, Pflanzenreich IV. 5(Heft 18): 79. 1903, Bot. Jahrb. **54**: 210. 1916, Nat. Pflanzenfam. ed. 2. **13**: 248. 1926; Dallimore & Jackson, Handb. Conif. 56.

1923, 1931, 83. 1948; Florin, Svenska Vet.-Akad. Handl. III. **10**: 280. 1931; Wasscher, Blumea **4**: 462. 1941.

A small tree, 10–23 m. tall, with numerous, scattered, sometimes opposite spreading branches. Vegetative buds small, ovate-acute; bud scales adpressed, acute, 1.5 mm. long. Leaves scattered below, but closely crowded near ends of twigs, thin-coriaceous, lanceolate, acute or obtuse at the apex, rarely mucronate, gradually narrowing to a short petiole; midrib broad, flat, not prominent above, scarcely prominent below; margins of blades not revolute, flat and [fide Wasscher (11)] with a distinct narrow shining line along the margins, 2.5–8 cm. long by 5–9 mm. wide. Transverse sections of the leaves show an interrupted upper hypoderm of very large fibers, no hypoderm fibers between the stomatal rows, vascular fibers usually present above the bundle, auxiliary sclereids absent in the mesophyll. Pollen cones unknown. Female cones axillary, solitary; peduncles slender, 3–8 mm. long; receptacle [fide Blume (1847)] twice as thick as the seed. Seed ellipsoid, 10 mm. long.

DISTRIBUTION: New Guinea.

New Guinea. NETHERLANDS NEW GUINEA: Lobo, *Zippel s.n.* (†ex Florin). PAPUA. Northern Division: Isuarava, *Carr 15395* (†A).

This species may be distinguished from those closely related to it by the small, thinner, flat leaves without prominent midrib above and the small terminal buds with very short scales. The margins of the leaves are not revolute as in *Podocarpus archboldii.* In both specimens the diameter of the hypodermal fibers is large, sometimes up to 70 μ.

25. **Podocarpus forrestii** Craib & W. W. Smith, Notes Bot. Gard. Edinburgh **12**: 219. 1920; Dallimore & Jackson, Handb. Conif. 46. 1923, 1931, 69. 1948; Florin, Svenska Vet.-Akad. Handl. III. **10**: 279. 1931.

A shrub up to 3.5 m. high with fairly stout branches. Vegetative buds small, ovate. Leaves 3.5–5.4 cm. long, 6.5–9 mm. wide, oblong or oblong-lanceolate, obtuse or rounded at the apex, gradually narrowing at the base into a short, winged petiole, dark green above, pale beneath; midrib broadly prominent above. Pollen cones unknown. Female cones usually solitary in the leaf axils, pedicels 8 mm. long, ovule on a short fleshy receptacle. Mature seeds unknown.

DISTRIBUTION: Eastern and western sides of the Tali Range in western China.

China. YUNNAN: Tali Range, *Forrest 6852* (†E).

Podocarpus forrestii is distinguished from *P. macrophyllus* var. *maki* by its dwarf habit and shorter, broader leaves. The upper midrib is not as abruptly prominent. I have examined the transverse section of leaves from only one specimen and I find that the leaf anatomy is very similar to that of *P. macrophyllus,* its var. *maki,* and *P. nakaii.* The interrupted upper hypoderm is of small fibers; rarely are there any vascular fibers, and I found no auxiliary sclereids. As the few differences seem to be only a matter of degree, it may well be that these are all forms of *P. macrophyllus.*

26. **Podocarpus pilgeri** Foxworthy, Philip. Jour. Sci. Bot. 2: 259. 1907, 6: 149. 1911; Pilger, Nat. Pflanzenfam. ed. 2. 13: 248. 1926; Florin, Svenska Vet.-Akad. Handl. III. 10: 280. 1931; Dallimore & Jackson, Handb. Conif. 54. 1931, 79. 1948; Wasscher, Blumea 4: 463. 1941.

Podocarpus celebica Warburg, Monsunia 1: 92. 1900, non Hemsley 1896; Pilger, Pflanzenreich IV. 5 (Heft 18): 78. 1903.

Podocarpus schlechteri Pilger, Bot. Jahrb. 54: 209. 1916, Nat. Pflanzenfam. ed. 2. 13: 248. 1926; Florin, Svenska Vet.-Akad. Handl. III. 10: 280. 1931; Wasscher, Blumea 4: 463. 1941.

Podocarpus costalis auct. non Pilger, Foxworthy, Philip. Jour. Sci. Bot. 6: 161. 1911.

A small tree or shrub, 2–15 m. tall, rarely taller, with scattered or verticillate branches. Terminal buds ovate-acute with narrowly triangular scales, sometimes long acuminate, keeled, to 4.5 mm. long. Leaves scattered or crowded near the tips of twigs, spreading, usually thick coriaceous, rigid, usually flat, linear-lanceolate to oblong, cuneately or more gradually narrowed to the short petiole, abruptly or rather gradually narrowed to an acute apex, sometimes apiculate, 1.5–8 cm. long, 4–13 mm. broad; midrib narrow and sharply prominent above, keeled, flat, or even channelled below. Transverse sections of the leaves show 1–3 vascular resin canals, the central one sometimes being larger; the upper hypoderm is usually of large isolated fibers, sometimes several in a group and rare fibers on the lower side between the stomatal rows; vascular sclereids or fibers are usually present. Male cones solitary, axillary, subsessile, scales ovate-triangular and acute, cylindrical, 1.5–5 cm. long, 2–4 mm. in diameter; microsporophylls broadly triangular, apiculate with a scarious margin. Female cones solitary, axillary; peduncles 3–12 mm. long; receptacle of two fused fleshy bracts, obtuse and free at the tips, 5–12 mm. long, 3–7 mm. thick, subtended by a pair of subulate bracts 1.5–2 mm. long. Seed elliptic-globose, obtuse, 8–8.5 mm. long, 7 mm. broad.

DISTRIBUTION: Mountains between 1400–3000 m. altitude on islands from the Philippines to the Solomons, and one collection from Siam.

Philippine Islands. LUZON: Tayabas, Mt. Banajao, *Foxworthy*, Bur. Sci. 2393 (†NY), *Gates 7254* (†F), *Copeland s.n.* (†UC); Lucban, *Elmer 7778* (A, †MO, NY); Rizal, *Loher* in 1914 (†UC). MINDORO: Mt. Halcon, *Merrill 5754* (†NY, isotype). NEGROS: Canlaon Volcano, *Merrill 241* (†A). MINDANAO: Misamis Prov., Mt. Malindang, *Mearns & Hutchinson*, Bur. Sci. 4673 (†BR, †NY); Agusan Prov., Cababaran, Mt. Urdaneta, *Elmer 14086* (A, F, GH, †MO, NY, †UC); Bukidnon Subprov., Mt. Lipa, *Ramos & Edanõ*, Bur. Sci. 38500 (A).

Celebes. Gowa, Lembaja, Boroe, *Boschpr. bb20437* (A).

New Guinea. NETHERLANDS NEW GUINEA: Idenburg River, Bernhard Camp, *Brass & Versteegh 13519A* (†A–2 sheets); NE Lake Habbema, Bele River, *Brass 11341* (†A, LAE); Subdistr. Manokwari, summit of Arfak Mountains, Vogelkop, Angi gita Lake, *Kostermans 2161* (†A), *2236* (†A), *2519* (†A). TERRITORY OF NEW GUINEA. Western Highlands District: Wahgi-Sepik Divide, *Womersley & Millar NGF6980* (A, LAE); Wahgi-Jimmi Divide, *Womersley NGF5316* (A, †LAE); Mt. Hagen, *Cavanaugh NGF3324* (†LAE). Bismark Mountains, *Schlechter 18780* (†BR, †UC). Morobe District: Wau-Mubo Road near Skindewai, *Womersley & Millar NGF8341* (A, LAE); NE Oberamnang, *Clemens 4569* (A), *4696* (†A); Edie Creek, *Womersley NGF5373* (A, †LAE); above Wau, *McAdam NGF440* (BRI, †LAE). PAPUA. Central Division: Mt. Tafa, *Brass 4034* (†NY); above the Gap, *Carr 13721* (†A); Boridi, *Carr 14563* (A), *14556* (†A); Mt. Obree, *Lane-Poole 357A* (†BRI). Milne Bay District: Maneau Range, north slopes of Mt. Dayman, *Brass 22811* (A).

Solomon Islands. SANTA ISABEL ISLAND: *Brass 3265* (†A). SAN CRISTOBAL ISLAND: on ridge, *Logie NGF354* (LAE).

Siam. Kao Knap, Krat, *Kerr 17809* (†BM).

This description has been limited to those specimens obtained from the higher altitudes. Therefore it includes all of the specimens from the Philippine Islands listed by Foxworthy (5) as *P. costalis* and which were later referred to *P. pilgeri* Foxw. by Wasscher (11). The name *P. schlechteri* Pilger is still being retained by some workers for specimens with small, linear-lanceolate leaves which are pointed at both ends. There is so much variation, however, in the foliage of *P. pilgeri,* even within the same specimen, that these must be included here.

Kerr 17809, from Siam, has exceedingly immature fruit, but the foliage is so like that of many specimens of *Podocarpus pilgeri* that I refer it to that species. It is said to be a small tree, 1.8 m. high, not uncommon in high evergreen forest. Transverse sections of the leaves show more abundant upper hypoderm fibers than most other specimens. This specimen and those from New Guinea often show a few auxiliary sclereids in the mesophyll, but these are lacking in the Philippine specimens.

27. **Podocarpus neriifolius** D. Don ex Lamb. Pinus ed. 1. 1: 21. 1824, ed. 2. **2**: 122. 1828 (in part); Endlicher, Syn. Conif. 215. 1847; Gordon, Pinetum ed. 1. 279. 1858, ed. 2. 343. 1875; Carrière, Traité Conif. ed. 2. 661. 1867; Parlatore, DC. Prodr. **16**: 514. 1868; Bertrand, Ann. Sci. Nat. V. **20**: 59. 1874; Van Tieghem, Bull. Soc. Bot. France **38**: 169. 1891; Kent in Veitch, Man. Conif. 152. 1900; Pilger, Pflanzenreich IV. **5**(Heft 18): 80. 1903, Bot. Jahrb. **54**: 210. 1916. Nat. Pflanzenfam. ed. 2. **13**: 248. 1926; Bernard, Beih. Bot. Centralbl. **17**: 293. 1904; Foxworthy, Philip. Jour. Sci. **2**: 258. 1907, **6**: 162. 1911; Dallimore & Jackson, Handb. Conif. 52. 1923, 1931, 77. 1948; Wilson, Jour. Arn. Arb. **7**: 41. 1926; Florin, Svenska Vet.-Akad. Handl. III. **10**: 279. 1931; Merrill, Contr. Arnold Arb. **8**: 15. 1934; Wasscher, Blumea **4**: 437. 1941.

Myrica esquirolii Leveillé in Fedde, Rep. Sp. Nov. **12**: 537. 1913; Rehder, Jour. Arnold Arb. **10**: 108. 1936.

Podocarpus bracteata Blume, Enum. Pl. Javae 88. 1827–8; Van Tieghem, Bull. Soc. Bot. France **38:** 169. 1891.

Podocarpus discolor Blume, Rumphia **3:** 213. 1847.

Podocarpus junghuhniana Miquel, Pl. Junghuhn **1:** 2. 1851; Van Tieghem, Bull. Soc. Bot. France **38:** 169. 1891.

Podocarpus leptostachya Blume, Rumphia **3:** 214. 1847; Van Tieghem, Bull. Soc. Bot. France **38:** 169. 1891.

Podocarpus macrophylla var. *acuminatissima* Pritzl, Bot. Jahrb. **29:** 213. 1900.

Podocarpus neriifolius var. *brevipes* Pilger, Pflanzenreich IV. **5**(Heft 18): 81. 1903.

Podocarpus neglecta Blume, Rumphia **3:** 213. 1847.

A medium sized tree up to 40 m. tall (rarely larger) with very spreading branches and numerous branchlets. Terminal buds ovate with ovate-triangular to long-subulate outer scales usually as long as or longer than the bud, 5–7 mm. long. Leaves scattered, usually large, 7–15 cm. long, 9–13 mm. wide (sometimes longer and up to 19 mm. wide), straight or falcate, spreading, usually very gradually narrowing to an acute apex, and less gradually to a short petiole; midrib narrowly prominent above, broad and prominent below. Transverse sections of the leaves show 3 vascular resin canals below the bundle, vascular sclereids or fibers usually present above the bundle and more rarely below; no auxiliary sclereids, the interrupted upper hypoderm in small groups of from 1–7 fibers, 20–40 μ in diameter, no hypodermal fibers between stomatal rows, palisade mesophyll of a single layer. Pollen cones solitary, sessile, axillary, ovate, large, with usually thick, coriaceous, acute outer scales, the inner scales thinner and scarious, mature cones 2–8.5 cm. long, 2.5–4.5 mm. in diameter. Microsporophylls narrow, short, acute or obtuse, often apiculate. Female cones solitary in leaf axils, usually remote, peduncles 3–24 mm. long; the fleshy receptacle subtended by two subulate bracts 2–6 mm. long. Seeds 9–16 mm. long, narrow ovoid, sometimes globose but gradually narrowed toward the tip.

Distribution: Subtropical evergreen forest, 650–1300 m. altitude in the Himalayas, eastward into China, and south into the Malay Peninsula; on insular lands from Japan south into Java, west to Sumatra and the Andaman Islands, eastward as far as the Fiji Islands.

India. Nepal: *Wallich 6052A* (Type, †BM, †BR, †NY, †P), *Wallich* in 1818 (MEL, MO), *Anon.* 1819 (BR), *Scheidweiler s.n.* (†BR), *Lambert 45* (†BR), *Martius* in 1819 (†BR). Assam: Khasia, Jowae, *Clarke 18362* (†A); Jaiutea Hills, *Mann s.n.* (A); tropical region, *Hooker & Thomson* in 1856 (†MEL, PH); Sibebiun (?), *Thomson s.n.* (GH); *Masters s.n.* (†P, †PH); *Simons s.n.* (†P). East Bengal: *Griffith 5006* (GH), *Clarke 19721* (MEL). **North Burma:** Ngawchang Valley, N of Htawgaw, *Ward 173* (†A, NY); between Htawgaw and Lanyang, *Ward 311* (NY).

China. Western China, *Wilson 3007* (A). Szechwan: Mt. Omei, *Fang 2346* (A, †NY, P), *Faber 985* (NY). Kweichow: Tsunyi, *Cheng 5317* (†NY); Lo, *Cavalerie 3463* (†A), *3465* (†P), *Esquirol 3223* (†A, †P). Chekiang: south of Ping Yung, *R. C. Ching 1982* (†A, GH, †UC). Yunnan: Seyemeo Ulo, *Henry*

12919 (A, †MO, NY–2 sheets). Kwangsi: Me-kon, Seh-feng Dar Shan, S. Nanning, *R. C. Ching 8417* (A–2 sheets, GH, †UC); Shang-sze Dist., Shap Man Taai Shan, *Tsang 24761* (MO, NY).

Siam: Bangkok, *Kerr s.n.* (†BM); Kao Sem, Kouate, *Kerr 9907* (†BM); Klawry Ton, *Kerr 14586* (†BM); Kao Knap, Krat, *Kerr 17833* (†BM); *Garrett 538* (†BM). **Indochina.** Annam: Tourane, *Clemens* in 1927 (†UC); *Bordeneuri 36731* (†P); *Forest Service 48* (†P). Cambodia: *Poilane 15209* (†P). Cochin China: Chiang in Prov. Bienhoa, *Pierre 5532* (†A, NY, †P); near Baria?, *Pierre 5532* (A).

Malaya. Perak: *Wray 2922* (A). Pahang: Fraser Hill, *Anon. 11024* (†A). Penang: Government Hill, *Haniff 334* (†BISH, NY), *Curtis 3079* (A); Balik Pulau, *Hu 9422* (A); Tulo, *Glandoger* in 1906 (†MO).

Japan. Kyushu: Urumai Prov., Higashikirishima, *Wilson 6210* (A–2 sheets); no locality, *Sargent* in 1892 (A). **LiuKiu Islands:** Mt. Genka, Kunchon, *Wilson 8153* (A). **Formosa:** Shinchiku Prov. beyond Nauvaheizan, *Wilson 10319* (A); Lake Candidius, *Kanehira 21309* (A, UC). **Philippine Islands.** Luzon: Benguet, Mt. St. Tomas., For. Bur. 31479, *Esquerra* (†NY); Bontoc, Mt. Data, *Clemens 16251a* (†CAS, UC), For. Bur. 10894, *Curran* (NY), For. Bur. 14422, *Darling* (NY); Tayabas, Mt. Binuang, For. Bur. 28635, *Ramos & Edanõ* (A). Polillo: *McGregor 10779* (†NY).

South Andaman: Anderson 26, *Kerr s.n.* (†P); *Dr. King 208* (A). **Sumatra:** NW Lake Toba near Piso Piso, *Bangham 1116* (†A, NY); road from east coast to Tapanoeli, *Bangham 1128* (A, †NY); Tapanoeli, Sipirok, Panobasan, Dk. Poehoeten Lajan, *van Steenis Boschpr. bb 30986* (MO). **Mentawei Islands:** Pulau Siberoet, Sebai-bai, *Anon. Boschpr. bb 17444* (A). **Borneo:** southern part, *Korthals s.n.* (†MEL).

Java. Prov. Preanger: above Tjibodas, *Christopherson 156* (†BISH), *Koorders 1243β* (A); Pangentjongan, forest Pasir Kajoejoetan, *Koorders 26553β* (†A–3 sheets), *Koorders 1260β* (A); Tjitjalengka, *Koorders 14206β* (†A); Parakansalak, G. Poetri, Tjikramat, *Koorders 39405β* (A); Tjilaki, southeast Java, *Forbes 924* (A, †MEL); Semarang Oengaran, *Koorders 1223β* (BRI); Mt. Kaukuban, Prau, *Anderson 69* (†MEL); Tjikramat, *Warburg 2678* (†NY); G. Tiloe, Pengalengan, *Warburg 11118* (NY); Boerangrang, Goenseng Soenda, *Bakhuizen Van den Brink 4586* (UC). Without locality: *Martius s.n.* (†BR), *Blume s.n.* (NY), *Junghuhn 2* (†GH) *Zollinger 2019* (BM, †MEL), *Anon.* (†MEL–3 sheets).

New Guinea. Netherlands New Guinea: Japen, Seroei, *Boschpr. bb30698* (†A), *bb30699* (A), *bb30727* (†MO), *bb30803* (A), *bb30903* (A); Dalman, Nabire, *Kanehira & Hatusima 12266* (A). Territory of New Guinea. Sepik District: Yellow River hills near Sepik River, *Womersley NGF3937* (LAE–2 sheets), *Womersley NGF3919* (†LAE–2 sheets). Eastern Highlands District: Aiyura Range, *Womersley NGF3374* (LAE). Madang District: Kani Gebirge, *Schlechter 16740* (UC). Morobe District: Boana vicinity, *Clemens 8158* (†A); Morobe, *Womersley NGF3128* (†BRI, LAE). Papua. Western Division: Palmer River below junction of Black River, *Brass 7299* (A, †LAE); Oriomo River, Wurio, *Brass 5907* (†A, BRI, CAS, MO, NY), *5908* (†A, BRI, NY); above sawmill, *Hart NGF5019* (†LAE). Gulf District: Murua River, *Brass 1344* (A). Northern Division: foothills of Hydrographer Range near new Inoto village, *Hoogland 3845* (†LAE); foothills of Hydrographer & Owen Stanley Range, *Lane-Poole 238* (A, †BRI), *275* (A, †BRI); Ioma, Manbare River, *Allen & Martin NGF3283* (A, †BRI, LAE); Dobodura Plain, near Embi Lakes, *Cavanaugh & Fryar NGF2087*

(BRI–2 sheets, LAE–2 sheets). Central District: Kokoda Track Plantation near Sogeri, *Womersley NGF4158* (†A, LAE); Sogeri, *Smith NGF132* (†BRI); Uberi, Eilogo Mill, *1 Aust. Ore. NGF E.24* (BRI), *Anon. NGF48* (LAE); Hombron Bluff, near Pt. Moresby, *Gray & McDonald NGF7137* (†LAE). Milne Bay District: Milne Bay area, Dawa Dawa River, *Smith NGF1322* (†LAE). Goodenough Island: east slopes, *Brass 25023* (A). NEW BRITAIN: Mavalu River, *Anon. NGF2897* (†A, †LAE). **Solomon Islands.** MALAITA: Dingali, interior from Quoimonapu, *Kajewski 2370* (A, †BISH, BM, BRI). NEW GEORGIA: *Waterhouse 209* (†K).

Fiji Islands. VITI LEVU: Mba, Singatoka River, *Gillespie 3866* (DS, NY, †UC, US); hills between Nandala and Nukumuku creeks, *Smith 6167* (A, †ILL); Naitasiri, vicinity of Nandarivatu, *Gillespie 4033* (†BISH), *4281* (†BISH); Sovutawambu, *Degener 14670* (†A, MO, NY, US); woods near road part Tamavua Village, *Gillespie 2143* (†BISH); Prince's Road forest, *Parham 805* (†A); Namosi, Voma Mountain, *Gillespie 2910* (†BISH), Naitarandamu Mt., *Gillespie 3363* (†BISH). VANUA LEVU: Mathuata, Seanggangga Plateau in drainage of Korovuli River, vicinity of Natua, *Smith 6721* (A, †ILL); south slopes of Mt. Numbiuloa, east of Lambasa, *Smith 6385* (A, †ILL), *Smith 6570* (A, †ILL). VANUA MBALANU: *Bryan 575* (BISH, †ILL). TAVIUNI: Somo Somo, *Gillespie 4840* (†BISH, NY, UC). OVALAU: near summit of range west of Levuka, *Gillespie 4433* (†BISH, †UC). NGAU: hills inland from Sawaieke, *Smith 7783* (†US). Exact locality not indicated: *Anon.* U. S. South Pacific Expl. Exped. 1838–43 (†US).

Without locality: *Horsfield Herb. s.n.* (GH), *Anon.* (GH), *Kurz* (ex Herb. Sulp. Kurz) (A).

Cultivated. JAPAN: *Oldham* in 1861 (GH), Hort. Grieb., *Anon.* in 1849 (MO). CEYLON: Peradeniya Gardens, *Galston 2486* (†UC). JAVA: Hort. Bogor. *V.F.33* (GH, NY), Bot. Hard. Buitenzorg, *Sargent* in 1903 (A). ENGLAND: Kew Royal Botanic Gardens, *Cook* in 1937 (†ILL).

The preceding description of *Podocarpus neriifolius* D. Don is limited to specimens from Nepal (the type locality), Bengal, Assam and northern Burma. This species has such a wide geographical range and varies so much from the type that it can be best understood by consideration of the specimens from separate regions. *Podocarpus neriifolius* occurs on the continent of Asia in China, to the east, and in Siam, Indochina and the Malay Peninsula, to the south, and on islands from Japan in the north, southward to Sumatra and Java, and eastward through Malaysia to the Fiji Islands.

Transverse sections of leaves of specimens from Nepal show leaves thin, often to the point that some, or all three of the vascular resin canals are obscured beyond recognition. There are no true auxiliary sclereids in the mesophyll but the cell walls are frequently thickened, without pits, and in many leaves the cells are large with little cytoplasm. Sometimes the upper hypoderm, between the margin and the midrib, exists as only a few isolated fibers of medium or even small diameter.

In China, the foliage is usually large and like that of the trees in Nepal. However, *Fang 2346* and *Esquirol 3223* have smaller leaves, not over 8 cm. long and 7.5 mm. wide, but the long-angustate apex is like that of the type, thus placing them in this species. Transverse sections of the leaves show essentially similar anatomy. The upper hypoderm is more abundant and in larger groups of fibers (up to 24) and vascular fibers are rarer above the vascular bundle. *Fang 2346* shows a few hypodermal fibers between the stomatal rows and this specimen and *Cheng 5319* have rare auxiliary sclereids in the upper and lower mesophyll. The male cones are sessile and are usually in fascicles of two or three.

The terminal buds of the Siamese specimens are larger than the twig, globose, with broad triangular scales, the outer of which are shorter than the bud. The leaves are large, those of *Kerr 17833, Kerr 9907* and *Garrett 538* being over 14 cm. long with a gradually narrowing acute apex. *Kerr 17833* has the narrowest, not over 10 mm. wide. *Kerr 14586* has wide leaves which narrow abruptly to a caudate acuminate apex. In all of them, the upper midrib is quite broadly prominent and the leaves are thicker as shown in the transverse sections by the often doubled palisade parenchyma. The upper hypodermal fibers are in small groups, sometimes up to 55 μ in diameter, and are not interrupted at the midrib. In *Kerr 14586* the hypodermal fibers interrupt the palisade which is then replaced by large cells with little cytoplasm. Auxiliary sclereids are found in the lower mesophyll.

Podocarpus neriifolius also occurs in Indochina and Cambodia. The *Clemens* specimen is said to represent "scattered trees along the river," and has leaves only 10 mm. wide. The leaves of all specimens are scattered and have the long-tapering acute apex typical of the species. Transverse sections of the leaves do not always show vascular fibers and only the *Clemens* specimen and one of *Pierre 5532* have auxiliary sclereids below the accessory transfusion tissue. *Pierre 5532* needs special comment, for two taxa are included under this number and the labels record two different collection sites, both questioned on the specimens. There are a number of sheets bearing this number in the herbaria of the Arnold Arboretum, the New York Botanical Garden and the Paris Museum, and, of these, only the specimens with large, scattered leaves having a long-tapering apex are *P. neriifolius*. The others are *P. annamiensis*, a new taxon in which the leaves are straighter, stiffer, somewhat more crowded, much smaller with more abruptly acute apices and the transverse leaf sections show two very large lateral vascular resin canals instead of three of almost uniform size.

Of the specimens from Malaya, *Anon. 11024* has very wide leaves with the apex abruptly narrowing to a caudate-acuminate tip and long acuminate-attenuate terminal bud scales. The upper hypodermal fibers are solitary or in very small groups and are rarely interrupted at the midrib. In *Anon. 11024* the palisade mesophyll is undeveloped but cells with dense cytoplasm lie between the upper hypodermal fibers. Leaves of the *Glandoger* specimen usually show two additional lateral vascular resin canals which are associated with the transfusion tissue and the upper hypodermal fibers are scant.

Kanehira 21309 from Formosa is not *Podocarpus nakaii*. It most closely resembles the specimens of *P. neriifolius* from the Fiji Islands.

On Luzon, in the Philippines, the leaves have very abundant upper hypodermal fibers with few or short interruptions in *Clemens 16251a* and *For. Bur. 31479*, but on Polillo, *McGregor 10779*, they are rare and in small groups of 1–4 fibers. There are rare lower hypodermal fibers between the stomatal rows in *For. Bur. 31479*. In leaves of *Clemens 16251a* the palisade is often a double layer, rare in this species.

West of the Malay Peninsula, *Podocarpus neriifolius* has been collected from South Andaman Island. The leaves are thin and wide with a caudate-acuminate apex. Transverse sections of the leaves of *Kerr s.n.* show upper hypodermal fibers in small groups, also interrupted at the midrib, and a palisade of short dense cells between the fibers.

Transverse sections of leaves of plants of this species from Sumatra usually have solitary scattered upper hypodermal fibers and the hypodermal layer is interrupted at the midrib. Leaves of *Bangham 1128* show a few auxiliary sclereids below the accessory transfusion tissue. The leaves of this specimen also have abruptly caudate-acuminate apices.

Most of the Javan specimens are like those from Nepal. Some have an abruptly acuminate or caudate apex to the leaf, especially if the foliage is quite large. The *Martius* specimen has leaves with the two lateral vascular resin canals larger than the central one. Two specimens, *Reinwardt s.n.* and *Anderson 69*, have five vascular resin canals, the two extra lateral ones being very near or in the transfusion tissue. Transverse sections of the leaves show the interrupted hypoderm with fibers averaging a little larger than those of the type, often scattered or even isolated; there are lower hypodermal fibers between the stomatal rows only in the *Reinwardt* specimen; auxiliary sclereids only in *Koorders 26553β*.

Only one of the specimens which I have seen from Borneo, *Korthals s.n.*, has the narrowly prominent midrib on the upper side of the leaf which is characteristic of *Podocarpus neriifolius*. This specimen has also terminal bud scales with long-acuminate or even foliaceous tips, to 1 cm. long. Blume cited this as one of the specimens in his *P. leptostachyus*, which has been placed in the synonymy of *P. neriifolius* by Pilger (1903). The Melbourne herbarium specimen, which I examined, has a solitary, expanded but very narrow male cone.

This species is a fairly common tree in New Guinea and seems to reach higher altitudes there than in other areas. Characteristics which were found most useful in delineating the species were the slender branches, the leaves with margins not parallel and with long-tapering acute or acuminate apices, a sharply prominent upper midrib, transverse sections showing three vascular resin canals, interrupted upper hypodermal fibers between the stomatal rows, and the lack of auxiliary sclereids in the mesophyll. The terminal bud varied from ovate to globose and the length of the bud scales did not seem to be critical. Male cone buds are small and usually in sessile clusters of one to three.

Other species of this group in New Guinea are *P. thevetiifolius*, *P. rumphii*, *P. ledermannii*, *P. archboldii* and *P. idenburgensis*. Reference to the key will indicate the essential differences.

The leaves of the specimens of *Podocarpus neriifolius* from the Solomon Islands are thin, broad and have a very acute or caudate-acuminate apex and the seeds are large, up to 14 mm. long. Transverse sections of the leaves show upper hypoderm and palisade as in the Borneo specimen.

Some of the specimens from the Fiji Islands cannot be clearly differentiated from the type of *Podocarpus neriifolius* in Nepal and thus are included in this species. With this inclusion the geographical range for *P. neriifolius* is greater than that of any other species. *Podocarpus oleifolius* in South and Central America extends for an almost equal distance north and south of the equator but there is little range of longitude. Here, in the Fiji Islands, *P. neriifolius* is a tree found in either open or dense forests at altitudes usually of less than 500 m. The leaves are quite thick and coriaceous, sometimes only 4 cm. long and 4 mm. wide on reproductive branches, and the margins tend to be revolute. The broad lower midrib may have an open groove, and transverse sections always show auxiliary sclereids. The pollen cones are usually clustered and sessile. Many of these specimens have been marked as *P. elatus*, a species which differs distinctly in having abruptly acute or obtuse, often mucronate tips to the leaves and continuous upper hypoderm is seen in transverse sections. One specimen, *Gillespie 2143*, has the immature seed elongate with a conspicuous crest and an elongated beak at the micropyle.

27a. **Podocarpus neriifolius** var. **atjehensis** Wasscher in Blumea 3: 450. 1941.

A small tree, 15 m. tall, with stout branches. Terminal buds large, the outer scales long-acuminate, to 10 mm. long, tips spreading. Leaves crowded, deflexed or drooping, linear-lanceolate, 7–18 cm. long, 5–8.5 mm. wide, very gradually narrowed to an acute, sometimes mucronate, apex, gradually narrowing to a short petiole at the base; midrib narrowly prominent above, sometimes limited by shallow grooves on either side, broadly prominent below. Transverse sections of the leaves show three vascular resin canals with the lateral sometimes larger and the median obscured, interrupted upper hypoderm of isolated fibers 23–37 μ in diameter, the layers interrupted at the midrib both above and below, rare vascular fibers only above the bundle, cuticle thick. Male cones solitary, axillary, sessile; scales acute-acuminate, up to 5 mm. long; mature cones 2–3 cm. long, 4–4.5 mm. thick. Female cones solitary in the leaf axils, crowded in the lower part of new growth; peduncles slender, 8–16 mm. long; receptacle narrowly fleshy, 7–9 mm. long, subtended by long bracts, up to 6 mm. Seed sub-elliptical, 9–10 mm. long, 7–8 mm. broad, apex obtuse.

DISTRIBUTION: In Atjeh in Sumatra, at elevations of 2250–3300 m.

Sumatra: Atjeh, Gajolanden, G. Kemiri, *Van Steenis 9614* (†A).

The above description was prepared from the type specimen, the only example seen.

27b. Podocarpus neriifolius var. degeneri, var. nov.

Frutex vel arbor parva; ramulis sparsis, subverticillatis; gemnis terminalibus magnis, ovoideis, squamis exterioribus attenuatis, e basi lato crescentibus. A specie differt foliis parvis maturis, plerumque minusquam 10 mm. latis.

Shrub or small tree; branches few, subverticillate; terminal vegetative buds large, ovoid, the bud scales with apices acuminate to long-attenuate or abruptly narrowed to a long apiculus. Leaves patent to spreading, thin-coriaceous, 6–12 cm. long, 6–10 mm. wide, linear-angustate, shiny above, dull-rusty beneath, the apices narrowly acute, the bases narrowed into short petioles; leaves on young shoots to 18 cm. long, 17 mm. wide. Transverse leaf sections show 3 vascular resin canals, hypodermal fibers of somewhat smaller diameter than those of the species, vascular fibers rarely present and auxiliary sclereids lacking in the mesophyll. Pollen cones axillary on growth of the previous year, sessile, cylindrical, up to 3 cm. long, 3–3.5 mm. in diameter, surrounded at the base by numerous thin, carinate, broadly ovate scales which are sometimes apiculate; microsporophylls with small, narrow, up-turned apiculi. Female cones axillary, solitary, on slender peduncles 7–12 mm. long, the receptacle of several fused scales, 8 mm. long, with small, spreading free tips, subtended by a pair of slender, thin, attenuate bracts up to 5 mm. long, and bearing 1–2 ovules. Seeds 9–12 mm. long, elongate, 5 mm. wide, bluntly crested; immature seeds narrowed at the base.

DISTRIBUTION: along streams in forests, 40–800 m. altitude, on Viti Levu in the Fiji Islands.

Fiji Islands. VITI LEVU: Mba, Nandarivatu, *Degener 14272* (TYPE, †A, MO, NY, US); Unidawa Road near Nandala River, *Gillespie 4137* (†BISH, †DS, NY, UC); hills between Nggaliwana and Nandala creeks, south of Nauwange, *A. C. Smith 5665* (A, †ILL), *5666* (A, †ILL); 3 miles south in valley of Nandala Creek, *A. C. Smith 6254* (A, †ILL); *Gillespie 4129* (†BISH); Singatoka River, *Gillespie 4282* (†BISH, US); forest at headwaters of stream which runs to Navua, *Gillespie 4250* (†BISH, NY, UC); Lautoka Mts., *Greenwood 50A* (†A, BRI, NY), *45A* (A, BRI); Namosi, above Waikava, *Parham 1701* (†A); Nandina River, *Gillespie 2531* (†BISH, UC); Waikava, *Parham 2154* (†A); Serua, banks of Navua River, *Gillespie 3382* (†BISH, UC). Locality not indicated: *Seeman 575* (†GH). *Horne 792* (†GH). **Cultivated.** VITI LEVU: Exp. Sta. 17 m. east of Suva, *Buchholz s.n.* (†ILL).

27c. Podocarpus neriifolius var. polyanthus Wasscher, Blumea 4: 455. 1941.

Tree to 40 m. tall, slightly fluted toward base. Terminal buds large, conical; outer scales acuminate or only acute, erect, stout, often shorter than the bud. Leaves spreading, more or less coriaceous, straight or somewhat falcate, lanceolate, gradually narrowing to a short petiole, abruptly or more gradually narrowing to the acute apex, 6–16 cm. long, 13–20 mm. broad (only 6–9 cm. long, 7–8.5 mm. broad in New Guinea); midrib narrowly prominent, broader and sometimes furrowed below. Male cones unknown. Female cones numerous, all over the new growth, in the axils of bracts as well as in those of the leaves and above the leaf scars; the few bracts sessile with a broad base, acute, to 1.5 cm. long, 2.5 mm. broad; peduncles thick, 1.5–5 mm. long; receptacle subtended by 2 subulate bracts to 3 mm. long, composed of 2–4 fused fleshy scales, only 1–2 fertile, short and thick cylindrical, 6–7 mm. long, 4–5 mm. broad. Seeds elliptical-ovate, 10 mm. long, 6 mm. in diameter.

DISTRIBUTION: In Sumatra (fide Wasscher) and New Guinea in rain forests, alt. 100–600 m.

New Guinea. PAPUA: Milne Bay District, *Smith NGF1322* (†BRI).

The specimen cited above has abundant very young ovules on the new growth at the twig tips. Dormant buds are connate to globose with short triangular obtuse scales. The leaves are small for *Podocarpus neriifolius* but they have the general shape of the species. Transverse leaf sections show the anatomy typical of *P. neriifolius* with interrupted upper hypoderm of small fibers and no hypodermal fibers between the stomatal rows of the lower side. One of the sectioned leaves shows a loosely organized palisade layer on the lower side of the leaf. This has not been found in any other specimen in Section *Podocarpus*.

27d. **Podocarpus neriifolius** var. **teysmannii** Wasscher, Blumea 4: 453. 1941.

Podocarpus Teysmannii Miquel, Fl. Nederl. Indië 2: 1072. 1859; Parlatore, DC. Prodr. **16**: 516. 1868; Gordon, Pinetum ed. 2. 348. 1875; Pilger, Pflanzenreich IV. **5**(Heft 18): 81. 1903; Dallimore & Jackson, Handb. Conif. 56. 1923, 1931; Florin, Svenska Vet.-Akad. Handl. III. **10**: 280. 1931.

A small tree with stout twigs. Terminal buds globose, flattened, with short, outer scales 2–3 mm. long, these closely appressed, rigid, broadly triangular, with obtuse-acute apex. Leaves scattered, spreading, broadly lanceolate, 8.5–17 cm. long, 16–26 mm. wide, abruptly narrowing to a short, thick petiole at the base, also abruptly narrowing to the caudate-acuminate apex; midrib very broadly prominent above, ridged, flat, prominent or even channelled below. Male cone buds solitary in the leaf axils, globose, large, 3 mm. in diameter; mature cones unknown. Female cones and seeds unknown.

DISTRIBUTION: At sea level or low altitudes on Sumatra and nearby islands.

Sumatra: *Teysmann 513* (†ex Florin, Berlin Herbarium); sea coast, *Teysmann s.n.* (MEL), *Teysmann s.n.* (†MEL); Tapanoeli, Angkola en Sipirok, Panobasan, Dk. Poehoetan Lajan, *Boschpr. bb30986* (MO). **Bangka:** kajoe sembliang, *Teysmann s.n.* (†MEL). **Karimata:** *Teysmann s.n.* (†MEL–2 sheets).

According to Wasscher (11), who combined this taxon with *Podocarpus* *neriifolius*, var. *teysmannii* differs from the species chiefly in the globose terminal buds, the broadly lanceolate leaves with shortly acuminate apex, and the large male cone buds.

Transverse sections of the leaves show anatomy in agreement with the species except for very rare auxiliary sclereids in the mesophyll between the accessory transfusion tissue and palisade layer. Orr's description (9) of the leaf anatomy of *Podocarpus teysmannii* must be referred to *P. philippinensis*, since the specimen he used (*Orolfo 3919* from the Selangen Islands) is here identified as the latter species.

Large, broad leaves with a caudate-acuminate apex are also found in Siam, the Malay Peninsula, the Andaman Islands, the Solomon Islands, etc. Such specimens may belong in this variety, but at present are placed in *Podocarpus neriifolius* because the terminal bud is either ovate or cannot be observed.

Wasscher (11) listed four varieties of *Podocarpus neriifolius* which must be recognized, although I have seen no specimens of any of these. They could not be included in the key to the species and varieties in this paper, therefore, but for completeness I quote the critical characters given by Wasscher and indicate the geographical location of each variety. *Podocarpus neriifolius* var. *bracteata* Wasscher, from Java, "differs . . . in the large, ovate-acute, male flower buds, with squarrose, ovate-triangular, acute bud scales." *Podocarpus neriifolius* var. *linearis* Wasscher, cited from four collections from Java, "differs . . . in the narrower leaves with margins parallel, the obtuse terminal buds and the large, ovate, male flower buds." *Podocarpus neriifolius* var. *membranacea* Wasscher, described from two collections from Celebes, "differs . . . in the membranaceous scales of the terminal buds and the ovate-acute male flower buds." *Podocarpus neriifolius* var. *timorensis* Wasscher, described from a single collection from Timor, "differs . . . in the indistinct, not or hardly prominent midrib, and the leaves shorter-narrowed toward the apex and often with a mucro, whereas the male flowers are thicker."

28. **Podocarpus polystachyus** R. Brown ex Mirb. Mém. Mus. **13**: 75. 1825 (nomen!), ex Bennet in Horsf. Pl. Jav. Rar. 40. 1838 (nomen!); Endlicher, Syn. Conif. 215. 1847; Gordon, Pinetum ed. **2**: 345. 1865; Carrière, Traité Conif. ed. 2, 662. 1867; Parlatore, DC. Prodr. **16**: 515. 1868; Bertrand, Ann. Sci. Nat. V. **20**: 59. 1874; Warburg, Monsunia **1**: 192. 1900; Pilger, Pflanzenreich IV. 5(Heft 18): 79. 1903, Nat. Pflanzenfam. ed. 2. **13**: 247. 1926; Merrill, Philip. Jour. Sci. **3**: 394. 1908; Foxworthy, Philip. Jour. Sci. **6**: 161. 1911; Stiles, Ann. Bot. **26**: 455. 1912; Dallimore & Jackson, Handb. Conif. 54. 1923, 1931, 79. 1948; Florin, Svenska Vet.-Akad. Handl. III. **10**: 280. 1931; Wasscher, Blumea **4**: 456. 1941.

Podocarpus littoralis Teysmann, Nat. Tijdschr. Ned. Ind. **36**: 237. 1876.

P. littoralis Hort. ex Biswas, Jour. & Proc. Asiatic Soc. Bengal [Calcutta] II. **28**: 374. 1933.

P. neriifolius D. Don in Lamb. Pinus ed. 2. **2**: 122. 1828.

A small tree up to 20 m. tall with a trunk up to 45 cm. in diameter and numerous subverticillate spreading twigs. Terminal buds ovate with keeled, narrow, acuminate, stiff scales sometimes becoming 10 mm. long. Leaves scattered, usually crowded toward the tips of the branches, coriaceous, shiny above, usually lanceolate to linear-lanceolate, flat, 4–8 cm. long, 6–10 mm. wide (rarely somewhat wider), abruptly narrowed to the mostly obtuse apex, sometimes mucronate, gradually narrowing at the base to a short petiole; midrib prominent above, broader and sometimes shallowly channelled below. Cross sections of the leaves show 3 vascular resin canals, interrupted upper hypoderm of very large fibers up to 70 μ in diameter, lower hypoderm absent between stomatal rows, vascular sclereids usually present above or below the bundle (mostly absent in Philippine specimens. Pollen cones fascicled 3–5 in leaf axils, sessile, cylindrical, 2–4.5 cm. long, 2.5–3 mm. in diameter, surrounded at the base by small, broad, spreading scales. Microsporophylls broadly ovate-triangular, acute to somewhat obtuse. Female cones axillary, solitary on peduncles 3–6 mm. long; receptacle of two fused fleshy scales, one somewhat shorter than the other, subtended by 2 subulate, early deciduous bracts. Seed globose or elliptical, about 10 cm. long.

DISTRIBUTION: Low elevations, often coasts, of islands south and east of the South China Sea, and the Malay Peninsula.

Philippine Islands. LUZON: Ilocos Norte, Burgos, Bur. Sci. 27146 *Ramos* (†A); Tayabas, Bur. Sci. *27325 Quieb* (†A, NY), Bur. Sci. 26902 *Edano* (BRI); For. Bur. 24264 *Cagayan* (A). PALAWAN: For. Bur. 3854 Curran (†NY), For. Bur. 904 *Foxworthy* (NY). NEGROS: western part, *Masias, Sareno & Torrible* in 1925 (†UC). Mindanao: Davao, Pendesan, *Kanehira 2623* (NY).

Malaya. PAHANG: *Henderson 18420* (†UC); Kioala, *Ridley 1441* (†BM). PULAU TIOMAN: Telok Paya, *Anon. s.n.* (†UC). SINGAPORE: Barnes' Island, *G. L. Smith s.n.* (TYPE, †BM); Forest de Kranjo, *Langlasse 72* (†P); *Wallich 6052B* (MO, †P); Mangrove swamp at New John's Street, *Sargent* in 1903 (A–2 sheets); Serangoon, *Ridley 3367* (†MEL); *Hooker & Thomson s.n.* (GH).

Borneo. *Teysmann s.n.* (†MEL). BRITISH NORTH BORNEO: Kuala Penyu, For. Dept. 1798, *Apostal 35* (†UC); Jesselton, *Clemens 51171* (†UC), *9659* (A, BRI, GH, †UC–2 sheets), *9568* (A); *Native collector 2353* (A); *Foxworthy s.n.* (†US).

Bangka: *Teysmann s.n.* (†MEL–2 sheets).

Cultivated. MALAY PENINSULA: Singapore, Bot. Gard., *Furtado* in 1931 (†BRI). JAVA: Buitenzorg Bot. Gard., *Warburg 1210* (†NY), V.F. 1, from Lingga, *Sargent* in 1903 (NY, †UC–3 sheets), *Anon. s.n.* (†DS), V.F. 17a, from Lingga, *Sargent* in 1917 (NY, UC), *Sargent* in 1903 (A–2 sheets, †MO–3 sheets); Bohn's Garden at Buitenzorg, *Sargent* in 1903 (A–2 sheets). AFRICA: Kisantu, Jardin Agronomique, *Vanderyst 31936* (†BR), *Vanderyst 31949* (†BR), *Vanderyst 36983* (†BR); Belgian Congo, Eala, *Corbisier-Baland 1136* (†BR, K, MO, †NY), *Corbisier-Baland 1353* (†BR, K, MO).

Podocarpus polystachyus is quite distinct in having often isolated, extremely large upper hypodermal fibers seen in transverse leaf sections. This character, together with the linear-lanceolate, rigid leaves and the male cones in bundles of 3–5, make possible the positive identification of the *Corbisier-Baland* and *Vanderyst* specimens from cultivation in Africa. Determination of the former had been questioned and of the latter unknown.

Transverse sections of the leaves do not show auxiliary sclereids in upper or lower mesophyll. However, some cells of the lower mesophyll have thickened and pitted walls but are not devoid of cell contents (except *Henderson 18420*).

The description of *Podocarpus polystachyus* by Wasscher (11) was the first to include specimens from the Philippine Islands. Foxworthy (5) took his description from that of Pilger (1903) which was, in turn, from specimens from the Malay Peninsula and Borneo only. Why Foxworthy was not certain that this species was distinct from *P. elatus* R. Br. is not clear except that the leaves of both are often mucronate. The leaves of *P. elatus* are larger, have parallel margins and the upper hypoderm of much smaller fibers is continuous.

28a. **Podocarpus polystachyus** var. **rigidus** Wasscher, Blumea **4**: 460. 1941.

Leaves thick-coriaceous, very rigid, more lanceolate and broader with margins not parallel, 3–7.5 cm. long, 8–14 mm. broad; midrib strongly prominent above, often distinctly, broadly and shallowly channelled beneath.

DISTRIBUTION: Riouw Archipelago and Borneo, on mountain slopes and summits.

Borneo: western part, G. Kelam, *Hallier 2373* (†NY).

Wasscher (11) described this variety as differing from the species in its leaf shape, the species having narrower, linear-lanceolate leaves. I do not find this difference so striking; many specimens having some leaves of the described shape must be assigned to the species, the leaves of which may be up to 13 mm. broad. However, in an examination of the transverse section of a leaf fragment from *Hallier 2373*, I find abundant large sclereids in the upper mesophyll which are entirely absent in the species. Some of the lower mesophyll cells show the same thickening of the walls as observed in the species proper. The shallow channel of the lower midrib of this specimen is so constricted as to eliminate the central vascular resin canal.

That *Podocarpus polystachyus* var. *rigidus* is found on mountain slopes and summits is more striking than the small differences in leaf anatomy. The habitat of the species is limited to the low elevations of sea coasts and estuaries.

29. **Podocarpus macrophyllus** (Thunb.) Don in Lamb. Pinetum ed. 1. **2**: 22. 1824, ed. 2. **2**: 123. 1828; Endlicher, Syn. Conif. 216. 1847; Blume, Rumphia 3: 215. 1847; Carrière, Traité Conif. 664. 1867; Parlatore, DC. Prodr. **16**: 517. 1868; Sieb. & Zucc. in Miquel, Fl.

Japon. 2: 70. 1870; Bertrand, Ann. Sci. Nat. V. 20: 59. 1874; Mahlert, Bot. Centralbl. 24: 281. 1885; Van Tieghem, Bull. Soc. Bot. France 38: 169. 1891; Shirasawa, Essenc. Forest. Japon. 1: 31. 1899; Warburg, Monsunia 1: 192. 1900; Kent, Vietch's Man. Conif. 150. 1900; Pilger, Pflanzenreich IV. 5(Heft 18): 79. 1903, Nat. Pflanzenfam. ed. 2. 13. 1926; Bailey, Cult. Evergreens 179. 1923; Dallimore & Jackson, Handb. Conif. 49. 1923, 1931, 73. 1948; Florin, Svenska Vet.-Akad. Handl. III. 10: 279. 1931; Metcalf, Fl. Fukien 1: 20. 1942.

P. chinensis Blume, Rumphia 3: 216. 1947 non Wall.; Mahlert, Bot. Centralbl. 24: 281. 1885; Florin, Svenska Vet.-Akad. Handl. III. 10: 279. 1931.
Podocarpus chinensis Wallich ex Parlatore, DC. Prodr. 16: 516. 1868.
Taxus macrophylla Thunberg, Fl. Japon. 176. 1784.

A tree 8–15 m. tall, with horizontal branches and numerous, crowded, leafy twigs. Terminal buds ovate, small, the scales ovate with acuminate tips. Leaves crowded, straight, green above, paler beneath, linear-lanceolate, apex long-angustate, acute or obtuse, gradually narrowing at the base to a short petiole, 5.3–10.3 cm. (usually 8–10) long, 6–10 mm. (usually 9–10) broad; midrib prominent above and rather broad, fairly prominent and broader below. Transverse sections of the leaves show 3 resin canals below the vascular bundle, interrupted upper hypoderm of very small fibers (16–20 μ in diameter), no lower hypodermal fibers between the stomatal rows, palisade of 2–3 layers of cells, vascular fibers often present below the vascular bundle and auxiliary sclereids usually absent from the mesophyll. Pollen cones fascicled 3–5, sessile, very narrow-cylindric, up to 3 cm. long, surrounded at the base by broad triangular, stiffly coriaceous scales. Microsporophylls obtuse with distinct apiculus. Female cones solitary, peduncles 16–17 mm. long; receptacle of 2–3 fused fleshy scales with free tips, subtended by 2 small, narrow, subulate scales 3–4 mm. long. Seeds ovoid, 10–12 mm. long.

China. KIANGSU: Soochow, Dang Wei, *Ching & Tso 785* (A); Kunshan, *Mrs. Tsiang Ying 1* (NY). SZECHWAN: *Fang 1963* (A). CHEKIANG: 20–40 miles west of Wenchow, *Ching 1892* (†UC); Wenchow, *Ling Kan*, Univ. Nanking 7308 (†UC); Yen Tang Shan, *Chiao*, Univ. Nanking 4737 (A, NY, †UC); Nan-Hoo, *H. H. Hu 191* (GH); King Yuan, *Ching 2439* (NY, †UC). CHUSAN: *Home s.n.* (MO). ANWEI: Chemen, *Chung 3124* (A). KIANGSI: south of Nanchong, Sang-su-ling, *Chung 2* (A); Lu Shan, *Chiao 18760* (A). FUKIEN: Amoy, Kulangsu, *Chung 5775* (A); Puchen, *Chung 3865* (A). KWANGTUNG: Koo Long Ue, *McClure B-2* (NY); Canton, *Chun 7731* (NY). YUNNAN: between Muang Hai and Keng Hung, *Rock 2495* (A), *Bonati 1802* (†UC). KWEICHOW: Tsunyi, *Tsiang* 5317 (A, NY).

Japan. HONSHU: Mt. Maya, Settsu, *Arimoto* in 1903 (†MO); Idsu (ex Herb. Sokurai), *Wilson* in 1910 (A). KYUSHU: Tairashima, Kawanabe Island, *Ushio* in 1917 (†A); Nagasaki, *Anon.* (ex Herb. Th. Porter) (PH), *Maximowicz* in 1863 (GH, †NY–2 sheets). LOO CHOO ISLANDS, *Wright 310* (GH, NY).

Cultivated. CHINA: Kwangtung, Tak-Hing, Heung Shan, C.C.C. 13193, *McClure* (†UC). JAPAN: Hondo, *Wilson* in 1911 (ex Herb. Sakurai) (A); Mino

Prov., *Shioto 8743* (A), *Ugai Kichigoro 4440* (A). PHILIPPINE ISLANDS: Luzon, Manila, *Fenix 161* (A). NEPAL: *Netla Thuret 1889* (A). SINGAPORE: *G.T.* (ex Herb. Hook. & Thomson) (GH). SWITZERLAND: Locarno, Bot. Gard., *Baenitz* in 1905 (ILL). ENGLAND: Kew, Royal Bot. Gard., *Cook* in 1937 (ILL). UNITED STATES: New York Bot. Gard. 3750, from C.P. 1900, *Hartling* in 1919 (ILL); California, Goleta, *Anon. s.n.* (†ILL). WEST INDIES: Jamaica, Chinchona Gardens, *Buchholz* in 1946 (ILL); Trinidad, Roy. Bot. Gard., *Ewan 17014* (†MO); Tobago, Castleton Gardens, *Harris 45, 50, Broadway 2934* (K).

Transverse sections of the leaves of *Podocarpus macrophyllus* and its varieties are ordinarily quite easily recognized by the thick, usually doubled, layer of palisade mesophyll and the interrupted upper hypoderm of small fibers. This is very useful as the species is highly successful in cultivation and the original source of the material has frequently long been forgotten. Often it seems to be misidentified as *P. elongatus*, an African species, which has distinct marginal resin canals.

Stiles (10) selected the leaf of *Podocarpus macrophyllus* for his description of the anatomy most typical of *Podocarpus.* That the plant he used was probably the variety *maki* does not invalidate the description, for the leaves have the same anatomy and are merely shorter and narrower. He indicated that he observed "slight" differences in the quantity of transfusion tissue, accessory transfusion tissue and sclerenchyma in *P. elatus* and *P. polystachyus*, but attributed these differences to external conditions. I find, however, on examination of a larger number of specimens, that continuous upper hypoderm is a consistent character of *P. elatus,* and the hypodermal fibers are much larger in diameter in *P. polystachyus.* Orr (9) found that the above characters provided distinguishing differences for these species.

29a. **Podocarpus macrophyllus** var. **angustifolius** Blume, Rumphia 3: 215. 1847; Pilger, Pflanzenreich IV. 5(Heft 18): 80. 1903.

This variety differs from the species in having narrower leaves which are quite variable in length, being both shorter and longer on a single plant than the extremes for the species. The linear-lanceolate leaves have also a more tapering apex.

DISTRIBUTION: A few specimens from both China and Japan but best known from cultivation in the United States.

China. KWANGTUNG: *Canton Christian College Herb. 13193* (†UC); Canton, *Read* (PH). KIANGSU: Tungtin, Soochow, Tai Hu Lake, *Ching & Tso 730* (A). **North Burma:** Nmai Hka Valley, *Ward 521* (A). **Japan.** HONSHU: Yamato River in Nara Park, *Wilson 7855* (A); Kanagawa-Ken, between Kamakura & Zushi, *Beattie & Kwihara 10449* (A). HACHIJO ISLANDS: Wilson *8391* (A). Locality not indicated: *Anon.* (ex Herb. Lugd. Batav.) (†BR–2 sheets, NY).

Cultivated. JAPAN: LiuKiu Islands, Yokohama Nursery, *Wilson s.n.* (A). JAVA: *Zollinger s.n.* (†BR). AUSTRALIA: Brisbane Bot. Gard., *White 9283* (A). EUROPE: Germany, Hannover Bot. Garden #6, *Zabel* in 1892 (A). WEST INDIES: Tobago Bot. Station, *Broadway 2934* (F, †MO–2 sheets, NY); Trinidad, Port of Spain, *Broadway* in 1933 (A); Trinidad, St. Augustine, *Baker 14554* (TRIN); Martinique, Basse Pointe, *Duss 2096* (†NY). CUBA: Prov. Santa Clara, Harvard Trop. Gard., *Jack 8353* (A, NY, US). UNITED STATES. California: Los Angeles, *Buchholz* in 1940 (A, †ILL–3 sheets), *Buchholz* in 1942 (†ILL), *van Rensselaer 1713* (ILL), *Brown* in 1938 (CAS), *Rollins & Chambers* in 1938 (GH), *Turner* in 1926 (CAS); San Francisco, Golden Gate Park Arboretum, *Buchholz* in 1942 (†ILL), *Walther* in 1942 (A); Santa Barbara, Orpets Nursery, *van Rensselaer 1718* (†ILL). Texas: Houston, *Fisher 44301* (F). New Jersey: New Brunswick, Rutgers Greenhouse 1B, *Johnston* in 1952 (†RUT), from CU1, Atkins Garden, Cuba, *Johnston* in 1952 (†RUT). New York: Botanical Garden Greenhouse #3635 from D.P.M. 1900, *Nash* in 1905, #3750 from D.P.M. 1900, *Taylor* in 1906, #15022 from Edinb. 1902, *Taylor* in 1905 (NY).

Podocarpus macrophyllus var. *angustifolius* is widely cultivated in southwestern and southern United States where it is used mostly in trimmed hedges, sometimes as a shrub or small tree. It is also extensively used as a green foliage in floral arrangements. It frequently passes under the names *P. chinensis* or *P. sinensis*, and is commonly called the "Southern Yew."

29b. **Podocarpus macrophyllus** var. **chingii**, var. nov.

Arbor columnaris, 8 m. alta, ramulis adscendentibus; foliis crassis rigidis, oblanceolatis, 1.2–3 cm. longis, 3–4 mm. latis, valde gradatim attenuatis in petiolo brevissimo, apicibus plerumque obtusis, marginibus interdum revolutis; strobilis masculis alabastris globosis, 1.5 mm. diametro, 1–3-fasciculatis, squamis tenuibus, late triangularibus, obtusis, imbricatis, strobilis maturis tenuibus, ad 2.5 cm. longis; strobilis femineis ignotis.

Tree with trunk up to 10 cm. in diameter; bark fibrous and brown; young twigs green. Terminal buds very small, conical; outer scales only up to 3 mm. long, carinate, somewhat tapered to the thick apex, the tips occasionally spreading. Leaves small, densely crowded, erect, linear-oblong to narrowly spatulate, the apex acute to rounded, the midrib very sharply prominent above, broader and flat below.

DISTRIBUTION: Known from only the type locality, in Chekiang, China.

China. CHEKIANG: 55 Chinese miles (li) west of Lung-sien, alt. 100 m., *Ching 2477* (TYPE, †A).

The striking columnar habit and the very small leaves distinguish this variety. It most closely resembles *Podocarpus macrophyllus* var. *maki*, the foliage being a miniature of that variety. The foliage does not differ greatly from that of *P. brevifolius* which has the leaves mostly larger and tapering more quickly toward the base. The latter species, however, is a tree with stout, spreading branches and solitary male cones.

29c. **Podocarpus macrophyllus** var. **maki** Endlicher, Syn. Conif. 216. 1847; Sieb. et Zucc. in Miquel, Fl. Japon. 2: 70. 1870; Dallimore & Jackson, Handb. Conif. 49. 1923, 1931, 74. 1948.

Podocarpus macrophyllus ssp. *maki* Sieb. Naamlijst 35. 1844; Pilger, Pflanzenreich IV. **5** (Heft 18): 80. 1903, Nat. Pflanzenfam. ed. 2. **13**: 248. 1926; Wasscher, Blumea **4**: 461. 1941.

Podocarpus chinensis Wall. in Endl. Syn. Conif. 215. 1847; Blume, Rumphia **3**: 216. 1847; Bertrand, Ann. Sci. Nat. V. **20**: 59. 1847; List N.6051 ex Carrière, Traité Conif. ed. 2. 658. 1867; Parlatore, DC. Prodr. **16**: 516. 1868; Warburg, Monsunia **1**: 192. 1900.

Podocarpus japonica Sieb. Ann. Soc. Hort. Pays-Bas 35. 1844.

Podocarpus makoyi Blume, Rumphia **3**: 215. 1847.

Podocarpus miquelia Hort. ex Parlatore, DC. Prodr. **16**: 516. 1868.

Podocarpus sinensis (?) Favre in Ann. Sci. Nat. V. **3**: 379. 1865.

Podocarpus vrieseana Hort. ex Parlatore, DC. Prodr. **16**: 516. 1868.

Small tree or shrub with erect branches and thickly leafy twigs. Leaves straight, erect to spreading, linear-lanceolate, obtuse or shortly angustate at the tip, gradually narrowing to the short petiole, 3.5–7 cm. long, 4.5–7 mm. wide; midrib narrowly prominent above. Male cones sessile, in clusters of 3–5 in upper leaf axils, strobili narrowly cylindrical, nearly filiform, 3–4.5 cm. long, 2–3 mm. in diameter; microsporophylls triangular, acute, apiculate. Female cones solitary in leaf axils on peduncles 5–11 mm. long; the fleshy receptacles of 2–3 fused scales subtended by 2 small subulate bracts. Seeds elliptical, 8–10 mm. long, 6–7 mm. in diameter.

DISTRIBUTION: A few specimens of this variety from China, North Burma, Japan and Formosa seem to have come from wild habitats. It is best known from its successful wide cultivation not only in Japan, its probable source, but throughout the world in the milder climates.

China. CHEKIANG: southern part, between Ping Yung and Tai Suan, *Ching 2168* (A, NY, †UC); Tsing-Yun Dist., Peach Mountain, *Keng 438* (A); Chusan & Ningpo, *Capt. Home* in 1892 (BM), *Ching 2439* (†UC). KWANTUNG: Wat Shui Shan, *Chun 7343* (A), *Wang & Ling 7343* (†UC); Su-liu-kwan, Lofou Shan, *Tsiang 1750* (A), Heunghsan, *Chun 97* (NY); Canton, *Anon.* in 1889 (†MO). Locality unknown: ex Herb. Prager, *Anon. s.n.* (†CAS), *Bonati & Lure 1802* (†UC), ex Univ. Nanking, *Chiao* in 1925 (†UC). **North Burma:** 'Nmai Hka Valley, *Kingdon Ward 521* (NY). **Japan.** HONSHU: Oshima, Prov. Izu, *Mizushima 815* (A); Hondo, *Shioto* in 1935 (†A); Hakone and Tokyo, *Hartshorne* in 1894 (PH); Sin, *Zollinger 161* (A). KYUSHU: Kagosima, *Masamune* in 1922 (NY). No specific locality in Japan: *Thunberg s.n.* (†UPS), *Lejeuni s.n.* (†BR), ex Herb. Lugd.-Batav., *Anon. s.n.* (†BR, NY), ex Scheidweiler Herb., *Anon. s.n.* (†BR), 6051A Wall. Cat., *Lindley s.n.* (NY), ex Herb. College S. S. Trin., *Harvey* (GH), ex Herb. Lugd.-Batav., *T. s.n.* (GH), *Anon. 2* (MEL), ex Hernhard Herb., *Goring 181* (MO). **Formosa:** Taitôtyô, Suibotei, *Suzuki-Tokio 19678* (A); Urajiro-maki Taichu Prefecture, *Hayata & Mori 7147* (A). Origin unknown: part of specimens on *Wall. 6052A*, not *P. neriifolius* (†BR).

Cultivated. CHINA. Kiangsu: Nanking, *Chen & Teng 4104* (UC); Maan Shan Inin Shan, *Tso 1634* (A); Tungting, Tai Hu Lake, Soochow, *Ching & Tso 731* (A). Hupeh: *Ho-Ch'ang Chow 1972* (A, NY). Fukien: Foochow, West Lake Park, *Chang 4360* (†MO); Wooshihshau, *Chung 2491* (A, UC); Electric Factory Garden, *Chung 2700* (A, UC); Hinghwa, *Chung 1304* (A), *7515* (A); Amoy region, Kulangser, *Chung 1635* (A, UC). SINGAPORE: Bot. Gard., *Sargent* in 1903 (A), Bohn's Gard., *Sargent* in 1903 (A). JAPAN: ex Hort. Cantab. *Anon.* in 184– (NY), Tokyo Gardens, *Faurie 59* (MO). CEYLON: Hakgala Bot. Gard., *Wilson* in 1921 (†A). MONACO: Hort. Monac., *Anon.* in 1824 (†BR). SWITZERLAND: Locarno, ex Schneider Herb., *Anon. s.n.* (†A). FRANCE: Riviera, *Schneider s.n.* (†A). ENGLAND: *Lucas 1777* (†BM), Kew, *Anon. s.n.* (MO). ITALY: ex Herb. R. Bot. Hort. Neap., *Anon.* in 1868. (†MO), ex Bernhardi Herb., *Anon. s.n.* (†MO), ex Horti Thenensis Herb. *Bossche 1375* (†BR). AFRICA: Cape of Good Hope, *Anon.* in 1836 (†MO), Hort. Daudin, *Anon.* in 1851 (†DS); Grootvaderbosch, *Thunberg s.n.* (†UPS). MAURITIUS OR MADAGASCAR: *Blackburn* in 1873 (†CU). VENEZUELA: Caracas, *Pittier* in 1924 (†VEN), *Orozco 324* (†F). BRAZIL: Rio de Janeiro Bot. Gard., *Curran* in 1915 (†US), *deLaubenfels* in 1952 (†ILL). WEST INDIES: *Broadway 2934* (†F); Trinidad, Port of Spain, *Broadway s.n.* (BM); Jamaica, *Chrysler 1914* (NJU), *Anon. s.n.* (†ILL). UNITED STATES. New York: New York Bot. Gard. 3750A from DPM 1900, *Taylor* in 1906 (NY), *Hartling* in 1914 (NY), *Nash* in 1905 (NY), *Anon.* in 1920 (ILL). New Jersey: Greenhouse at Rutgers, *Johnson* in 1952 (†NJU). District of Columbia: Washington, Congressional Garden, *Parry* in 1918 (US). South Carolina: Columbia, *Hough* in 1916 (CAS); Charleston, *Sargent* in 1914 (A). Georgia: Augusta, *Cuthbert* in 1896 (NJU); Cairo, *Wight* in 1948 (†ILL). Florida: Gotha, Nehrling's Place, *Rehder* in 1920 (A); Glen St. Mary, *Hume* in 1926 (A); Winter Haven, *McFarlin 4944* (MICH); Panama City, Tyndall Field Hospital area, *Gray* in 1945 (†ILL); Jacksonville, *Huger* in 1922 (NY), *Dahlgren* in 1945 (F). Missouri: St. Louis, Bot. Gard., *Woodson 321* (MO), *Irish* in 1896 (MO), *G. E.* in 1873 (MO), *Engelmann* in 1877 (MO). Louisiana: New Orleans, *Kock* in 1936 (CU). California: Hales place, Santa Barbara, *Walther* in 1921 (†CAS). JAVA: Hort. Bot. Gard. Buitenzorg, VF 18, *Anon.* 1903 (NY–2 sheets), VF 16, *Anon.* in 1903 (NY). NEW GUINEA: Aiyura, *Womersley NGF3397* (LAE). AUSTRALIA: Brisbane, private garden, *White 3311* (A).

This variety is distinguished from the species by the narrower and shorter leaves, not over 7 cm. long nor 7 mm. wide. The anatomy of the leaf in transverse section does not differ from that of the species.

LITERATURE CITED

1. BAKER, R. T., AND H. G. SMITH. A research on the pines of Australia. Sydney. 1910.
2. BUCHHOLZ, J. T., AND N. E. GRAY. A taxonomic revision of *Podocarpus*. I. The sections of the genus and their subdivisions with special reference to leaf anatomy. Jour. Arnold Arb. **29**: 49–63. 1948; IV. The American species of section *Eupodocarpus*, subsections C and D. *Ibid.* 123–151.
3. COMPTON, R. H. Gymnosperms. Jour. Linn. Soc. Bot. **45**: 421–434. 1922.
4. FLORIN, R. Untersuchungen zur Stammesgeschichte der Coniferales u. Cordaitales. Erster Teil. Morphologie und Epidermisstrukture der Assimilations-organe bei den rezenten Koniferen. Svenska Vet.-Akad. Handl. III. **10.** 1931.
5. FOXWORTHY, F. W. Philippine gymnosperms. Philip. Jour. Sci. Bot. **6**: 149–177. 1911.
6. GIBBS, L. S. A contribution to the flora and plant formation of Mt. Kinabalu and the highlands of British North Borneo. Jour. Linn. Soc. Bot. **42**: 1–240. 1914.

7. Lee, I. Early explorers in Australia. From the log-books and journals, including the diary of Allan Cunningham, botanist, from Mar. 1, 1817 to Nov. 19, 1818. London. 1925.
8. Metcalf, F. P. Flora of Fukien and floristic notes on southeastern China. Lingnan University. 1942.
9. Orr, M. Y. The leaf anatomy of *Podocarpus*. Trans. Proc. Bot. Soc. Edinburgh **34**(1): 1–54. 1944.
10. Stiles, W. The Podocarpeae. Ann. Bot. **26**: 442–514. 1912.
11. Wasscher, J. The genus *Podocarpus* in the Netherlands Indies. Blumea **4**: 359–481. 1941.

Agnes Scott College
Decatur, Georgia

ONTOGENY OF THE SPORANGIA IN XIPHOPTERIS SERRULATA AND PYRROSIA NUDA [1]

KENNETH A. WILSON

IN SPITE OF ALL the recent discussion of relationships and classification of such well-known genera as *Vittaria* and *Polypodium*, and such of their presumed allies as *Dipteris*, *Cheiropleuria*, and *Platycerium*, no attempts appear to have been made to correlate the details of sporangial structure with cytological and other morphological evidence (e.g., the nature of the gametophytes) which has recently been accumulating. It is surprising that, in view of the emphasis which is placed on the reproductive parts of flowering plants, the sporangial structure has for so long escaped detailed investigation. Undoubtedly one of the main factors in causing this delay in their study is the opinion that the sporangia of the "higher" or polypodiaceous ferns are so simple that they do not by themselves give adequate evidence of relationship (Holttum, 1954). It is true that these minute sporangia are deceptively similar in appearance. However, before one can determine accurately whether sporangial structures are comparable it is important to know the precise details of leptosporangial ontogeny. Ontogenetic knowledge should lead to (1) clearer concepts of homology between parts of sporangia of different species, and (2) demonstrations that some apparent homologies do not exist. Only then can the details of the mature sporangium be clearly understood, and only then can there be a basis for the interpretation of presumably homologous parts of a large number of mature sporangia.

In an earlier paper (Wilson, 1958), the ontogenetic steps in the formation of the mature sporangium of *Phlebodium aureum* (L.) J. Sm. (Polypodiaceae sensu strictu) were presented. It was shown that the sporangial stalk results from cells intercalated in the first segments of the sporangial primordium rather than by the activity of an apical cell as has been generally believed. Furthermore, it was found that the stalk of the sporangium and the jacket of the capsule are produced by the subdivision of 5 initials or "segments." Segment 0 contributes only to the formation of the stalk, segment I to a portion of the stalk and part of the proximal face of the capsule, segment II to the stomial region, the stalk, and to the proximal and distal faces of the capsule, and segments III and IV to the rest of the annulus and to both the proximal and distal faces of the capsule.

However, the study of sporangial ontogeny in *Phlebodium* still left several questions unanswered. *Phlebodium* has a two-rowed stalk; how is a one-rowed stalk produced? Do the sporangia of another genus in the same family develop in the same manner? What difference, if any,

---

[1] A portion of a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University of Michigan.

would be found in the ontogeny of the sporangia in a species of a different family?

In an attempt to answer these questions two fern species were chosen for study: *Xiphopteris serrulata* (Sw.) Kaulf. (Grammitidaceae) and *Pyrrosia nuda* (Gies.) Ching (Polypodiaceae). In the present paper, the developmental sequence in the formation of the sporangia in the two species is described and a comparison is made with the ontogeny of the sporangia in *Phlebodium aureum.*

ACKNOWLEDGMENTS

I am particularly indebted to Dr. Warren H. Wagner, Jr. for his patient and helpful directions and criticisms during the entire course of this investigation. The material of *Xiphopteris serrulata* used in this study was collected by me during an expedition to Jamaica, The West Indies. I am deeply grateful to Dr. Grady L. Webster and to Professor H. H. Bartlett for making this field study possible.

MATERIAL AND METHODS

The plant material of *Xiphopteris serrulata* was collected in Portland Parish, Jamaica, in 1954 (*K. A. Wilson & W. Murray 588*). *Pyrrosia nuda* is growing at the Botanical Gardens of the University of Michigan, and the material was collected there (UMBG *19980*; from Assam, India, *W. Koelz 11716A*). Specimens of both species have been deposited in the Herbarium of the University of Michigan, and duplicates of *Xiphopteris serrulata* have been distributed to several other herbaria.

Young sori which had been preserved in F.A.A. were selected, embedded in paraffin, and sectioned. *Xiphopteris* was sectioned at 12 microns, while *Pyrrosia,* because of the larger size of the young sporangia, was sectioned at 15 microns. The sections were stained in Conant's quadruple stain (Johansen, 1940). Sori in various stages of development were also cleared by the sodium hydroxide technique (Foster, 1949) and then stained in 3 per cent tannic acid in 50 per cent alcohol and 3 per cent ferric chloride in 50 per cent alcohol. After dehydration in alcohol, the sporangia were teased out and mounted in Diaphane. Because of the thickness of the frond of *Pyrrosia* and the deeply sunken sori, the above method, which was successful for *Xiphopteris,* proved to be of value only for the sporangia in the later stages of development. In order to study the earlier stages, 75-micron sections of fixed *Pyrrosia* material were cut on the freezing microtome. These sections were cleared and stained as outlined above and then mounted in Diaphane without further dissection. When bleaching was necessary, a 50 per cent aqueous solution of Clorox was used. The mature sporangia were studied in water mounts since dehydration led to the dehiscence of the capsule. All illustrations were made with the aid of a camera lucida.

MORPHOLOGICAL OBSERVATIONS

1. Xiphopteris serrulata

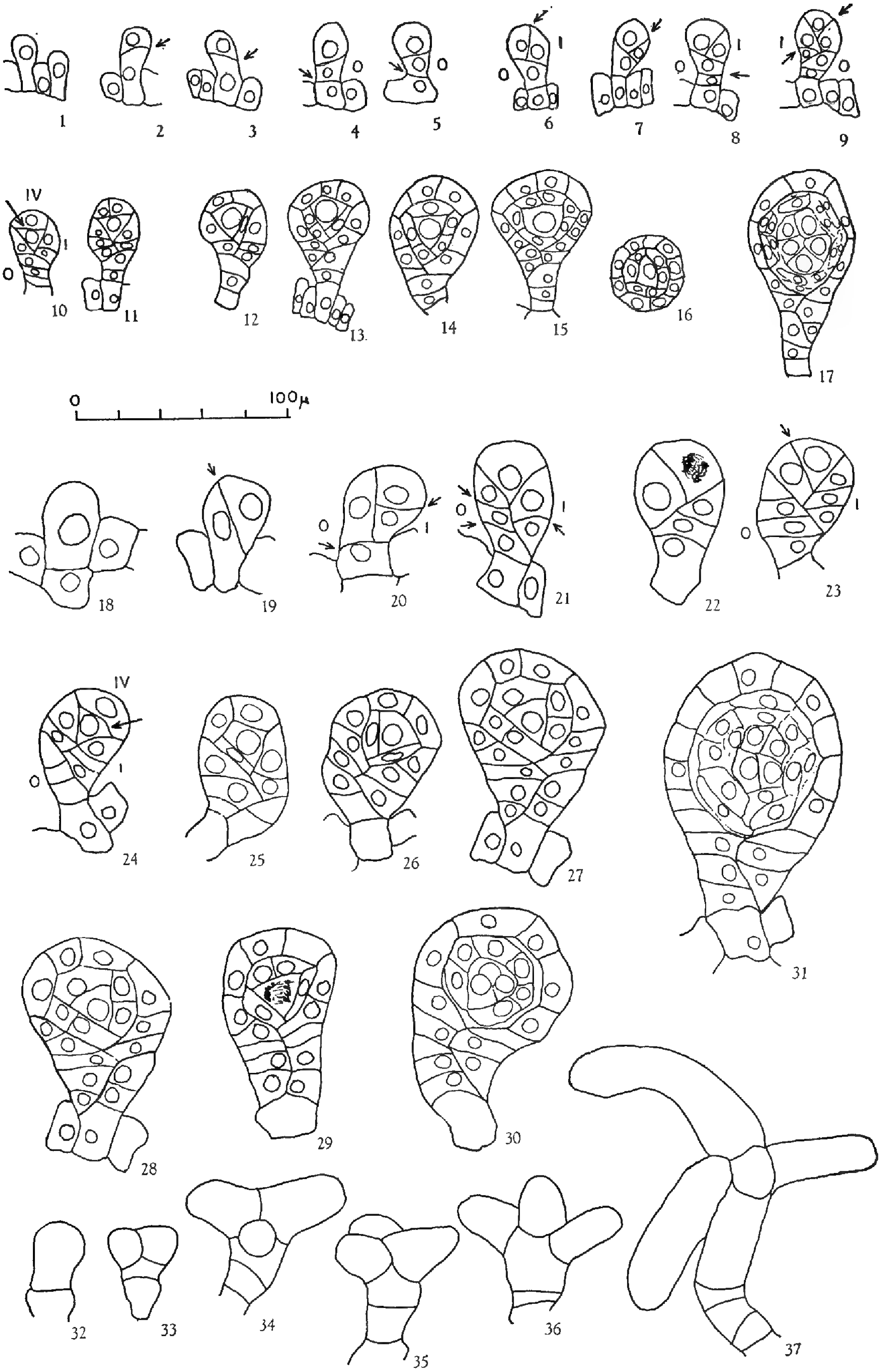
The swollen sporangial initial of *Xiphopteris serrulata* is first divided by a cell-wall which is slightly inclined but which never reaches the level of the receptacular cells (*figs. 2, 3*). This division is soon followed by the formation of a second wall which is transverse and intercalated in the lower cell of the initial (*figs. 4, 5*). This wall is produced on a level with the surface of the adjacent receptacular cells, and separates the sporangial primordium from a basal cell. The basal cell undergoes no further division and takes no part in the subsequent development of the sporangium. The sporangial initial at this stage consists of two cells: a proximal cell, segment 0, and a distal cell, the mother initial.

The mother initial divides and cuts off, by a series of three oblique walls, segments I, II and III, which contribute to the jacket layer of the capsule and the distal, three-rowed portion of the stalk (*figs. 6–9*). In the meantime, horizontal intercalary divisions take place in segment 0 (*figs. 8, 9*). After the formation of segments I, II, and III, the mother initial, now shaped like an inverted three-sided pyramid, divides horizontally and produces a transverse wall which cuts off segment IV and thereby becomes completely enclosed by its daughter cells (*fig. 10*).

The enclosed tetrahedral mother initial divides in the same manner and in the same order as it did in producing segments I, II, III, and IV, so that it becomes enclosed by four cells, the tapetal initials, which separate it from the cells of the sporangial wall (*figs. 12–14*). Each of the tapetal initials becomes partitioned into four cells by means of a vertical and a horizontal anticlinal wall (*figs. 13–16*), and all sixteen cells produced by these divisions then divide periclinally to form a two-layered tapetum, which soon disorganizes, surrounding the inner sporogenous cells (*fig. 17*).

After the mother initial divides to produce the four tapetal initials, the activity of the central cell changes and it divides equally to form the sporocytes (*fig. 17*).

FIGS. 1–37. SPORANGIAL ONTOGENY IN *Xiphopteris serrulata* AND *Pyrrosia nuda*: INTERNAL SEGMENTATION. FIGS. 1–17, *Xiphopteris serrulata*: 1, Protruding initial; 2, 3, Formation of first wall; 4, 5, Formation of segment 0; 6, 7, Formation of segment I; 8, Intercalary division in segment 0; 9, Formation of segment II or segment III, intercalary division in segment I; 10, Formation of segment IV; 11, Intercalary division in segment IV; 12–15, Formation of tapetal initials; 16, Cross section of primordial capsule; 17, Formation of sporocytes. FIGS. 18–37, *Pyrrosia nuda*: 18, Protruding initial; 19, Formation of first wall; 20, Formation of segments 0 and I; 21, Intercalary divisions in segments 0 and I; 22, 23, Formation of segment II or segment III; 24, Formation of segment IV; 25–28, Formation of tapetal initials; 29–31, Formation of sporocytes; 32–37, Various stages in the ontogeny of the paraphyses. Arrows point to newly formed walls. Roman numerals identify sporangial segments.



FIGS 1–37. SPORANGIAL ONTOGENY IN *Xiphopteris serrulata* AND *Pyrrosia nuda*.

All divisions that take place in segment 0 are horizontal; there are never any vertical walls formed in the segment. As a result of the position and inclination of the first wall formed in the sporangial initial, segment I never reaches the level of the cells of the receptacle. Therefore, since only segment 0 contributes to the base of the sporangial stalk, and since the divisions within this segment are only transverse, the stalk of the mature sporangium consists of a single row of cells at its base (*figs. 59–61*). On the other hand, the upper portion of the stalk beneath the capsule is three-rowed. The cells in the lower portion of segments I, II, and III each contribute to the formation of one of the three rows of cells which subtend the capsule.

While the tapetal initials and sporogenous cells are dividing, the jacket initials are becoming partitioned anticlinally to produce the exterior layer of the capsule. The first two divisions in segment I are transverse (*figs. 41–45*), and these are followed by the formation of still another cross wall in the distal portion of the segment so that segment I becomes composed of a linear series of four cells (*figs. 46, 47*).

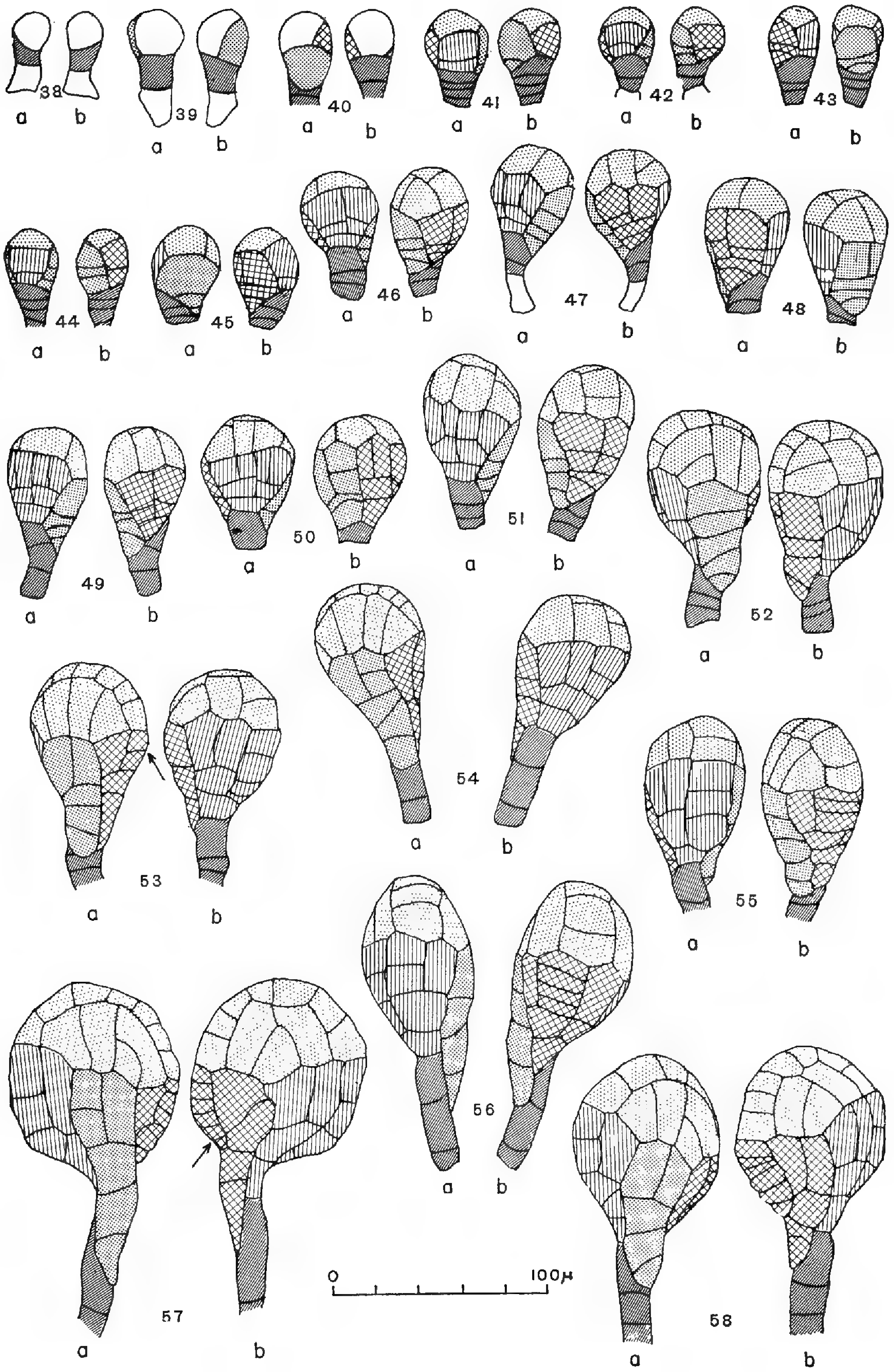
Both segment II and segment III become similarly partitioned by cross walls; however, segment II is divided by two transverse walls, while segment III becomes partitioned by only one such wall (*figs. 42, 43a*).

The cleavages in the first three capsular segments are accompanied, or soon followed, by a division in the cap cell, segment IV, which produces a wall, difficult to see in whole cleared sporangia, that extends from segment II to segment III (*fig. 45a*; *figs. 62, 63*, wall *v*). Following the first division of segment IV into two cells, each one of the cells undergoes a division by a wall perpendicular to the first one (*fig. 46b*; *figs. 62, 63*, walls *h*).

The uppermost of the four cells of segment I divides, by the formation of a vertical wall, into two cells of approximately the same size (*fig. 48b*; *fig. 63*, wall *v*). This vertical division is at times followed by a horizontal division in one of the two cells (*figs. 54a, 57a*); more frequently, however, these cells remain undivided (*figs. 53a, 58a*). The distal cells of segment I are immediately recognizable in mature sporangia and may be seen to form a portion of the capsular jacket on one side, the proximal face, of the sporangium (*figs. 59, 61*). The three cells below them, on the other hand, produce one of the three rows of cells at the base of the capsule.

The division pattern of the other capsular segments is more complex and may be understood more easily by considering the sequence of division in each of the segments separately. As the developing sporangium continues to enlarge, the uppermost of the three cells of segment II becomes divided by a vertical wall (*fig. 45b*; *fig. 63*, wall *v*), and each of the cells thereby produced now divides by forming a horizontal wall (*fig. 48a; fig. 63*, walls *h*). The cells next to segment III do not become further divided, and they can be recognized in the mature sporangia as forming part of one of the lateral walls of the capsule (*fig. 60*). These first divisions in segment II are essentially identical to those of segment I, and, as will be shown later, a similar division sequence occurs in segment III.

Additional divisions in segment II all contribute to the formation of the



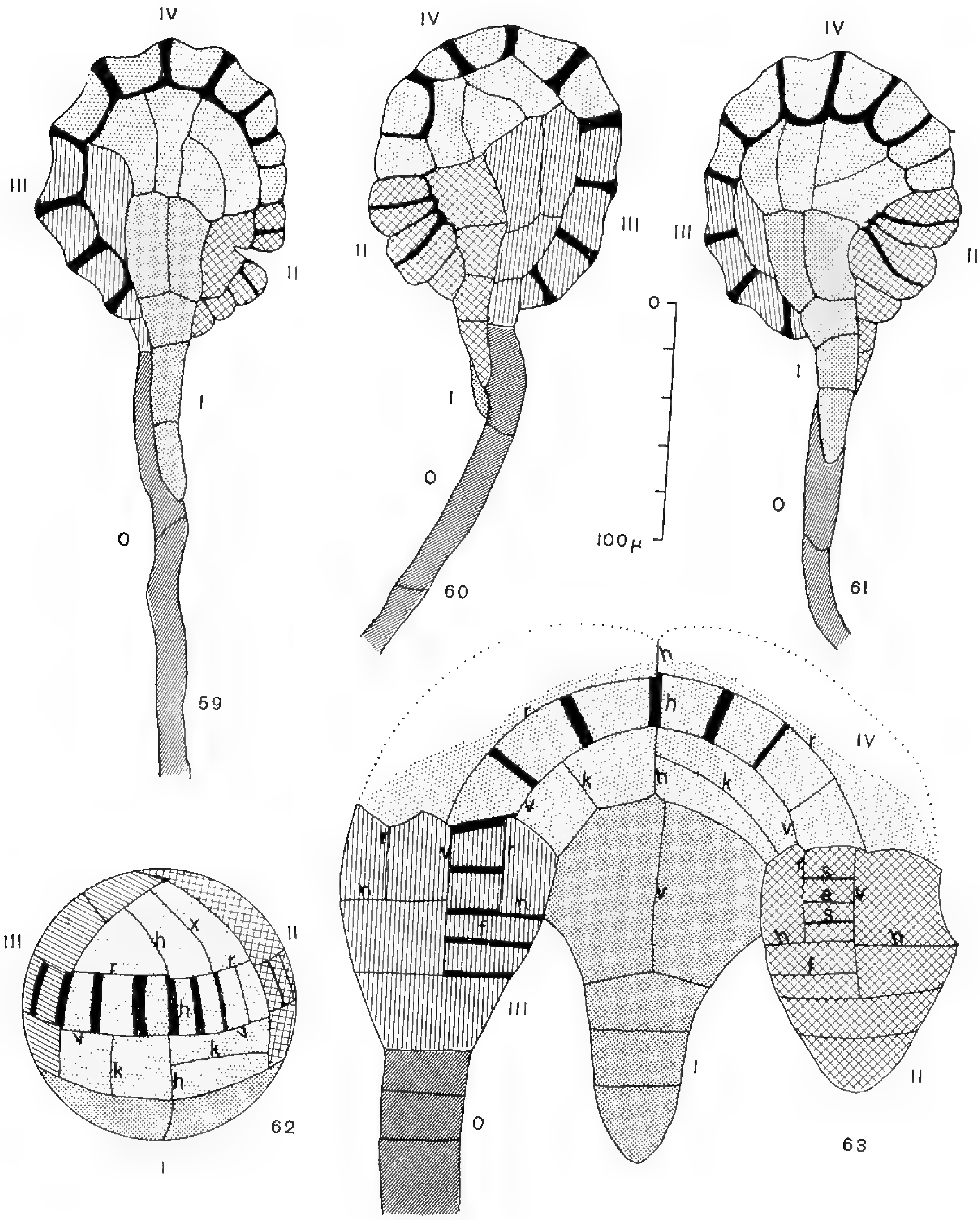
FIGS. 38–58. SPORANGIAL ONTOGENY IN *Xiphopteris serrulata*: SUPERFICIAL SEGMENTATION. Both sides of each sporangial primordium are illustrated and are designated by the letters "a" and "b." For explanation of shading see FIGS. 64–78.

stomium and its associated cells. The cell which undergoes the first division is directly related to the position of segment II with respect to segment I. It is always the uppermost cell contiguous to segment I which becomes partitioned by a vertical wall. It must be pointed out here that, in contrast to *Phlebodium aureum*, segment II is very rarely produced on the left side of segment I; in the great majority of sporangia segment II will be found to be lying to the right of segment I.

The distal cell of segment II which is contiguous to segment I becomes partitioned by a vertical wall (not shown in its first appearance; see wall *r*, *fig. 63*). The uppermost daughter cell which borders on segment I undergoes no further divisions and contributes to the formation of part of a lateral wall. However, the other daughter cell becomes partitioned by the intercalation of a horizontal wall (shown by arrow, *fig. 53a*; *fig. 63*, wall *e*). An additional horizontal wall partitions each one of these last-formed cells and produces the stomial cells (*fig. 56b*; *fig. 63*, walls *s*). As a rule the distal cell next to segment III remains undivided; however, on occasion it may become partitioned by a vertical wall (*fig. 58b*). Before the formation of the stomium, a horizontal wall is usually intercalated in the cell directly beneath the one which is divided by the vertical wall (i.e., the distal cell contiguous to segment I; shown by arrow, *fig. 57b*; *fig. 63*, wall *f*). Following the divisions which produce the stomium, no additional cleavages occur in segment II. The two lowermost cells of segment II form part of the three-rowed stalk at the base of the capsule (*fig. 60*).

Occasional failure of wall formation in segment II may lead to the formation of unusually large cells in the stomial region, as may be seen in *figure 61*. This condition is a result of the absence of the vertical wall which delimits the annular cells in segment II. A similar situation has been observed in segment III, which would result in the formation of large bow cells (*fig. 55a*).

As was stated above, the distal cell of segment III becomes dissected first by a vertical wall (*fig. 63*, wall *v*) and then by two horizontal walls (*fig. 63*, walls *h*) in much the same manner as segment II. The next divisions mirror those of segment II except for the formation of an additional wall. Both of the distal cells become divided by the formation of a vertical wall (*figs. 50a, 51a*; *fig. 63*, walls *r*), after which the cell adjacent to the one which borders on segment I is partitioned by a horizontal wall (*fig. 56a*). One wall forms in the cell below (see wall *f*, *fig. 63*), and with the production of this series of cells the subdivision of segment III is completed. As the sporangium enlarges and matures, the walls of the smaller cells in segment III, which are aligned in a vertical series, become thickened to form the cells of the bow, while the lowermost cell of this segment contributes to the formation of the three-rowed stalk (*fig. 59*). The cells between the bow cells and the cells of segment II do not become further subdivided after the division of the distal cell by the vertical wall. These cells all contribute to the formation of part of the lateral face (*fig. 60*), while the cell on the opposite side of the annular ring and in contact with segment I contributes to the other side of the capsular face (*fig. 59*).



Figs. 59–63. Mature sporangium of *Xiphopteris serrulata*. 59, Proximal face; 60, Distal face; 61, Proximal face: segment II with abnormally large stomial region; 62, 63, Diagrammatic analysis of segment derivatives in the mature sporangium; 62, Top view: segment IV (adapted from Kündig); 63, segments I, II, III (adapted from Müller). Roman numerals identify sporangial segments. For explanation see text.

The first divisions of segment IV into four cells are followed by a division of the two cells contiguous to segments II and III, which produces in each cell a wall that is parallel to the first-formed wall. In other words, these walls are intercalated in the sector of segment IV on that side of the first-formed wall which is away from segment I (see walls *r, fig. 63*). This division sets the boundaries for the formation of the annular cells in the cap segment. A series of walls perpendicular to the first-formed wall and to the wall parallel to it produces a series of cells which differentiate into the top of the annulus. The greatest variation in the division pattern of *Xiphopteris serrulata* is seen in the partitioning of segment IV. Generally this segment contributes seven cells to the annulus; however, it may at times be observed that only six cells are produced in this series (*fig. 60*). The portion of segment IV which contributes to the proximal face of the sporangium usually becomes divided by walls formed in different planes: one wall is formed vertically while the other is variously inclined (*figs. 59, 61*; walls *k, figs. 62, 63*). The placement of the last cell wall in the sector of segment IV in the distal face of the sporangium also varies (wall *x, fig. 62*; *figs. 52b, 57b*).

2. Pyrrosia nuda

One of the most striking differences in the young sporangia of *Pyrrosia nuda* from those of *Xiphopteris*, as well as from those of *Phlebodium*, is in their size. The sporangial initials are themselves almost twice as large as those of *Phlebodium*, and well over twice the size of those of *Xiphopteris* (*fig. 18*). However, in spite of the size of the sporangial initial, the first two divisions are the same as those of *Phlebodium*. The first wall formed is oblique and extends to the level of the receptacular cells or below it (*fig. 19*). The second wall is horizontal and in line with the surface of the cells of the receptacle (*fig. 20*).

There seems to be some variation in the orientation of the wall which produces segment I. It may be noted that at times this wall is formed in such a way that it does not bisect the wall of segment 0, as it does in *Phlebodium*, but rather is so oriented that segment I fails to include the entire basal portion of the initial which is not occupied by segment 0. Consequently, the lower portion of the mother initial reaches the base of the primordium (*fig. 65*). In such circumstances, when segment II is formed it will extend to the very base of the sporangial primordium (*figs. 67a, 70a*)! This is a rare occurrence. Usually the divisions are as in *Phlebodium* and the base of the primordium is occupied by segment 0 and segment I only (*fig. 69*), resulting in a two-rowed stalk. When, however, the wall of segment I is so placed that segment II reaches the base of the sporangium, the entire stalk of the mature sporangium will be three-rowed. Although such stalks are rare, they have been observed in mature sporangia of *Pyrrosia*.

The details of the further development of the sporangium do not vary from those of either *Xiphopteris* or *Phlebodium*. Of some significance may be the fact that a larger number of cells form the bow in *Pyrrosia* than in either of the other two genera (segment IV contributes twelve cells to the annulus), but they are formed in the same manner as has been described for *Xiphopteris* (see *figs. 18–31, 64–84*).

Stellate paraphyses occur intermixed with the sporangia of *Pyrrosia* (*fig. 85*). These arise from superficial cells of the receptacle which become divided by a transverse wall (*fig. 32*). Following the initial transverse divisions, the terminal cell of the developing paraphysis becomes bisected by a vertical wall (*fig. 33*). These two terminal cells continue to elongate, and soon, as a result of a protrusion and expansion of the cell wall beneath them, a third cell is initiated (*fig. 34*). Elongation of these cells apparently does not take place at the same rate; the newly formed cells appear to elongate more rapidly. This process is repeated many times (see *fig. 37*) and gives rise to the many-celled paraphyses. Vertical divisions in the stalk may be seen to accompany the formation of the elongated cells. On the other hand, no walls are formed in the terminal cells of the paraphysis. The elongation of the terminal cells ceases soon after the walls at their bases become thickened.

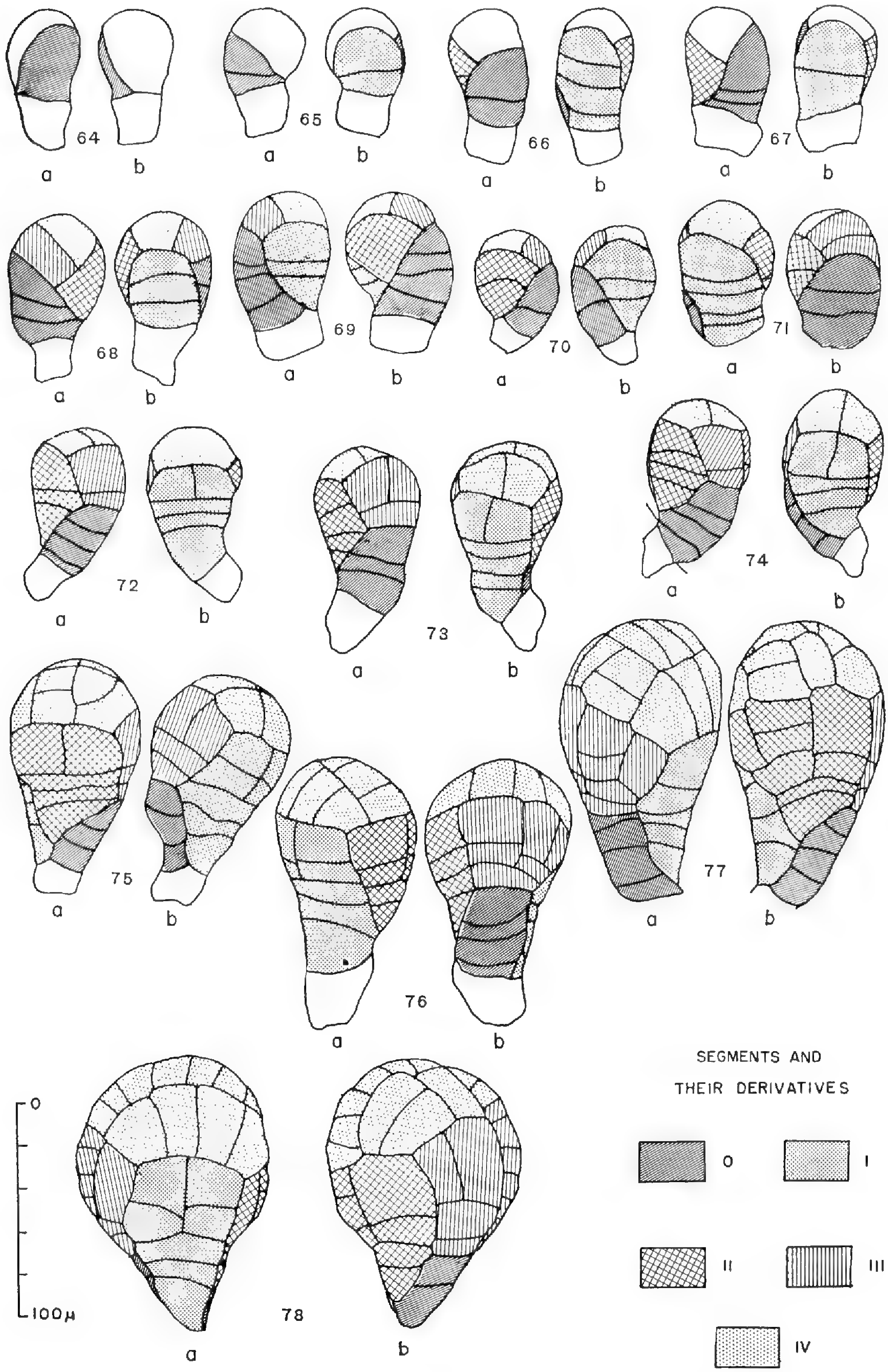
DISCUSSION

The orientation of the first division of the sporangial initial is not always the same in different species. In *Pyrrosia nuda*, as well as in *Phlebodium aureum*, the first wall formed is oblique and reaches the level of the receptacular cells. On the other hand, the first wall in *Xiphopteris serrulata* is essentially transverse and well above the cell surface of the receptacle.

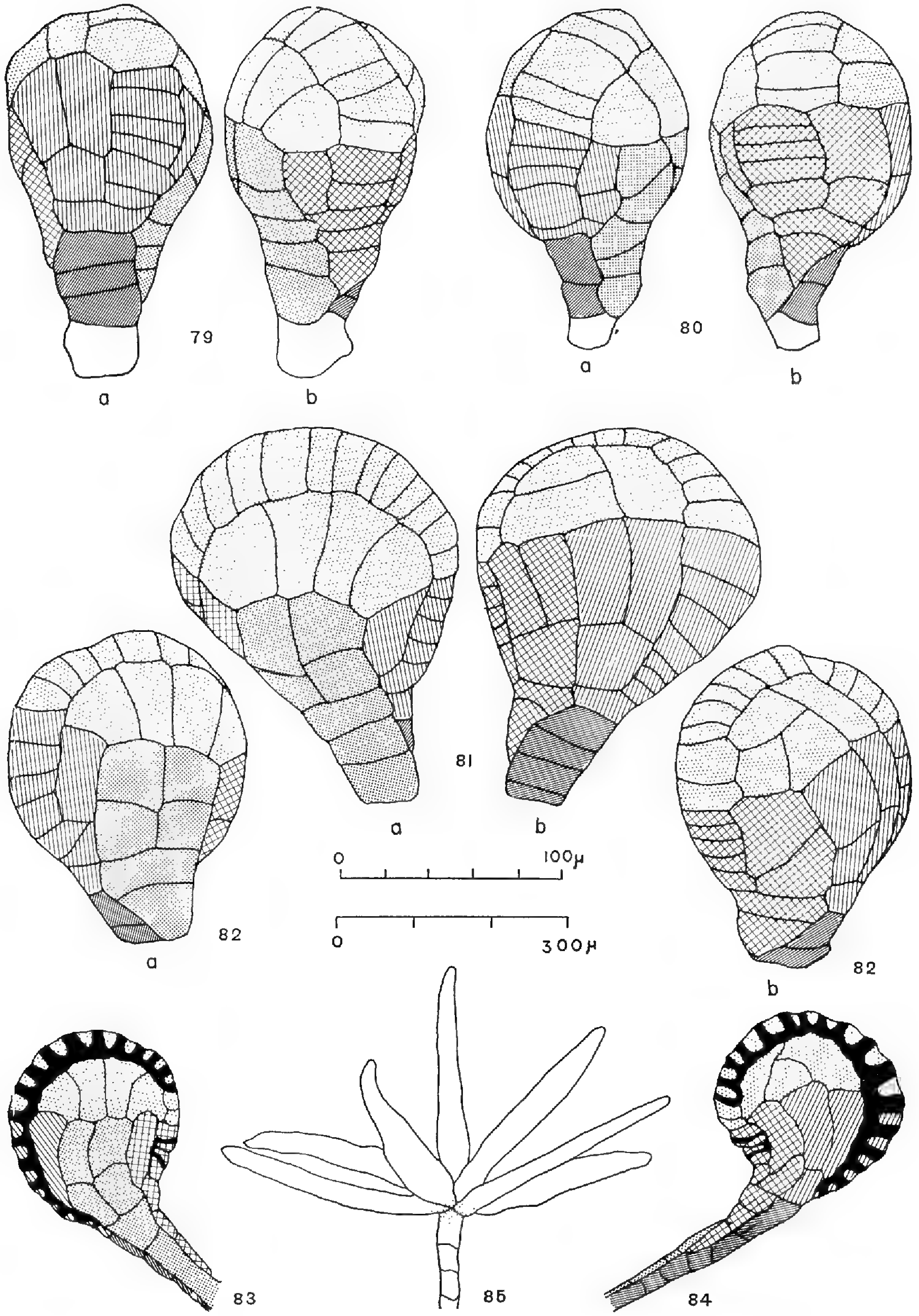
Wagner (1952) has shown the same variation in the species he examined. The first division of the sporangial initial of *Diellia* and *Asplenium* is transverse, while in *Nephrolepis* and *Davallia* it is oblique. Kündig (1888) was the first to notice the two different orientations of this cell wall. According to him, the first wall is oblique in *Asplenium* and all the other species he investigated, except *Polypodium vulgare*, where the first wall is transverse. The observations on *Asplenium* and *Polypodium* are no doubt in error, and the correct interpretation would be the reverse of that given by Kündig. As will be explained below, the structure of the mature stalk directly reflects the orientation of the first division of the sporangial initial.

Although no division figures were seen in the stalk-forming segments of *Xiphopteris serrulata* and *Pyrrosia nuda*, there is no evidence to indicate that the walls are not intercalated to produce the sporangial stalk in these species as they are in *Phlebodium aureum*. There is certainly no indication that the stalk is produced by the activity of an apical cell.

Wagner (1952) postulated that the two-rowed stalk is produced entirely by the oblique orientation of the first wall, and the one-rowed stalk results from the transverse position of this first-formed wall. The sporangial stalk of *Xiphopteris* is one-rowed and is indeed a direct result of the horizontal orientation of the first wall. All cell walls intercalated are transverse, never



FIGS. 64–78. SPORANGIAL ONTOGENY IN *Pyrrosia nuda*: SUPERFICIAL SEGMENTATION, EARLIER STAGES.



FIGS. 79–85. SPORANGIAL ONTOGENY IN *Pyrrosia nuda*. 79–82, Superficial segmentation, later stages; 83, 84, Mature sporangium; 83, Proximal face; 84, Distal face; 85, Mature paraphysis.

longitudinal. Stalk formation in *Xiphopteris* agrees with that in *Diellia*. However, one may question Wagner's conclusion with regard to the development of the two-rowed stalk. In *Phlebodium aureum* the sporangial stalk is always two-rowed and the first division is oblique. The first wall formed in the sporangial initial of *Pyrrosia* is also oblique, but the stalk is not always two-rowed: it may be three-rowed instead. As has been pointed out in *Pyrrosia*, the two-rowed condition is not solely the result of the orientation of the first wall, but depends also on the placement of the wall which forms segment I. When segments 0 and I do not include the entire basal portion of the initial, the stalk will be three-rowed as a result of the cells contributed to it by segment II. The significance of the first wall in the structure of the stalk may then be summarized in this manner: The one-rowed stalk is produced entirely by the orientation of the first division,[2] while the two- and three-rowed stalks depend on the orientation of both the first division and that which produces segment I. The distal portion of the stalk is always three-rowed and is formed by the lower cells of segments I, II, and III.

Bower (1915) reported on the development of the sporangia of *Dipteris* and *Cheiropleuria*. The sporangial stalks of these ferns are four-rowed, and, according to him, the segmentation of the young sporangium "appears to show a regular cleavage of the segments *in two opposite rows*," and the "subdivision of the two rows of segments of the stalk by walls in the plane of the drawings has given rise to the four rows of cells of the stalk, as seen in later stages." In view of the preceding discussion which points out that there is no apical cell activity in the production of the stalk in the species examined, I suggest that a reinvestigation of the sporangia of both *Cheiropleuria* and *Dipteris* should be made, stressing stalk formation and, because of its potential morphological significance, the inner and outer segmentations of the capsule. For the present, Bower's conclusions must be accepted with reservation.

The internal divisions following the formation of segment IV are the same in *Xiphopteris serrulata*, *Pyrrosia nuda* and *Phlebodium aureum*. The four tapetal initials are produced by the mother initial in the same sequence and in the same manner as are the four capsular segments (segments I–IV). Only after the enclosed mother initial has produced the tapetal initial does it undergo a change in activity and begin to divide equally to produce the sporocytes. Moreover, as in *Phlebodium aureum*, there is no evidence to indicate that the derivatives of the tapetal initials are potentially sporogenous, nor is there any to support the view that any of the derivatives of the inner cell behave in the manner of a tapetal cell. Thus, in view of the manner in which the tapetal initials are formed, the opinion that they are better considered as inner wall cells, at least ontogenetically, is strongly supported. The central cell may be considered sporogenous only after these initials have been cut off from the mother initial.

There has been much disagreement in the application of the term "arche-

---

[2] A possible exception may be found in the sporangial stalk of *Dictymia*, which possesses a single cell at its base.

sporium." Kündig (1888), Müller (1893), Campbell (1905), Bower (1923), and Smith (1938) used it to refer to the central tetrahedral cell before the tapetal initials are formed. However, Kny (1895) and more recently Troll (1954) have limited its usage to the central spore-producing cell. Since the term "archesporium" is intended to refer to the first cell generation of the sporogenous tissue, it should be used only to designate the truly sporogenous initial. A more comprehensive survey of the use, or perhaps misuse, of this term was made by Bower (1908), who suggested that it be retained "merely in a descriptive sense, in those cases where the cell or cells which give rise to the sporogenous group are obvious, but in a descriptive sense only." It might be better still to avoid the use of the term and prevent confusion. This has been done by Eames (1936) and Wagner (1952), although Eames considered the central cell, prior to the formation of the tapetal initials, to represent the "primary sporogenous tissue."

Eames also reported that from the "primary sporogenous tissue" are cut off by "periclinal divisions one or two layers of thin cells which become the tapetum." I have not seen any evidence to support this statement. All of my material indicates that only one layer of tapetal initials is cut off, which, as a result of periclinal and anticlinal divisions, develops into a two-layered tapetum. It may be possible that in some ferns two series of tapetal initials are produced, but there is no evidence at present to support this statement.

The subdivision of the capsular segments is remarkably similar in *Xiphopteris*, *Pyrrosia* and *Phlebodium*. In all three, segment I contributes to a portion of the stalk and part of the proximal face of the capsule, segment II to the stomial region and the stalk, and segments III and IV to the rest of the annulus. The proximal face is formed from cells of segments I, II, III, and IV, and the distal face from those of segments II, III, and IV.

As has been pointed out by Wagner, a comparison of the "eusporangiate method" of sporangial development with the "leptosporangiate method" is highly desirable. Bower (1923) described a series showing gradual steps from the segmentation typical of eusporangiate ferns to that of leptosporangiate ferns. Similar series are also described by him for the sporangial stalk and for the capsule. His conclusions indicate that there is little fundamental difference between the two types and that the facts "appear to establish the general sequence of forms from the Eusporangiate to the Leptosporangiate, as a valid evolutionary progression."

I have shown that there has been a great deal of misunderstanding of the ontogeny of the polypodioid leptosporangium, and, in view of this, comparisons based on data of uncertain validity may be seriously questioned. A review of the literature on the development of the sporangium of the Marattiaceae and the Ophioglossaceae shows that little is known about the process and that the various authors do not agree. (For a summary of this information see Campbell, 1911, and Bower, 1923).

Before any detailed comparison can profitably be made between the two types of development, new investigations should be made of the ontogeny of the sporangium of the eusporangiate ferns, and of the so-called "primitive" leptosporangiate ferns.

Pirard (1947) discussed the stellate paraphyses of *Niphobolus* [*Pyrrosia*] *lingua*, but these do not agree in their details with those of *Pyrrosia nuda*. The paraphyses of *P. nuda* do not have the thickenings in the cell walls of the stalk as do those of *P. lingua*, nor are the elongated cells borne on a swollen cell, but rather on one of approximately the same dimensions as the cells of the stalk. Since the various types of stellate paraphyses have been used as taxonomic characters in the genus (Giesenhagen, 1901), it is hardly surprising that those of these two species should be different.

SUMMARY

In a study of the ontogeny of the sporangia of *Xiphopteris serrulata* and *Pyrrosia nuda*, it is shown that the sporangial stalk is produced by the intercalation of cell walls in the first-formed segments of the sporangial primordium. A one-rowed stalk results directly from the horizontal orientation of the first division of the sporangial initial; two- and three-rowed stalks are produced by an oblique first division, and the number of rows depends upon the orientation of the wall forming segment I. The stalk is produced from the division products of the initial designated as segment 0 and the lowermost cells formed from segments I, II, and III. The stomial region develops in segment II, and the remainder of the annulus forms in segments III and IV. It is again suggested that the tapetal initials are better interpreted as inner wall cells of the capsule, and that the term "archesporium" be limited to designate the cell which directly gives rise to the sporocytes. Comparison of the leptosporangium with the eusporangium must be deferred until more information on both sporangial types is available. The paraphyses of *Pyrrosia nuda* are also described.

ARNOLD ARBORETUM AND GRAY HERBARIUM
HARVARD UNIVERSITY

LITERATURE CITED

BOWER, F. O. 1908. The Origin of a Land Flora. 727 pp. MacMillan, London.

———. 1915. Studies in the phylogeny of the Filicales. V. *Cheiropleuria bicuspis* (Bl.) Presl, and certain other related ferns. Ann. Bot. **29**: 495–529.

———. 1923. The Ferns. Vol. I. Analytical Examination of the Criteria of Comparison. 359 pp. University Press, Cambridge, England.

CAMPBELL, D. H. 1905. The Structure and Development of Mosses and Ferns. 657 pp. MacMillan, London.

———. 1911. The Eusporangiatae. The comparative morphology of the Ophioglossaceae and Marattiaceae. Carnegie Inst. Wash. Publ. **140.** 229 pp.

EAMES, A. J. 1936. Morphology of Vascular Plants. Lower Groups. 433 pp. McGraw-Hill, New York.

FOSTER, A. S. 1949. Practical Plant Anatomy. Ed. 2. 228 pp. D. Van Nostrand, New York.

GIESENHAGEN, K. 1901. Die Farngattung *Niphobolus*. 223 pp. Gustav Fisher, Jena.

HOLTTUM, R. E. 1954. The classification of ferns: The present position and some thoughts on future developments. Huitième Congr. Intern. Bot. Rapports & Communications, Sect. 2, 4, 5, 6: 5–8.

JOHANSEN, D. A. 1940. Plant Microtechnique. 523 pp. McGraw-Hill, New York.

KNY, L. 1895. Entwickelung von *Aspidium Filix mas* Sw. Botanische Wandtafeln mit erläuterndem Text, Abt. **9.** 411–438. Paul Parey, Berlin.

KÜNDIG, J. 1888. Beitrage zur Entwicklungsgeschichte des Polypodiaceensporangiums. Hedwigia **27:** 1–11.

MÜLLER, C. 1893. Zur Kenntniss der Entwickelungsgeschichte des Polypodiaceensporangiums. Ber. Deutsch. Bot. Ges. **11:** 54–72.

PIRARD, N. 1947. Sporanges, paraphyses, et organes connexes chez les fougères. Cellule **51:** 155–184.

SMITH, G. M. 1938. Cryptogamic Botany. Vol. II. Bryophytes and Pteridophytes. 380 pp. McGraw-Hill. New York.

TROLL, W. 1954. Allgemeine Botanik. Ein Lehrbuch auf vergleichend-biologischer Grundlage. 749 pp. F. Enke, Stuttgart.

WAGNER, W. H., JR. 1952. The fern genus *Diellia*. Its structure, affinities and taxonomy. Univ. Calif. Publ. Bot. **26:** 1–212.

WILSON, K. A. 1958. Ontogeny of the sporangium of *Phlebodium* (*Polypodium*) *aureum*. Am. Jour. Bot. **45:** 483–491.

THE DIRECTOR'S REPORT

THE ARNOLD ARBORETUM DURING THE FISCAL YEAR ENDED JUNE 30, 1958

IT IS WITH PLEASURE that I report another year of excellent progress in the care and use of the living collections, the improvement of the herbarium and library and the contributions of the various staff members. A dry summer, followed by a wet winter marked the climatic year; nevertheless, the fine display of flowering shrubs, trees and vines seen in the Arboretum during the spring gave evidence of the care they had received throughout the months of difficult weather conditions. An increasing number of visitors has been recorded and, of these, the registration book in the Administration Building indicates visitors from thirty-eight states and seventeen foreign countries. In addition to the regular work assignments of the staff, the answering of all types of horticultural questions by letter, by phone, or for individuals calling at the office in person consumes a considerable proportion of the staff working hours and is an indication of the confidence which the public places in the Arnold Arboretum.

Among the highlights of the year were the visits of distinguished colleagues from this hemisphere and abroad. In all, directors or representatives of twenty-three botanic gardens and arboreta visited the Arnold Arboretum during the year. The visit of Dr. George Taylor, director of the Royal Botanic Gardens, Kew, a newly appointed member of the Board of Overseers Committee to Visit the Arnold Arboretum, was of special interest and pleasure.

The Staff:

I am pleased to report the approval of the Harvard Corporation for the promotion and appointment without limit of time of Dr. Carroll E. Wood, Jr., as associate curator of the Arnold Arboretum. This appointment is well deserved and is indicative of the contribution which he has made to the Arboretum.

Mr. Roger Coggeshall, who has been chief propagator at the Arboretum since 1954, resigned to accept a position with a private nursery in Massachusetts. Mr. Coggeshall has done an excellent job in increasing the living collections, in research on the propagation of woody plants and in teaching popular classes in the education program conducted by the Arboretum. We regret his leaving the staff, but wish him success in his newly chosen field. He will continue, however, to assist in the instruction program in plant propagation at the Arboretum.

Mr. Alfred Fordham has been reassigned and promoted to the position of chief propagator. Mr. Fordham began his work at the Arnold Arboretum as assistant to Mr. William Judd in plant propagation. He received further training in this field as an exchange student from the Arboretum to the Royal Botanic Gardens, Kew, England, before the beginning of World War II. Upon his return to the Arboretum, following a leave of absence for war service, he was appointed assistant superintendent of buildings and grounds. We are pleased that Mr. Fordham is again serving in a capacity which will permit him to use his specialized training.

During the year Dr. Frans Verdoorn, holder of the honorary appointment as research associate at the Arnold Arboretum since 1942, accepted a new position as director of the Biohistorical Institute at the University of Utrecht, Holland. Dr. Verdoorn was born in Holland and thus that country regains not only a citizen but a remarkable botanical historian, as well.

Three holders of joint annual appointments with the Gray Herbarium accepted other positions at the end of 1957. Dr. Howard F. L. Rock, who was on the curatorial staff in the herbarium, accepted a position at the University of Tennessee. Drs. Robert Bennie Channell and Charles W. James, who, with Dr. Wood, were working on a flora of the southeastern states, accepted teaching appointments at Vanderbilt and the University of Georgia, respectively. To fill one of the latter positions, the joint appointment was made for Dr. Kenneth Wilson to work with Dr. Wood on this project.

Horticulture:

During the summer of 1957 the Arboretum experienced the worst drought on record. All but one of the ponds on the grounds dried up completely and the remaining one retained but a few inches of water. As the drought lengthened and the available water in the soil was exhausted, wilting became a familiar sign in all shrub and tree collections. Emergency steps were taken to water all recently planted trees and shrubs and those others growing in especially dry areas. A pressure-driven deep-watering system was employed to supply water directly at the roots of some of the larger trees, especially those in the conifer collection. Although injury resulted to many of the plants in spite of our efforts, it now appears that only a few plants were killed completely.

In the late fall and winter the situation was reversed, with rains so unusually heavy that the ponds filled and overflowed with floodings that blocked the meadow road for a period of several days. With the assistance of maps from the City of Boston Parks Department, some long-unused drainage channels were relocated and opened to lower the water level. It would seem that this excessive rainfall during a period of mild temperatures partly offset the dry summer season. Flowering was affected in many plants, particularly the azaleas, and much branch damage was noted, which required heavy pruning during the spring.

A number of improvements have been made on the grounds during the year. The spectacular collection of torch azaleas on the South Street bank was thinned and weeded, a retaining wall was built around the

Kalopanax pictus bordering one of the ponds and in the lilac collection many older varieties between the path and the road were removed to locations farther up the bank, allowing newer varieties to be placed in the more conspicuous locations. It is our aim to bring together in a central location the Lilac Committee's "100 best lilacs." About half of these, all young plants, are now in their new locations.

A major adjustment was attempted in the *Carya* collection where a very few species and varieties dominated the area. A number of duplicate trees were removed, these to be replaced with taxa not currently in our collection. The area was cleaned to allow access to the newly opened woodland along Center Street, which is the area proposed for an expanded planting of *Ilex pedunculosa*, its relatives and other rarer species.

The Boston Parks Department continued cleaning the cobblestone gutters. The main portion of the Arboretum between the Arborway and Walter Street has been completed and work has started on the Peters Hill tracts. This work, neglected for many years, makes a striking difference in the appearance of the grounds. Unfortunately, it also calls attention to the poor condition of the roads in many places, a condition which we hope can be handled by spot repairs immediately and eventually by retarring or resurfacing throughout.

Increased police protection was also granted by the Police Department, which assigned two mounted patrolmen to the Arboretum grounds during the spring season. Men on horseback are better able to patrol the remote areas of the Arboretum and can reach areas not accessible by patrol cars. The impressive riders and steeds have attracted considerable attention and have been photographed almost as much as the famed *Davidia.*

One new pest, the dogwood twig borer, was discovered in our collections this year. A heavy infestation of this insect was found in the *Viburnum* collections, apparently attacking all species, which may be the reason why some of the Viburnums have not appeared to be doing well. The location of the pest is extremely difficult. We now spray for this borer, combining the spray program with that for borers in the locust and mountain ash collections.

Dr. Donald Wyman has continued to act as co-ordinator for a group of botanic gardens and arboreta working in conjunction with the Horticultural Crops Research Branch of the U. S. Department of Agriculture. This group is responsible for bringing into the United States for trial growth under quarantine conditions those plants whose entry previously has been prohibited by law. Such plants are grown in special houses at Glen Dale, Maryland, for two or more years before being turned over to the arboretum or garden responsible for their introduction. During the year the Arnold Arboretum received a quarantine release on twenty plants previously held at Glen Dale. These plants originated in England, Germany and the Netherlands.

In continuation of the program of plant distribution established at the Arnold Arboretum seventeen years ago, fourteen new species and varieties were made available to cooperating nurserymen for propagation. In all 650

Above: "Up the hill." Photo and print by Mr. Henry Soron awarded a prize as the best black-and-white picture taken in the Arboretum.

Below: Officers Donahue and McNeil, two of the mounted policemen of the Boston Police Department now patrolling the Arboretum.

plants were distributed to thirty-four domestic nurseries, four foreign nurseries and ten arboreta and botanic gardens.

The number of new plantings on the ground during the year was slightly less than average. Individual plants added to the collection totaled 463, representing 221 species and varieties. Forty-one are new to our collections and eight are probably new to the United States.

Experimental work in the field of plant propagation, involving 646 species and varieties, continued in the greenhouses. One program concerned the propagation of native hybrid azaleas which are considered impractical to root on a commercial scale. A similar program for rooting Ghent azaleas under plastic was attempted. Various hormone concentrations were tried, with Hormodin No. 3 giving the best results. Once the cuttings were rooted the plants were placed under continuous light. Daylight was supplemented with artificial light for continuous illumination for a period of three months. The extended period of light caused a break in bud dormancy and the plants grew continuously. This appears to be a method for establishing hardier plants capable of being transplanted at an earlier age.

In a continuing experimental program of rooting Asiatic maples from cuttings, it was established that wounding the cuttings was definitely advantageous and that Hormodin No. 3 proved to be the best rooting hormone.

We were able to overcome the common double dormancy in seeds of *Cotoneaster* with the use of concentrated sulphuric acid. Seeds were soaked for two hours in the acid, washed well and stratified in plastic bags for three months at forty degrees Fahrenheit. This treatment produced a percentage of germination at the end of one year comparable to that normally obtained in the standard two-year treatment for seeds of this genus.

During the year 136 shipments, totalling 1137 species and varieties of seeds, living specimens, and propagating material, were received from institutions in the United States and ten other countries. We sent 26 shipments of seeds of 141 species and varieties and 320 shipments of propagating material or plants comprising 1328 taxa to sixteen countries besides the United States.

Two pieces of property owned by the Arboretum were recommended to the Corporation for sale and both were sold during the fiscal year. The tract of land at 310 South Street consisting of a house and barn with two acres of land was the gift of Mrs. Andrew J. Peters in 1953. After expending a considerable sum to fence the property and tear down a rambling frame addition to the basic brick house, it was discovered that the house was not structurally sound and could not be used as a staff residence. The property was on the Boston tax rolls at an inflated valuation, the taxes exceeding $1500 a year. Protecting the property from vandalism proved difficult and its sale was recommended. The receipts from the sale of this property will be added to the Arboretum endowment.

The second property sold was the Butler property on Center Street, acquired as a residence for Dr. Merrill while he was director of the Arboretum and occupied by him until his death in 1956. Since the cost of repairing this house was prohibitive, it was sold, together with the land on which it stands, and the proceeds of this sale will also be added to the endowment. By the disposition of these two pieces of property the Arboretum has been freed of two costly maintenance items.

Case Estates:

The plantings at the Case Estates include demonstration plots, nursery stock and plantings for hardiness testing. This area is attracting an increasing number of visitors each year. Particularly noticeable is the increase in requests from garden clubs and other horticultural organizations for guided tours through the area. During the year portions of the land were made available to staff members and graduate students of the Cabot Foundation, the Bussey Institution and the Biology Department for their individual projects, in addition to the land used for Arboretum purposes.

The desire of the Town of Weston to acquire portions of the Case Estates for schools was mentioned in the report for 1956–57. Both the director of the Arboretum and the Corporation made it clear throughout that the land would not be sold and that the town must take this tract by eminent domain. In a special town meeting in 1957 it was voted to take approximately seventy of the one hundred and forty-five acres then in the property. However, further recommendations of the School Site Committee resulted in a reappraisal of the town's school needs. After much discusssion by the committees, officials and residents, the town finally voted to take a smaller tract of land, which proved to contain thirty-two and one-half acres, but at the end of the fiscal year the formalities involved in taking this land by eminent domain had not been completed.

The loss of this area will necessarily reduce our opportunity for expanding the work carried on at Weston, and will also reduce the usefulness of the Case Estates to Harvard students, the Arboretum adult education classes and groups from the Weston schools. Any further inroads on the Arboretum land in Weston would raise serious problems affecting our abilty to continue the important work now being carried on there.

During the early town meetings called for discussing the Weston school needs, there was a group which favored locating a new high school on the Case Estates in addition to the elementary school previously proposed. However, this proposal did not receive the necessary support and the town voted to acquire a privately held property some distance from the Case Estates for this purpose.

Education Program:

Two series of classes consisting of lectures, field trips and demonstrations were presented in the regular fall and spring adult education program this year. The field trips conducted by Dr. Wyman at Jamaica Plain remain extremely popular and were supplemented by a series of field trips called "Field Botany," conducted by Drs. Howard and Wood at the Case Estates in Weston. All classes were open to the public, with advance registration essential, since in nearly all cases the class size was restricted. The courses are stimulating to students and instructors alike, but, regrettably, can not be expanded beyond the present effort. There seems to be an increasing demand for education in horticulture and botany through more popular, non-credit courses such as those offered in this program. Fortunately, five other organizations in the Boston area are now offering similar courses.

For nearly two months (from the last part of April until the middle of June), numerous groups visit the Arboretum for guided tours through the collections. Such tours are scheduled in advance and a maximum of six tours in one day has been accommodated. During other seasons the requests for tours are less frequent.

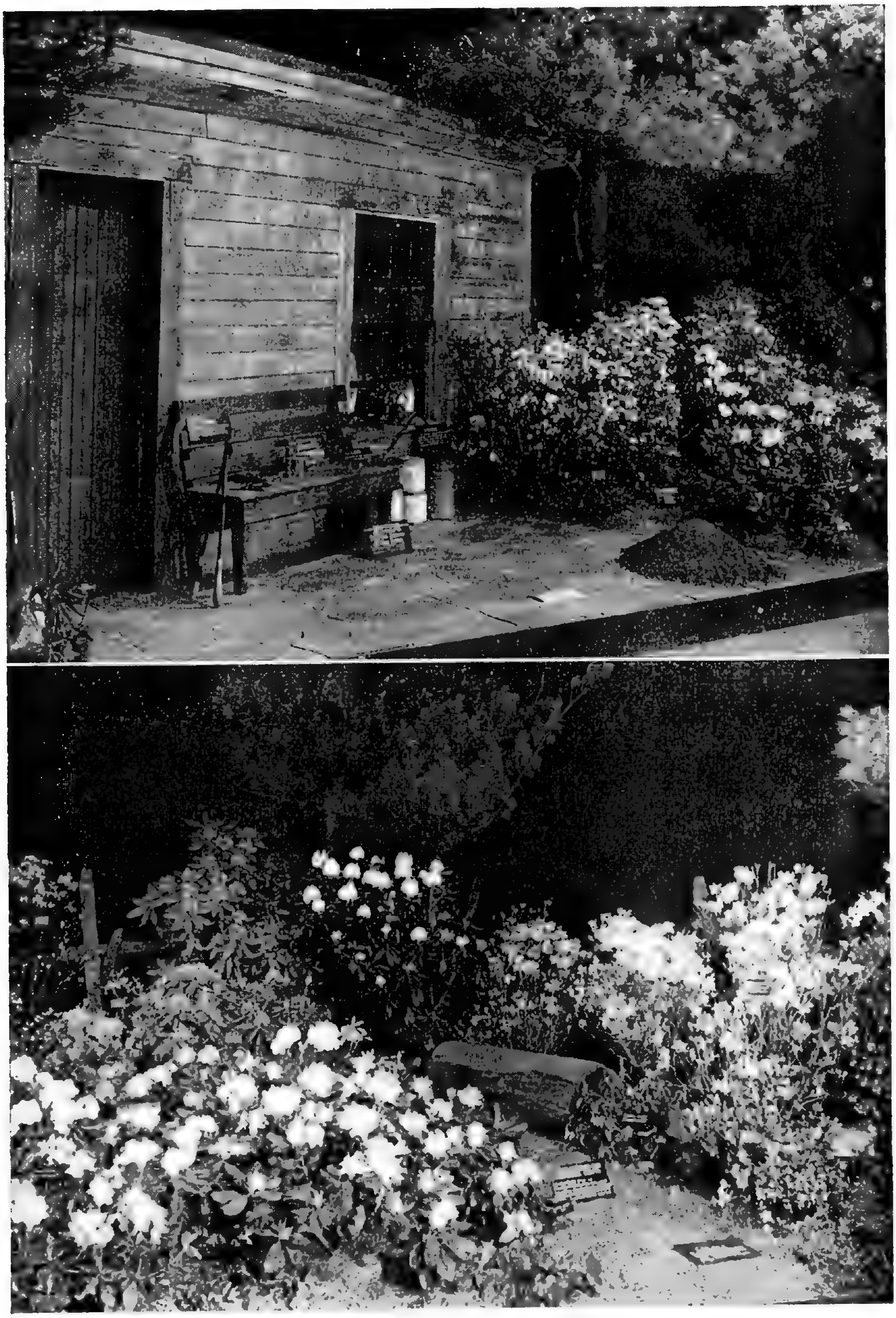
For the New England Zone meeting of the Garden Club of America which was held at the Arboretum in May, the staff assisted with a tour and the presentation of a display of tree peonies arranged by Mrs. George L. Batchelder, Jr. and Mrs. Ellery Sedgewick. The Librarian's Club of Boston also met at the Arboretum with the supervision of our librarian, Mrs. Schwarten. Tours of the grounds and a discussion of the services of the Arboretum staff were arranged. All available staff members were required during the Annual Field Day of the Massachusetts Horticultural Society held at the Arboretum. Seven buses were used for transportation during a two-hour conducted tour of the grounds. Since the buses could not seat all those who wished to take advantage of the tour, a separate caravan of cars supplemented the buses.

The Arboretum sponsored a special colloquium open to the public at the Biological Laboratories when Dr. George Taylor of the Arboretum Visiting Committee spoke on his work in Tibet. Colored slides illustrated his talk for the audience which nearly filled the hall.

Staff members represented the Arboretum at various meetings during the year. Dr. Howard gave the general lecture at the banquet of the Nurseryman's Short Course at the Waltham Field Station. Dr. Wyman took part in the refresher short course for arborists, also held at the Waltham Field Station. Dr. Sax attended the rootstock conference of the American Society for Horticultural Science and lectured on the production of dwarf fruit trees to the Plant Propagators Society and the New England Association of Nurserymen at their annual meetings. Drs. Howard, Kobuski and Sax attended the American Institute of Biological Sciences meetings in Palo Alto, California. Dr. Sax was reappointed as an American Institute of Biological Sciences lecturer and during the year visited Reed College, Lewis & Clark College and Whitworth College in Oregon and Washington, where he gave a series of lectures on world agriculture and population growth.

Exhibits and Displays:

The Arboretum exhibit at the Spring Flower Show of the Massachusetts Horticultural Society again won a gold medal as well as two special awards. One of the latter, from the Massachusetts State Department of Agriculture, was a new award at the show this year. The exhibit theme, "A Hobbyist's



Two views of the exhibit of the Arnold Arboretum at the Spring Flower Show held at Mechanics Hall. The exhibit was titled "A Hobbyist's Rhododendron Garden."

Rhododendron Garden," attempted to show the full program of care and selection necessary in producing fine rhododendrons. The Beatrix Farrand Silver Bowl for the best display of rhododendrons was won by this exhibit.

The open house held at Weston in early May was announced in the Weston and Wellesley papers and was well attended by people from these areas. We trust that those who attended gained a better appreciation of the function of the Case Estates in the program of the Arboretum. It is pleasing to learn that many garden clubs now carry the open house date on their schedule of coming events.

In co-operation with the Boston Camera Club, a contest was held for the best black-and-white photographs and the best kodachrome slides taken in the Arboretum during the past year. It was interesting to the staff, who acted as judges in the contest, to get a glimpse of those scenes and those individual plants which caught the eye and the imagination of the outsider. The best black-and-white print was made by Mr. Henry Soron of Arlington and showed a small boy walking on Bussey Hill in the elm collection. The best kodachrome slide of a general scene was taken by Robert Spooner of Brookline and showed the Sargent cherries near the Administration Building and the open field of daffodils and narcissi. Mrs. Karin Engstrom of Buzzards Bay won two prizes for the best close-up and the best pattern shot. The former was of *Magnolia soulangiana* var. *rubra* showing a mature flower and a pubescent bud. The latter was a beautiful picture of the trunk and adventitious shoots of *Cercidiphyllum japonicum* enhanced by backlighting. The contest for the best slide showing the horticultural value of a single plant had the most entries and the judges concluded that the outstanding slide was of a *Pseudolarix amabilis* in fall foliage taken by Mr. George Taloumis of Salem. The contest served to bring photographers to the Arboretum at all seasons of the year, judging from the entries.

Library:

The year 1957–58 brought to a completion the first stage in combining the non-horticultural collections of the Arboretum with those of the Gray Herbarium and several other selected collections. Mrs. Schwarten and her staff have successfully united, recatalogued and reconditioned these books in the Harvard University Herbarium Building. This action was voted by the Harvard Corporation on January 19, 1953, and progress toward this end has been indicated in previous annual reports. The physical properties of air conditioning, providing controlled humidity and temperature in a dust-free atmosphere, ensure a longer life for these books. The new arrangement has already demonstrated that increased efficiency is possible in the use, as well as in the care of these volumes. Only the pamphlet collection remains in need of reorganization.

In the course of this project, a relatively small number of duplicate books were found and set apart as reserves; these are shelved in a separate section of the library. These include volumes which are not presently needed and those held as replacements for volumes which receive much use. Duplicates of monographic treatises and special family studies have been placed on special shelves in the herbarium adjacent to the herbarium specimens of the families concerned. The unification program also allows greater office use or long-term use of these duplicate volumes by staff members.

In the course of the unification work in the library, the director and the librarian of the Museum of Comparative Zoology made available for our use a large room for work and storage. We are particularly indebted to them for this kindness.

The bound volumes added to the library during the year numbered 465. These included 212 volumes transferred to our library from the libraries at Widener, the Biological Laboratories and the special paleobotanical library. Also included are 145 volumes dealing with horticulture which were added to the library in Jamaica Plain. The total number of bound volumes accessioned now is 50,204. Pamphlets totalling 305 were added to the collection which numbers 16,573.

The horticultural library in the Administration Building in Jamaica Plain was also reclassified and portions of it rearranged for more convenient use by the staff. Additional library shelving was erected on the second floor to house special collections. As previously indicated, 145 bound volumes were added to this collection. The renumbering of all volumes in the horticultural library has been initiated.

A set of the Gray Herbarium Index to American Plants is maintained at Jamaica Plain and 3,000 cards in four issues were received and are being added to this collection.

Again this year the number of requests for books on interlibrary loan remains inconveniently high. Much as we wish to aid other workers, it is impossible to honor all requests for books to be sent on loan to other institutions. Where possible, requests for descriptions or passages are met by sending typed, photocopied or microfilmed copies of the pages needed and many other requests are referred to libraries within the home state of the individual requesting the loan. In addition, no book over one hundred years of age is ever sent from our library on interlibrary loan. Nevertheless, 217 volumes were sent out. The postage on such loans is usually paid by the borrowing library, but the general wear and often the real damage to the books is an expense we must bear. In contrast to the herbarium, where loans sent to staff members in other institutions may be somewhat offset by those received for the use of our own staff members, the interlibrary loan requests made by Arboretum staff members rarely exceed a dozen in the course of a year.

I wish to express my appreciation to Mrs. Schwarten and her staff for the concentrated effort they have made and the results they have obtained in bringing the library to its present excellent condition.

Herbarium:

It is now possible to report significant progress in the unification of the non-horticultural herbarium of the Arboretum with that of the Gray Herbarium. This work should be completed within the ensuing year. The additional funds made available for this task by the Harvard Corporation have enabled us to employ additional botanists who, with the herbarium staff, have made excellent progress. The details of this work have been discussed in previous reports. During 1955–56, the first year of this work, 103 families were integrated. In 1956–57, an additional 66 families were completed. During the last fiscal year 94 families were organized, leaving only 43 from a total of 306 families represented in our herbarium to be integrated. However, these 43 families include such large woody groups as the Rosaceae and the Leguminosae, as well as primarily herbaceous families such as the Gramineae, Cyperaceae, Compositae, Liliaceae and Ranunculaceae. The progress that has been made is satisfactory and the results encourage an even greater effort. The ease in using the reorganized and combined collections has demonstrated that the integration is well worth the time and effort expended.

As the work proceeds, excessive duplication in some areas within the collections has become evident. For example, in an experimental project it was found possible to remove 1058 sheets (either Arnold or Gray) from the Pinaceae and 23 sheets from the genus *Asimina*. Such sheets are either exact duplicates or sterile specimens represented by better material from the same geographical location. The unification procedure also has revealed a large number of herbarium sheets needing repairs. During the course of the year our mounter repaired 2302 sheets in addition to mounting for insertion 5535 sheets. The total number of specimens in the Arboretum herbarium as of July 1, 1958, therefore, is 699,452.

During the year 11,516 specimens were received by the herbarium. We received by exchange 6970, by subsidy 2708, by gift 1055, by special exchange 682 and for identification 101 specimens. The collection obtained by subsidy represented a set of plants obtained by Mr. Leonard Brass during the Fifth Archbold Expedition to New Guinea and adjacent islands. While the Arnold Arboretum had subsidized and handled all the botanical collections of the earlier expeditions, it was not able to do so in this case. A special collection of plants from Hong Kong and the vicinity was obtained in exchange for publications. In total, we received 993 specimens from the Western Hemisphere and 10,523 from institutions in or working on the floras of the Old World. These figures reflect the Arboretum's historical interest in the flora of Asia.

As a service to our colleagues, specimens from the herbarium of the Arnold Arboretum are sent on loan to recognized institutions. In turn, our staff borrows specimens from other herbaria to assist in their studies. The shipment of specimens on loan is necessarily an involved bookkeeping procedure. If the request is specific it may be necessary to send only a single specimen. Often, however, the request will be for a group of species, a genus, specimens from a certain geographic area, or representatives of several families. Each loan request must therefore be handled individually and may involve a few minutes or a full week of work. When the specimens have been withdrawn from the herbarium, a record of the loan is made in the herbarium and in special files. Thus we know at all times the location of our herbarium material. The specimens, carefully packed to prevent breakage, are shipped by express collect within the United States, but must be prepaid and insured when shipped outside of the United States. Notice of the loan and the total count is sent in a separate letter with a return slip to indicate the safe arrival of the loan. When the borrower has finished his studies the specimens should be packed with equal care and returned promptly. All specimens returned are immediately fumigated, counted and checked against the original record to insure the receipt of the material originally sent. The herbarium sheets are then examined to determine the conclusions of the study and, if the sheets are properly annotated, they are filed according to the classification suggested. Specimens of cultivated plants from the horticultural herbarium in Jamaica Plain are added to the loans of spontaneous plants or sent separately for special study as required. Thus a great deal of time is consumed in the preparation and return of a simple loan request.

During the past year the staff sent from the combined herbaria 95 loans averaging 141 sheets and totalling 13,411 sheets. Sixty of these loans went to institutions within the United States and 36 to institutions outside of the country. In contrast, during the same period our thirteen staff members and students made 71 requests for loans from 44 American and 27 foreign herbaria, for a total of 8,614 specimens borrowed.

Routine work continues on the herbarium of cultivated plants in Jamaica Plain. A start has been made on the project of locating the type specimens of horticultural taxa described by Professors Alfred Rehder and Charles Sargent. During the year there was an increase in the requests for representative specimens, kodachromes or black-and-white pictures of cultivated plants.

In preparation for his "Manual of Cultivated Trees and Shrubs" and the "Bibliography of Cultivated Trees and Shrubs," Professor Rehder maintained a card file of references to original publications and to illustrations of cultivated plants. After Rehder's death the administrative decision was made to curtail that work. This decision was unfortunate, since the reference file soon became of limited value. With the recent adoption of an international code of nomenclature for cultivated plants, the need for an up-to-date index of published cultivar names, together with references to illustrations, became imperative. Therefore, during the past year Miss Ethel Upham, formerly of the Arboretum staff, began the work of bringing up to date the "Rehder Index." Over six hundred cards have been added to the file in the past year and it is expected that in two years the index will be current.

The staff members continued to spend a small part of their time on individual research projects. Unfortunately, this time has been limited in the past three years and will continue to be for the ensuing year or until the herbarium integration is complete.

Dr. Howard continued his several projects supported by special research grants. Progress was made in the survey of the anatomical structure of the petioles of flowering plants and a report on this work was given at the International Horticultural Congress. His work on the West Indian vegetation was restricted to the vegetation in relation to bauxite subsoils, and the flora of the Lesser Antilles. A monographic study of the genus *Coccoloba* continues with final treatments prepared for the Lesser Antilles and Trinidad and the record of the genus in cultivation.

Dr. Perry returned from her trip to Europe, having profitably studied the New Guinea collections at herbaria in Great Britain, the Netherlands and Switzerland. In addition to herbarium work, Miss Perry continues her study of the materials from the 4th Archbold Expedition collected by Leonard Brass in New Guinea.

Dr. Hu had previously been working on a Flora of China supported by grants for that specific purpose. When the financial support was exhausted, Dr. Hu devoted her attention to regular Arboretum projects and has undertaken to identify the large accumulation of Chinese plants acquired by Dr. Merrill shortly after the end of the war. As sizable numbers of duplicates of these collections occupy our storage areas, the identification of the main set will enable the staff to distribute these collections within the next few years. Studies of the Compositae in China and miscellaneous monographic studies for the Flora of China have been completed and await publication.

Dr. Jarrett continued her work on the Moraceae and prepared several papers on *Artocarpus* for publication. Miss Jarrett has also developed an interest in the flora of the Philippines and is continuing that work which has been a tradition at the Arboretum.

Dr. Johnston reports that his work concerns the Boraginaceae of Texas and that work is in progress on the Chenopodiaceae and on the gypsum and serpentine floras.

Dr. Kobuski's heavy curatorial responsibilities which include supervision of the herbarium integration, have left him little time for his own research. The Theaceae continue to be his interest with special studies in progress on the genus *Ternstroemia*.

Dr. Wood assumed the responsibilities of editor of the Journal of the Arnold Arboretum with the January number of the current volume. He continued during the year his studies on the genera of seed plants of the southeastern United States; the genera comprising the woody families of the Ranales as they occur in that area were prepared for publication.

Mrs. Weber and Dr. Wilson, both of whom are on special projects, devote their full time to these. As a hobby of botanical interest, Mrs. Weber has prepared for publication a check list of the plants and plant families represented in philately. Dr. Wilson has readied several of his studies on ferns for publication and devotes his current research to further studies on this group of plants.

Comparative Morphology:

The assistance of I. W. Bailey, Professor of Plant Anatomy, *emeritus*, as curator of the wood and pollen slide collections is greatly appreciated by the staff. A number of wood samples and slides were added to the collections during the year. Requests for wood samples for study were mainly from scientists wishing to add such data to their taxonomic monographs. Fourteen such requests were filled from the wood collection and the herbarium.

During the year Professor Bailey received a grant from the American Philosophical Society in support of his research. His interest in the use of pollen in morphological studies centers now on the variations between fresh and processed pollen grains from herbarium material or fossil deposits. Professor Bailey's study of the anatomical structure of the stem in the Cactaceae continues to develop and he is accumulating samples for further work.

Cytogenetics:

Dr. Karl Sax, his assistant and students have reported the following contributions in the field of cytogenetics:

The mature trees of *Malus sikkimensis*, *M. toringoides* and an *M. sargentii* hybrid (AA 33340) usually breed true from seed when open pollinated, but occasionally they produce some segregates which differ from the typical in having larger flowers and fruits. Cytological studies show that the present trees are triploids.

The maternal-type progeny are also triploids, but the large-fruited types are tetraploids. Apparently the triploid parents are facultative apomicts which usually produce triploid progeny, but occasionally produce sexual segregates arising from a triploid egg cell and a haploid pollen grain from a nearby diploid species. Such progeny would resemble the maternal parent because of the excess maternal chromosomes.

Both *Malus sargentii* and *M. sargentii rosea* are facultative apomicts. Pollinated with pollen from a diploid *Malus* species, the progeny of the triploid *M. sargentii rosea* range from nearly diploid to approximately tetraploid, while the sexual progeny of the tetraploid *M. sargentii* are triploids.

Apparently the triploid parent produces egg cells ranging from haploid to triploid, although the apomictic progeny are triploids.

An issue of Arnoldia was published during the year reporting on the juvenile characters of trees and shrubs. Cuttings from suckers from the base of a seedling apple tree were found to root much more readily than cuttings from the fruiting branches of the same tree. The basal suckers are also juvenile in their leaf characters.

Instruction:

Although no formal courses were offered by staff members during the past year, both Dr. Howard and Dr. Sax continued to work with graduate students on special problems. Mr. Claud Brown completed his work with Dr. Sax on pine hybrids and, after receiving his Ph.D. degree, accepted a position in forest genetics at Texas A. & M. College.

A series of luncheon seminars was conducted throughout the year in the lecture room at the Harvard University Herbarium Building. These seminars, in which the herbarium staff take part, provide an opportunity for the staff and graduate students to meet informally to hear papers by representatives of each group. The seminars also provide a means for visiting scientists to meet and talk with the staff without the usual disruption of work schedules.

Travel and Exploration:

Travel by staff members during the past year was divided between attendance at professional meetings, the presentation of invitational lectures and specialized field work connected with research programs.

The annual meeting of the American Institute of Biological Sciences is held each fall at a college campus in the United States. As such meetings offer the opportunity of observing other biology departments, gardens and herbaria, as well as of meeting with professional colleagues, staff members are encouraged to attend when possible. The 1957 meetings were held on the campus of Stanford University at Palo Alto, California, and Drs. Howard, Kobuski and Sax made the special trip. The California flora, both native and introduced, is strikingly different from that seen in New England and scheduled field trips for interested registrants afforded the opportunity of seeing the coastal range vegetation as well as a bit of the redwood forests. Special trips were made by Drs. Howard and Kobuski to the California Academy of Sciences to confer with colleagues there and to the Strybing Arboretum in Golden Gate Park. Mr. Coggeshall attended the Plant Propagators Annual Meeting at Cleveland and Dr. Sax attended the American Society for Horticultural Science rootstock conference at Geneva, New York.

Every three years an International Horticultural Congress is held which is attended by persons interested in horticulture from all over the world. The Fifteenth International Horticultural Congress was held in Nice, France, April 11–18, 1958. Dr. Howard represented the Arnold Arboretum at these meetings, presenting one paper and reading another for Dr. Kobuski. Prior to the meetings Dr. Howard visited botanic gardens in Denmark and Switzerland. During the Congress field trips were conducted to allow the registrants an opportunity of seeing the natural vegetation of the area and the commercial and private aspects of horticulture.

Following the meetings, Dr. Howard visited Paris for some work at the Muséum National d'Histoire Naturelle and also visited many of the famous parks and gardens of Paris. In and around London a schedule arranged by Dr. George Taylor allowed Dr. Howard to see several famous arboreta such as Westonbirt and many gardens, both public and private.

Dr. Hu attended the 9th Pacific Science Congress held in Bangkok,

Above: A group of the participants at a plenary session of the XVI International Horticultural Congress held in Nice, France.

Below: Members of the Congress during a visit to the Exotic Gardens at Monaco.

Thailand, and presented four papers at these meetings. Arranging her trip eastward and circling the globe, she was able to visit botanic gardens and herbaria in England, France, Italy, Switzerland, India, and several countries of Asia. Following the congress Dr. Hu visited Hong Kong and Macao for field work and study furthering her work on the flora of China. An exchange of specimens was also arranged by Dr. Hu between the Arnold Arboretum and both the Gardens Department, Hong Kong, and the Department of Botany, National Taiwan University.

Field work associated with individual research projects was carried on by several staff members. Drs. Wood and Wilson collected materials for their work on the flora of the southeastern states in Florida, where they were the guests of Mr. and Mrs. George R. Cooley.

Dr. Johnston spent the summer months doing field work in Texas.

Dr. Howard made another trip to Jamaica to continue his study of the vegetation on bauxite soils when several additional areas in St. Elizabeth Parish became available. The results of earlier studies showing the nature of plantings desirable for the rehabilitation of mined-out bauxite pits is now becoming evident as the mining scars are gradually being covered with forage grasses, crop plants and forest trees. A survey trip was also made to Hawaii to examine areas being considered for mining operations there. Following this trip Dr. Howard accepted an invitation to serve as advisor to the Commissioner of Public Lands for the Territory of Hawaii. He is to give special consideration to the problems of vegetation loss in strip-mining operations and to advise regarding rehabilitation procedures if mining is conducted in the Territory.

Gifts and Grants:

The response of the Friends of the Arnold Arboretum to the annual appeal made during the spring was most generous. Most gifts received were unrestricted and were assigned to the "gifts for cultural purposes" fund which is used to employ additional summer labor on the grounds where needed. This fund also supports a research assistant for Dr. Sax and an assistant in the greenhouses to help on plant propagation.

A special grant was awarded to Dr. Sax from the Massachusetts Society for Promoting Agriculture for work on rootstocks and for methods for promoting the growth and fruiting of fruit trees in New England. This project is being carried on in conjunction with the Bussey Institution.

Dr. Howard received a three-year grant from the National Science Foundation to continue work leading to a flora of the Lesser Antilles. Mr. George Proctor of the Institute of Jamaica, Kingston, Jamaica is co-worker on this project and will do the field work. During the last year Mr. Proctor visted Grenada and St. Lucia for major field work and spent a few days on other islands. Mrs. Dudley Hall assists Dr. Howard in the herbarium work of this project and is also supported by this grant.

A number of outstanding plant species were given to the Arboretum, either as living plants or as propagating material. The plants received from Mrs. J. Norman Henry, and Mr. Orlando Pride were particularly noteworthy. Mr. A. G. Rotch presented to the Arboretum a portrait of the Arnold family painted by an unknown artist. He accompanied this with a genealogical summary which is a valuable addition to our historical records. The portrait, of considerable value beyond its special interest to us, is at present under the care of the staff of the Fogg Art Museum.

Publications:

Dr. Wyman edited the twelve numbers of Arnoldia, a bulletin of popular information which appeared during the year and Dr. Kobuski edited the Journal of the Arnold Arboretum, the quarterly issues of which serve the staff as an organ for the publication of scientific articles. Staff members have priority in placing manuscripts in the Journal and contributions from other individuals are by invitation or are papers based largely on the plant materials in the living collections or the herbarium and wood collections of the Arboretum. The Journal serves also as a medium of exchange for similar publications from other scientific institutions. The standards of the Journal have always been high and the excellence of the editorial work, together with the quality of the printing, has earned for it a good reputation in the field of scientific publications. For the last nine years the editor of this publication has been Dr. C. E. Kobuski, who has long been on the editorial board associated with the Journal. In fact, excepting only his leave of absence from the staff for war service, he has served continuously as associate editor or editor of the Journal since his appointment to the Arboretum staff in 1927. To him the Journal owes its direct, lucid style which, with characteristic regular date of issue, has become a hallmark of this publication. Dr. Kobuski has now asked to be relieved of his editorial duties in order to devote more time to his curatorial responsibilities in the herbarium and to his own research. Thus, with this volume the Journal becomes the editorial responsibility of Dr. C. E. Wood, Jr. Special acknowledgment to Dr. Kobuski was made in the January number of Volume 39.

One special publication was issued during the year. This was a photoreprint of "The Genus Pinus" by George Russell Shaw, issued previously as "Publication of the Arnold Arboretum, No. 5," in 1914. This publication has been out of print for many years but sufficient back orders had accumulated to merit a reprinting. To date, over 150 copies of this still important work have been sold.

It is with considerable pleasure that we note the presentation to Mrs. Susan D. McKelvey of the Sara Gildersleeve Fife Memorial Award, which was given in recognition of Mrs. McKelvey's contributions to botanical and horticultural literature. Mrs. McKelvey's works include "The Lilacs," "Yuccas of the Southwestern United States" and the recently published "Botanical Exploration of the Trans-Mississippi West 1790–1850." A full citation of the award was given in the Garden Journal of the New York Botanical Garden.

Bibliography of the Published Writings of the Staff and Students July 1, 1957 — June 30, 1958

BAILEY, IRVING WIDMER. Additional notes on the vesselless dicotyledon, Amborella trichopoda Baill. Jour. Arnold Arb. **38**: 374–380. *pl. 1, 2.* 1957.

———. Aggregations of microfibrils and their orientations in the secondary wall of coniferous tracheids. Am. Jour. Bot. **44**: 415–418. 1957.

———. The potentialities and limitations of wood anatomy in the study of the phylogeny and classification of angiosperms. Jour. Arnold Arb. **38**: 243–254. 1957.

———. Die Struktur der Tüpfelmembranen bei den Tracheiden der Koniferen. Holz als Roh- und Werkstoff **15**: 210–213. 1957.

———. Need for a broadened outlook in cell wall terminologies. Phytomorphology **7**: 136–138. 1958.

———. The structure of tracheids in relation to the movement of liquids, suspensions, and undissolved gases. *In*: The physiology of forest trees. p. 71–82. 1958.

COGGESHALL, ROGER GIBBS. Asiatic maples, their propagation from softwood cuttings. Arnoldia **17**: 45–56. *pl. 11, 12.* 1957.

———. The propagation of some little-used shade and street trees. Proc. 33rd Nat. Shade Tree Conf. 37–43. 1957.

HOWARD, RICHARD ALDEN. The Director's Report. The Arnold Arboretum during the fiscal year ended June 30, 1957. Jour. Arnold Arb. **38**: 389–403. 1957.

———. Studies in the genus Coccoloba, IV. The species from Puerto Rico and the Virgin Islands and from the Bahama Islands. Jour. Arnold Arb. **38**: 211–242. 1957.

———. Studies in the genus Coccoloba, V. The genus in Haiti and the Dominican Republic. Jour. Arnold Arb. **39**: 1–48. 1958.

———. The meadow. Arnoldia **18**: 17–24. *pl. 3–5.* 1958.

——— (with GEORGE R. PROCTOR). New records of Jamaican flowering plants, I. Jour. Arnold Arb. **39**: 101–106. 1958.

HU, SHIU-YING. Oriental Hollies. Nat. Hort. Mag. **36**: 31–64. *illus. 11–20.* 1957.

JARRETT, FRANCES M. A note on the identity of the genus Balanostreblus (Moraceae). Jour. Arnold Arb. **39**: 107–110. 1958.

JOHNSTON, IVAN M. Borraginaceae. *In*: Steyermark, Julian, et al. Contributions to the flora of Venezuela. Fieldiana. Bot. **28**: 1080–1082. 1957.

———. Studies in the Boraginaceae, XXIX. Echiochilon and related genera. Jour. Arnold Arb. **38**: 255–293. 1957.

——— (with C. R. MCCULLOUGH & J. M. PARKER). Terrain study of the Panama Canal zone with specific reference to the Fort Sherman area and vicinity. North Carolina State College, Department Engineering Research. 1–267. 1956.

KOBUSKI, CLARENCE E. The horticultural herbarium. Arnoldia **18**: 25–28. 1958.

SAX, KARL. The control of vegetative growth and the induction of early fruiting in apple trees. Proc. Am. Soc. Hort. Sci. **69**: 68–74. 1957.

———. The effect of ionizing radiation on chromosomes. Quart. Rev. Biol. **32**: 15–26. 1957.

———. Experimental control of tree growth and reproduction. *In*: The physiology of forest trees. p. 601–610. 1958.

———. The genetic future of man. *In*: The Population Ahead. 1958.

———. The juvenile characters of trees and shrubs. Arnoldia **18**: 1–6. *pl. 1.* 1958.

Schwarten, Lazella. Index to American Botanical Literature. Bull. Torrey Bot. Club **84**: 324–336, 398–411, 459–471. 1957; **85**: 78–88, 146–155. 1958.

Weber, Claude. Les mauvaises herbes d'origine Européenne en Nouvelle-Angleterre. Bull. Cercle Vaudois Bot. Lausanne **8**: 34–39. 1957 (1958).

———. Etude phytosociologique des prairies du Canton de Genève et de ses environs immédiats. Trav. Soc. Bot. Genève **4**: 20–38. 1956–57 (1958).

———. Note sur la colonisation des digues artificielles de galets en aval de l'Usine de Verbois (Genève). Trav. Soc. Bot. Genève **4**: 39–41. 1956–57 (1958).

———. La végétation de la Pointe à la Bise (Genève). Trav. Soc. Bot. Genève **4**: 47–53. 1956–57 (1958).

Wilson, Kenneth Allen. Ontogeny of the sporangium of Phlebodium (Polypodium) aureum. Am. Jour. Bot. **45**: 483–491. 1958.

Wood, Carroll E., Jr. (with R. K. Godfrey). Pinguicula (Lentibulariaceae) in the southeastern United States. Rhodora **59**: 217–230. 1957.

Wyman, Donald. Broad-leaved evergreens in the Arnold Arboretum. Arnoldia **17**: 61–76. *pl. 15, 16.* 1957.

———. Hollies for hedges, screens, and barriers. Nat. Hort. Mag. **36**: 139–146. *illus. 47–50.* 1957.

———. The new horticultural color chart. Arnoldia **17**: 57–60. *pl. 13.* 1957.

———. Winter injury — 1957. Arnoldia **17**: 37–44. *pl. 10.* 1957.

———. A spring walk through the Arnold Arboretum. Arnoldia **18**: 13–16. 1958.

———. Two new Mahoberberis hybrids. Arnoldia **18**: 9–12. *pl. 2.* 1958.

———. A new color chart for horticulture. Nat. Hort. Mag. **37**: 47–49. 1958.

Richard A. Howard, *Director*

Staff of the Arnold Arboretum

1957–1958

RICHARD ALDEN HOWARD, Ph.D., Arnold Professor of Botany, Professor of Dendrology, and Director.

IRVING WIDMER BAILEY, S.D., Professor of Plant Anatomy, *Emeritus*.
JOSEPH HORACE FAULL, Ph.D., Professor of Forest Pathology, *Emeritus*.

MICHAEL ANTHONY CANOSO, M.S., Curatorial Assistant.*
ROGER GIBBS COGGESHALL, Propagator (Resigned April 15, 1958).
ALFRED JAMES FORDHAM, Propagator (Appointed April 15, 1958).
HEMAN ARTHUR HOWARD, Assistant Horticulturist.
SHIU-YING HU, Ph.D., Botanist, Flora of China Project.
FRANCES MARY JARRETT, Ph.D., Botanist and Assistant Editor.
IVAN MURRAY JOHNSTON, Ph.D., Associate Professor of Botany.
CLARENCE EMMEREN KOBUSKI, Ph.D., Curator.*
MARGARET CATHERINE LEFAVOUR, Herbarium Secretary.
SUSAN DELANO MCKELVEY, A.B., Research Associate.
LILY MAY PERRY, Ph.D., Botanist.
KARL SAX, S.D., Professor of Botany.
LAZELLA SCHWARTEN, Librarian.*
CLAUDE WEBER, Botanist, Special Project.*
STELLA MABEL WHITEHOUSE, Business Secretary.
KENNETH ALLEN WILSON, Ph.D., Botanist, Southeastern Flora Project.*
ROBERT GEROW WILLIAMS, B.S., Superintendent.
CARROLL EMORY WOOD, JR., Ph.D., Associate Curator and Editor.
DONALD WYMAN, Ph.D., Horticulturist.

* Appointed jointly with the Gray Herbarium.

INDEX